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DESCRIPTIONS OF THIRTY-TWO NEW SPECIES OF BIRDS FROM THE HAWAIIAN ISLANDS: PART I. NON-PASSERIFORMES

ORNITHOLOGICAL MONOGRAPHS

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DESCRIPTIONS OF THIRTY-TWO NEW SPECIES OF BIRDS FROM THE HAWAIIAN ISLANDS: PART I. NON-PASSERIFORMES.

BY

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INTRODUCTION

Although the birds described here are known mainly from their bones, they are very much a part, perhaps the most important part ecologically and evolutionarily, of the modern avifauna of the Hawaiian Archipelago. Had not *Homo sapiens* arrived in these islands some 16 centuries ago, these birds would still be alive today—skin, feathers, songs, enzymes and all. The poor remnants of fauna and flora that still persist in the Hawaiian Islands evolved alongside and interacted with a diverse array of browsing, seed-eating, frugivorous, insectivorous, malacophagous, and raptorial birds whose former existence had never been suspected. Consequently, the distribution, adaptations, and history of the existing biota of the islands can no longer be sensibly interpreted without consideration of the fossil record.

We refer to the remains of prehistorically vanished birds as "fossils" in the sense of something dug up, as objects studied by paleontologists with paleontological techniques, in order to distinguish these specimens from those of "modern" species collected in the historic period. But the majority of these bones are not permineralized. Chemically they are essentially modern bone, little altered from their original composition when once part of a living organism. The mineral components of these bones can be dissolved away to leave a perfectly formed "ghost" of the organic protein matrix, just as in modern bone. The birds represented by these bones are not some temporally distant reminders of a long bygone age but were significant members of ecosystems that still exist, although these ecosystems are now greatly altered.

Factors that may have contributed to the extinction of these birds include direct hunting by man, predation by introduced mammals (rats, and perhaps pigs and dogs), and possibly to prehistorically introduced diseases. But the most severe reduction in species diversity of birds was probably due to the habitat destruction that resulted from the use of lowland environments by Polynesians for the extensive systems of agriculture that were so conspicuously manifested at the time of the first western contact in 1778. These perturbations began with the arrival of Polynesians, perhaps as early as 300 A.D. (Kirch 1985:68), were exacerbated by the arrival of Europeans with new farming methods and livestock, and have continued to the present. Not only did the birds themselves suffer an ill fate, but even their bones are now imperiled, as rampant development in the Hawaiian Islands is yearly destroying potential fossil sites, making paleontological exploration of the archipelago all the more imperative.

It took nearly two centuries for the historically known species of birds of the Hawaiian Islands to be discovered and described, beginning with the first specimens collected on Captain Cook's final voyage in 1778–1779 and ending with the description of *Melamprosops phaeosoma* in 1974 (Casey and Jacobi 1974). The names of some 30 authors are formally associated with the valid generic, specific, and subspecific names of Hawaiian birds, and dozens of other workers have studied and published on the systematics, evolution, morphology, and biogeography of this avifauna. A very liberal assessment of the number of endemic species in the historic fauna (Table 1) gives a figure of 55, whereas in a more conservative, traditional treatment the number would be about 40.

TABLE 1

ENDEMIC TAXA OF HISTORICALLY KNOWN (I.E., NON-FOSSIL) LAND BIRDS OF THE
HAWAIIAN ISLANDS[1]

1	*Certhia coccinea* Forster, 1781
2	*Gracula nobilis* Merrem, 1786
3	*Certhia obscura* Gmelin, 1788
4	*Certhia pacifica* Gmelin, 1788
5	*Certhia sanguinea* Gmelin, 1788
6a	*Certhia virens* Gmelin, 1788
7a	*Rallus sandwichensis* Gmelin, 1788
8	*Muscicapa obscura* Gmelin, 1788
9a	*Muscicapa sandwichensis* Gmelin, 1788
10	*Loxia psittacea* Gmelin, 1789
11a	*Fringilla coccinea* Gmelin, 1789
	PSITTIROSTRA Temminck, 1820
	DREPANIS Temminck, 1820
	VESTIARIA Jarocki, 1821
	6b *Nectarina flava* Bloxam, 1827
	11b {*Fringilla rufa* Bloxam, 1827}
	Strix sandwichensis Bloxam, 1827 = *Asio flammeus* (Pontoppidan, 1763)
	MOHO Lesson, 1831
12	*Bernicla sandvicensis* Vigors, 1834
	HEMIGNATHUS Lichtenstein, 1839
13a	*Hemignathus lucidis* Lichtenstein, 1839
	LOXOPS Cabanis, 1847
14	*Buteo solitarius* Peale, 1848
15	*Corvus hawaiiensis* Peale, 1848
16	*Entomiza angustipluma* Peale, 1848
17	*Fulica alai* Peale, 1848
	HIMATIONE Cabanis, 1850
	[*Himatione chloris* Cabanis, 1850 = 6b]
18	*Himatione maculata* Cabanis, 1850
19	*Mohoa braccata* Cassin, 1855
20	{*Hemignathus ellisiana* Gray, 1859}
	PHAEORNIS Sclater, 1859 = *MYADESTES* Swainson, 1838
21	*Moho apicalis* Gould, 1860
	CHAETOPTILA Gray, 1869
	ONYCHOTES Ridgway, 1870 = *Buteo* Lacépède, 1799
	LOXIOIDES Oustalet, 1877
22	*Loxioides bailleui* Oustalet, 1877
	Gallinula sandvicensis Streets, 1877 = *Gallinula chloropus* (Linnaeus, 1758)
23a	*Anas wyvilliana* Sclater, 1878
24	*Fringilla anna* Dole, 1879
	PENNULA Dole, 1879 = *Porzana* Vieillot, 1816
	7b *Pennula millsi* Dole, 1879
	11c {*Hypoloxias aurea.*—Finsch, 1880}
25	*Chasiempis sclateri* Ridgway, 1882
26	*Himantopus knudseni* Stejneger, 1887
	9b *Chasiempis ridgwayi* Stejneger, 1887
27	*Chasiempis ibidis* Stejneger, 1887
28	*Phaeornis myadestina* Stejneger, 1887
29	*Himatione parva* Stejneger, 1887
	{*OREOMYZA* Stejneger, 1887 = *Oreomystis* Stejneger, 1903}

[1] Species are listed in chronological order by date of original description in the genera in which originally proposed. Each endemic species is numbered. Subspecies have the same number as the nominate form and are lettered. For nomenclatural reasons, names in braces { } had to be replaced by subsequent names that appear farther along in the list under the same number. Names in brackets [ ] have been commonly used but are junior synonyms of names appearing earlier in the list under the number indicated. Equivalents are provided for generic names that are nearly universally regarded as invalid. This list recognizes more taxa at the species level than is customary (e.g., in *Chasiempis* and the *Hemignathus obscurus* group) in the belief that this is preferable for distinctive, allopatric insular forms.

TABLE 1

CONTINUED

30	*Oreomyza bairdi* Stejneger, 1887
	CHLORIDOPS Wilson, 1888
31	*Chloridops kona* Wilson, 1888
32	*Hemignathus stejnegeri* Wilson, 1889
20	*Hemignathus lichtensteini* Wilson, 1889
	13b *Hemignathus hanapepe* Wilson, 1889
	[*Hemignathus procerus* Cabanis, 1890 = 32]
33	*Loxops flammea* Wilson, 1890
	CHRYSOMITRIDOPS Wilson, 1890 = *Loxops* Cabanis, 1847
34	*Chrysomitridops caeruleirostris* Wilson, 1890
35a	*Himatione montana* Wilson, 1890
36	*Himatione stejnegeri* Wilson, 1890
	TELESPIZA Wilson, 1890
37	*Telespiza cantans* Wilson, 1890
38a	*Phaeornis lanaiensis* Wilson, 1891
39	*Himatione mana* Wilson, 1891
	[*Chasiempis gayi* Wilson, 1891 = 27]
40	*Himatione dolei* Wilson, 1891
	CIRIDOPS Newton, 1892
	PORZANULA Frohawk, 1892 = *Porzana* Vieillot, 1816
41	*Porzanula palmeri* Frohawk, 1892
42a	*Tatare familiaris* Rothschild, 1892
43	*Himatione fraithii* [= *freethii*] Rothschild, 1892
	RHODACANTHIS Rothschild, 1892
44	*Rhodacanthis palmeri* Rothschild, 1892
45	*Rhodacanthis flaviceps* Rothschild, 1892
	VIRIDONIA Rothschild, 1892
46	*Viridonia sagittirostris* Rothschild, 1892
	11c *Loxops ochracea* Rothschild, 1892
	23b *Anas laysanensis* Rothschild, 1892
	PALMERIA Rothschild, 1893
	13c *Hemignathus affinis* Rothschild, 1893
47	*Hemignathus lanaiensis* Rothschild, 1893
	PSEUDONESTOR Rothschild, 1893
48	*Pseudonestor xanthophrys* Rothschild, 1893
49	*Acrulocercus bishopi* Rothschild, 1893
	6c *Himatione wilsoni* Rothschild, 1893
	35b *Himatione newtoni* Rothschild, 1893
	11b *Loxops wolstenholmei* Rothschild, 1893
50	*Phaeornis palmeri* Rothschild, 1893
51	*Heterorhynchus wilsoni* Rothschild, 1893
	38b *Turdus oahuensis* Wilson and Evans, 1899
	CHLORODREPANIS Wilson and Evans, 1899
	{*ROTHSCHILDIA* Wilson and Evans, 1899 = *Loxops* Cabanis, 1847}
52	*Drepanis funerea* Newton, 1894
	NESOCHEN Salvadori, 1895
	DREPANORHAMPHUS Rothschild, 1900 = *Drepanis* Temminck, 1820
	PAROREOMYZA Perkins, 1901
	OREOMYSTIS Stejneger 1903
	38c *Phaeornis rutha* Bryan, 1908
53	*Telespiza ultima* Bryan, 1917
	HORIZONETTA Oberholser, 1917 = *Anas* Linnaeus, 1758
	DYSMORODREPANIS Perkins, 1919
54	*Dysmorodrepanis munroi* Perkins, 1919
	42b *Conopoderas kingi* Wetmore, 1924
	MAGUMMA Mathews, 1925 [replaces *Rothschildia*]
	PSEUDOMOHO Mathews, 1925 = *Moho* Lesson, 1831

TABLE 1

CONTINUED

	MOHOHINA Mathews, 1925 = *Moho* Lesson, 1831
	MOHORNIS Mathews, 1925 = *Moho* Lesson, 1831
	MELAMPROSOPS Casey and Jacobi, 1974
55	*Melamprosops phaeosoma* Casey and Jacobi, 1974
	9c *Chasiempis sandwichensis bryani* Pratt, 1979

The first fossil bird was described from the Hawaiian Islands in 1943, based on some very fragmentary remains of a goose that had been discovered in 1926 (Wetmore 1943). Thereafter, avian paleontology ceased in the islands until Joan Aidem discovered bones of extinct birds in sand dunes on the island of Molokai in the early 1970's (Stearns 1973). Two new genera and species were named from these discoveries (Olson and Wetmore 1976). Since 1976, through our own collecting efforts and those of the Bishop Museum, with major assistance from many interested volunteers, tens of thousands more fossils have been collected from the main islands (Olson and James 1982a, b; 1984; James 1987; James et al. 1987). We are prepared at this time to describe 32 new species from this material, which, with the 3 fossil species already named, brings the named extinct fossil avifauna to 35 species. Perhaps as many as 22 additional species are represented by material that is either not sufficiently diagnostic or that requires more intensive analysis in order to resolve species' limits. Thus, we find ourselves faced with the problem of documenting and describing, in a relatively short period of time, a fauna that in size and complexity exceeds the entire historically known avifauna, which took dozens of researchers almost two centuries to discover and describe.

The systematists who preceded us had an easier task in many respects. Original descriptions of new species of historically known Hawaiian birds were often based on a single study skin, or at most a small series of study skins. Such descriptions were essentially of a single object from which 4 or 5 measurements might be taken. Discussion of variation within species at most entailed the mention of juvenile and female plumages when these were known and differed from that of the adult male. Descriptions were usually very brief and not comparative. A selection of 15 species named by Lord Rothschild took an average of 15 lines, or a little over 100 words, to describe, including measurements, statement of range, and remarks. Four of Rothschild's genera took even less space, from 5 to 13 lines, for an average of less than 80 words.

By contrast, our fossil species may be known from thousands of bones from dozens of individuals. At times nearly complete skeletons of single individuals may be available, but just as frequently we must deal with masses of unassociated material. Each major bone in the skeleton may potentially have diagnostic features and may yield numerous different measurements. The simple physical processes of cleaning, sorting, cataloging, numbering, and storing such vast amounts of material is staggering by comparison with the curatorial responsibilities of the skin taxonomist. On the other hand, certain species are as yet known from very fragmentary or extremely poorly preserved remains, such that in many cases,

although we can be certain that new species are represented, their generic relationships may be uncertain and they cannot really be properly diagnosed. There is the additional factor of potential variation through time and of geographic variation between islands or between sites at different elevations that may complicate interpretations of the fossil record.

We had first thought to proceed by taxonomic groups, combining descriptions of new fossil species with systematic revisions of modern taxa. The need for a timely overview of the collecting localities and their faunas was so pressing, however, that we decided on a preliminary treatment in which no new taxa were named, the extinct fossil species being referred to only by informal designations (Olson and James 1982b). That publication was significantly out-of-date by the time it was issued, owing to the discovery by R. Michael Severns of great bone deposits in lava tubes on Maui, an island for which we had previously had a very meager fossil record. Some of the material from Maui was included in a briefer summary of Hawaiian fossil birds (Olson and James 1984), and the geology and chronology of one of the major fossil sites on Maui has been dealt with in some detail (James et al. 1987).

Although the Hawaiian fossils deserve detailed analysis in connection with studies of evolution, phylogeny, biogeography, functional morphology, taphonomy, and other stimulating lines of investigation, we cannot proceed without having names for the organisms to be discussed. Therefore, it is our intention at this time simply to satisfy the protocol for the establishment of new taxa, with little further elaboration. In the present monograph, we propose formal scientific names for 3 new genera and 16 new species of non-passerine birds. These descriptions are supplemented by brief discussions of unnamed forms that may prove to be new species but for which we prefer to defer formal nomenclatural designation. An additional 4 new genera and 16 new species of passerines are treated in an accompanying monograph (James and Olson 1991).

MATERIALS AND METHODS

All fossil material is housed either in the National Museum of Natural History, Smithsonian Institution, or in the B. P. Bishop Museum. Modern comparative material examined is listed under individual accounts of genera. In most instances we had many more fossil specimens available than have been cited in the descriptions and diagnoses. We have specifically designated only enough paratypical material for adequate specific diagnoses, so that in cases where differences between species are based mainly on size, the paratypical series will be larger than otherwise. In a sense, all specimens of new species in our collections identified prior to 1988 could be regarded as paratypes, many of which are still uncataloged. To list them all, however, would consume an inordinate amount of time and space.

Within related groups of species, the sequence of presentation is geographical, proceeding from west to east within the islands. This is intended as a convenience in the presentation of data, as in tables, which are read from left to right, and also incidentally reflects the ages of the islands, beginning with the oldest and proceeding to the youngest. SYSTAT (Wilkinson 1989) and SYGRAPH (Wilkinson 1988) software were used for statistical tests and box plots.

Museum acronyms used in this monograph are as follows:

AMNH—American Museum of Natural History, New York.
BMNH—British Museum (Natural History), Tring.
BBM, BBM-X, BPBM—Bernice P. Bishop Museum, Honolulu.
KU—Museum of Natural History, University of Kansas, Lawrence.
MVZ—Museum of Vertebrate Zoology, University of California, Berke-
    ley.
NHMW—Naturhistorisches Museum, Wien [Vienna].
PIN—Paleontological Institute of the U.S.S.R. Academy of Sciences,
    Moscow.
RMNH—Rijksmuseum van Natuurlijke Historie, Leiden.
UMZC—University Museum of Zoology, Cambridge, England.
USNM—National Museum of Natural History, Smithsonian Institution,
    Washington, D.C.

RECAPITULATION OF FOSSIL LOCALITIES

Fossils of prehistorically extinct species of birds have been found on five of the main Hawaiian Islands (Fig. 1) and come from a variety of geological settings, including sand dunes, limestone sinkholes (both flooded and dry), lava tubes, a crater lake bed, and archeological midden deposits. Details of geography and chronology of most of the fossil sites may be found in our previous publications (Olson and James 1982b, 1984; James 1987; James et al. 1987). Therefore, only summaries are presented here, along with brief descriptions of newer sites not heretofore mentioned. With two exceptions, all radiometrically dated fossil deposits are Holocene in age.

KAUAI

Makawehi dunes: These are dunes of calcareous sand perched above sea cliffs on the southeast coast of Kauai, about 2 km E of Poipu, between Makahuena Point and Kamala Point (Olson and James 1982b:22). Fossils were confined mainly to discrete areas that were detected by finding larger bones exposed at the surface, each site being designated individually by number (Olson and James 1982b). Radiocarbon ages of associated land snail shells and crab claws gave dates of 6,740 ± 80 and 5,145 ± 60 yr BP, respectively. These are considered to be maximum ages because these animals sometimes incorporate older environmental carbon in their shells (Olson and James 1982b:30).

→

FIG. 1. Map of the main Hawaiian Islands showing some of the principal fossil localities and the relationship of the main group to the Northwestern chain (inset). All fossil localities on Maui occur in the shaded portion; mainly in the western third thereof. The dashed line indicates the approximate extent of the coalesced island of Maui Nui that existed during low sea-level stands. The Kona and Kohala areas of Hawaii are each divided into northern and southern districts that are not shown.
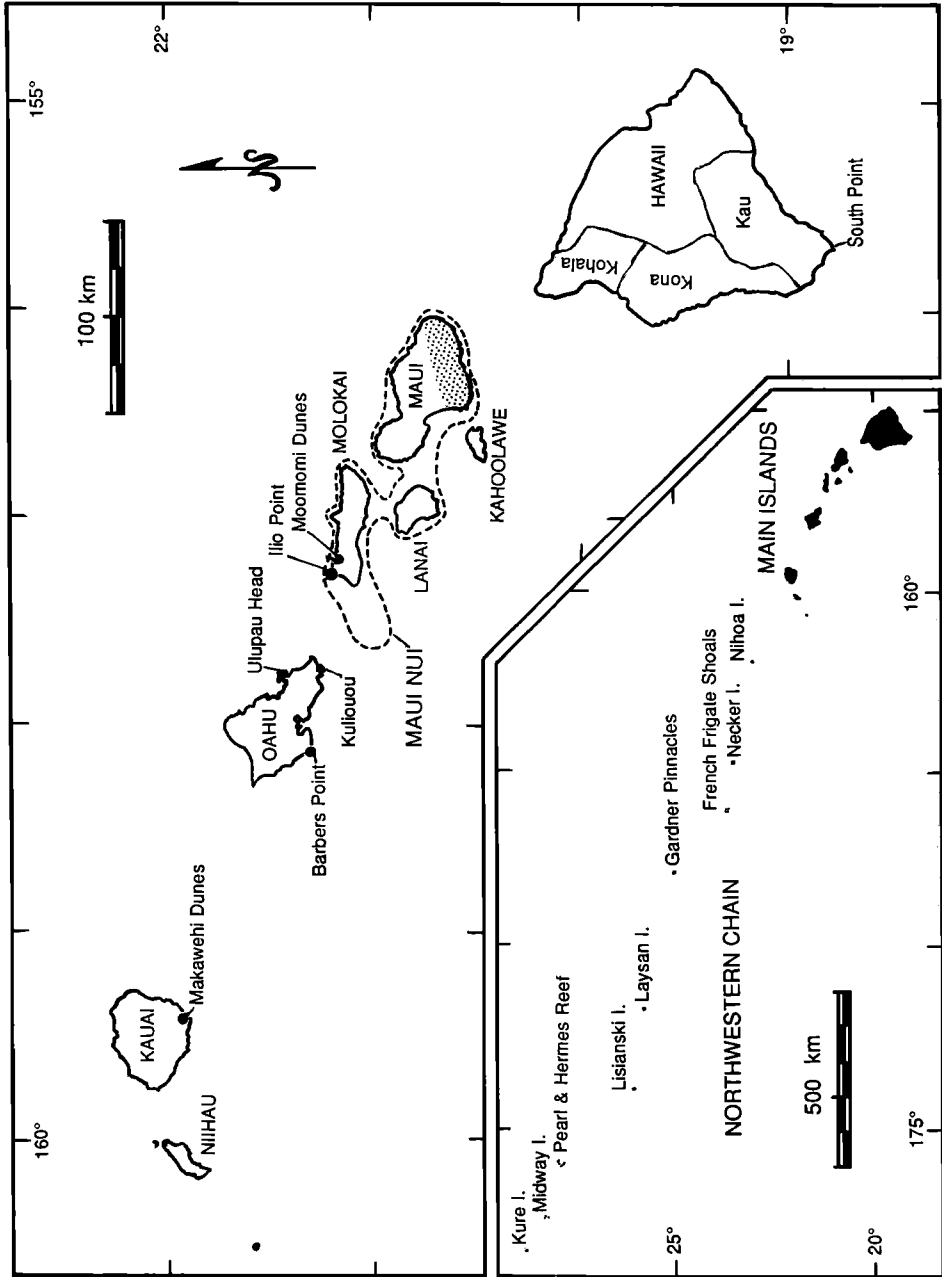
OAHU

Barbers Point: Fossils occur here in karstic features in a raised (ca. 7 m ASL) limestone reef on the Ewa Plain in the southwestern portion of the island near Barbers Point. Most specimens were found in sediment that had accumulated in sinkholes of varying size, a number of which show evidence of Polynesian occupation or modification. All such sites have received either Bishop Museum or State of Hawaii archeological site numbers (or both), which we have indicated here only in the case of holotypes. Radiocarbon dates on material from sinkholes near Barbers Point fall in the latter half of the Holocene. An exceptional site at Barbers Point was an enclosed cavern (Site 50-Oa-B6-139) partly filled with brackish water. At the bottom of this cavern were many bird bones, including associated skeletons of *Chaetoptila* and two large species of *Corvus.* It is likely that the associated specimens were deposited when there was no water in the cavern, presumably when sea level was lower. These fossils may be older than most others from Barbers Point (Olson and James 1982b).

Kuliouou Shelter: This is an archeological site near the southern shore of the southeastern corner of Oahu that has yielded a few bones of extinct birds (Olson and James 1982b:29).

Ulupau Head: Numerous bird bones have been recovered from Pleistocene lacustrine sediments in the crater at Ulupau Head, Mokapu Peninsula, on the southeastern coast of Oahu (James 1987). These sediments are probably considerably younger than 800,000 yr, the age of the oldest rocks in the volcanic series forming the crater, and older than 120,000 yr, the age of the overlying marine deposits of the Waimanalo Formation (James 1987).

MOLOKAI

Moomomi dunes: Bones occurred rather commonly at the surface of "blowouts" in the very extensive dunes of calcareous sand on the northwest coast of Molokai in the vicinity of Moomomi Beach. The various individual sites here and at Ilio Point are numbered as outlined in Olson and James (1982b). The only date for this area as yet is from land snail shells associated with the articulated complete skeleton of the holotype of *Thambetochen chauliodous* Olson and Wetmore (1976), which indicated an age of about 25,000 yr (Stearns 1973). Because of difficulties with exogenous carbon in land snail shells, this must be regarded as a maximum age. The specimen of *Thambetochen* came from a very low level in the dunes, just above sea level, and is probably older than the majority of fossils recovered here. Some of the surface finds may be anthropogenic midden materials (Olson and James 1982b).

Ilio Point dunes: Dunes similar to those at Moomomi also occur at the northwesternmost tip of Molokai at Ilio Point. Radiocarbon dates from two different kinds of land snails from one of the most productive fossil sites here were 5,510 ± 65 yr BP and 5,245 ± 60 yr BP, which again, are maxima (Olson and James 1982b:30).

MAUI

Fossils from Maui have come almost exclusively from lava tubes that accumulated bones primarily through acting as pitfall traps. In most such cases, in-

dividual skeletons were found lying exposed on the floor of these caves, where the bones tend to settle into crevices in the rubbly *aa* lava and are frequently damaged. In some caves, deep, well-stratified fossiliferous alluvial sediments were present. When known, we have given coordinates and elevations for each site. These are approximations only, pending more accurate determinations using satellite tracking systems. Coordinates in degrees and minutes of north latitude and west longitude are presented in simplified format (viz., 2037/15615 = 20°37′N, 156°15′W). Quadrangles refer to U.S. Geological Survey 7.5 minute series topographic maps.

Kahawaihapapa Cave: (Lualailua Hills Quad., 2037/15615, 15 m). This lava tube near Kahawaihapapa Point on the southern shore of east Maui, formerly served as a water source for the prehistoric inhabitants of the region as well as a trap for birds. The entrance is a skylight with a vertical drop of approximately 4 m. The downslope portion of the tube extends only a short distance, where it is inundated with brackish water. The upslope portion is quite long, perhaps 1 km, with a few short side channels. The fossils collected here in 1988 occurred on the floor and ledges of the upslope portion and include ibises, petrels, a bat, and a goose (*Branta*), the last found together with bone fishhooks, bone fishhook blanks, and files of sea urchin spine and coral.

Crystal Cave, Manawainui Gulch: (Lualailua Hills Quad., 2038/15614, 183 m). This rather complex lava tube is in the Manawainui Gulch (one of several by that name on Maui) that is located about midway along the southern coast of east Maui. The cave extends more or less horizontally from its entrance, which is on the steep cliff of the gulch itself, so that the cave would have been inaccessible to non-volant birds, and did not function as a pitfall trap. The only fossils here were associated skeletons of passerines found on the rock surface of the cave floor, usually encrusted with mineral. The cave is shaped like a hairpin, extending back into the cliff, then dropping down and turning back in the direction of the entrance.

Puu Naio Cave: (Makena Quad., 2037/15624, 305 m). This lava tube with a collapsed ceiling is situated above La Perouse Bay at the southwest corner of East Maui, near the hill called Puu Naio, and has been described in detail by James et al. (1987). Fossils occurred at the surface in both the upslope and downslope portions of the tube, and more importantly, in deep, finely stratified sediments that washed into the upslope portion of the cave. Radiocarbon dates of purified collagen from bones indicate that fossil deposition in these sediments took place more or less continuously from approximately 8,000 yr ago to the present (James et al. 1987). Excavations in 1984 and 1988 in the sediments of the upslope portion of the tube produced at least 28 species of endemic birds.

Lua Lepo: (Lualailua Hills Quad. [western edge, almost on Makena Quad.], 2038/15620, 808 m). This is the second of a linear series of three lava tubes located about 3.5 km northwest of the Lualailua Hills on the southern slopes of Mt. Haleakala. Access to the entrance is through a steep-sided gulch with large boulders of collapsed roof-fall that leads to a 2.25 m dropoff at the mouth of the cave that would have prevented the escape of flightless birds. The cave has only a downslope branch, which is 55 m long with a stratified deposit of moist clayey alluvium extending 25 m from the entrance. Excavation of this deposit in 1988 produced bones of a variety of flightless birds, passerines, and petrels, many of the larger species being recovered as associated skeletons in exceptionally fine condition.

We coined the name from the Hawaiian *lua,* a cave or hole, and *lepo,* filth, from the damp, muddy conditions under which we worked here.

Auwahi Cave: (Makena Quad., 2040/15621; 1,463 m). This lava tube is located in the Auwahi district on the southwest slope of Mt. Haleakala, East Maui. There are two pitfall entrances leading into downslope portions. Bones of extinct birds, almost exclusively flightless species (anatids, ibises, and rails), occurred in profusion at the surface and in the thin deposits of sediment that accumulated in some portions of the cave. Most of the bones are very well preserved and unmineralized.

Hukihuki Cave: (Makena Quad., 2041/15621, 1,220 m). Entry to this lava tube, located 2.5 km NNW of Puu Makua at an elevation of 1,220 m, was gained by descending an 11 m vertical pipe. Egress during our collecting forays in 1988 was facilitated by pulling the climbers up on a rope attached to a jeep, hence the name of the cave, from Hawaiian *huki,* pull. The cave has an insignificant upslope branch and an extensive downslope branch that preserved skeletons of flightless birds, weakly volant geese, and a lesser number of volant birds (ducks, gallinules, and crows). These were found lying on the floor amongst lava rubble. Evidently the vertical entry pipe was long and narrow enough to trap volant as well as the usual flightless species.

Waihou Spring Cave: (Makena Quad., 2040/15621, 1,463 m). This is a short, walk-in lava tube on the western slope of Puu Makua near Waihou Spring. It contained bones of a few individuals of flightless birds on bare lava rock.

Puu Makua Cave: (Makena Quad., 2040/15621, 1,463 m). This is a deep and spacious lava tube located near the eastern flank of Puu Makua. It is entered through a skylight in the ceiling of a large chamber that has a cinder cone at its center, the top of which is 16 m below ground level, with the lowest part of the floor of the entry chamber 21 m below ground level. The cave has both upslope and downslope branches, both containing associated skeletons of flightless birds lying amongst the lava rubble on the floor. Volant animals included gallinules, an eagle, owls, bats, and various passerines. Most of the passerines were recovered from an excavation in 1988 of a deposit of clayey alluvium that encircles the cinder cone in the entry chamber.

Owl Cave near Puu Makua: (Makena Quad., 2040/15621, 1,402 m). This rather insignificant portion of a lava tube is one of several in the vicinity of Puu Makua Cave. The entrance is not a pitfall and the cave extends upslope for a distance of only a few meters. The only fossil bird found here was a nearly complete, though partially disintegrated, skeleton of the extinct endemic owl, found lying directly on the surface of the lava floor.

Upper Kipahulu Valley: (Nahiku Quad., Lua Manu 1,830 m, Puka Moa 1,860 m). Two lava tubes in the rain forest of the upper Kipahulu Valley, East Maui, are the only Hawaiian fossil sites yet found that are still in an ecosystem not totally altered by man. The caves were found by personnel of the National Park Service, who also made arrangements for collecting. The names coined for these caves are Lua Manu (= Bird Cave; at first called Lua Iwi), and Puka Moa (= Fowl Hole). Both caves feature vertical entrances that trapped flightless birds, the waterlogged bones of which were collected in 1984 (Bishop Museum collections) and 1988 (Smithsonian collections) (see Medeiros et al. 1989). The only remains of

volant birds were those of *Pterodroma phaeopygia,* a thrush, and one individual of a new genus of finch-billed drepanidine.

Lower Waihoi Valley Cave: (Kipahulu Quad., 424 m). This is a lava tube in the Lower Waihoi Valley, about 4.8 km south of Hana, at the eastern end of east Maui. Bones of an ibis and several rails were found on the rock floor of this cave (Olson and James 1982b:15).

HAWAII

We have yet to find any fossil sites on the island of Hawaii that contain a reasonably representative sample of birds. The first fossil bird described from the archipelago was the goose *Geochen rhuax* Wetmore (1943), represented by some very poorly preserved fragments of bone found under 25 m of lava flow in the vicinity of Pahala, on the southern side of the island. We have bones of an additional species of extinct goose from lava tubes in the Kona and Kohala Districts and bones of extinct rails from deposits at South Point and various archeological sites on the island. Because we name no new species from the island of Hawaii here, we shall defer any further discussion of its fossil sites.

SYSTEMATIC PALEONTOLOGY

Order PROCELLARIIFORMES
Family PROCELLARIIDAE
Genus *Pterodroma* Bonaparte, 1856

The new species described below shows no tendency in either the wing or hindlimb toward the diving adaptations seen in *Puffinus* or *Pelecanoides*. It is much larger than any species of Oceanitidae, lacks the elongation of the area of the skull between the ectethmoid and the nasofrontal hinge, with the concomitant anterior elongation of the lacrimal typical of that family, and lacks the shortened wing elements and femur and elongated tibiotarsus and tarsometatarsus of the more specialized genera of the Oceanitidae (Olson 1985a). Its osteology is typical in most respects of the gadfly petrels of the genus *Pterodroma*. The lacrimals are fused, unlike in the very closely related genus *Bulweria* (Olson 1975a), and the limb proportions are likewise more like those of *Pterodroma* than *Bulweria* (Olson 1975b).

Comparative material examined: Skeletons (USNM) of all of the genera and most of the species of Procellariiformes, including in particular *Pterodroma hypoleuca* (23), *P. nigripennis* (1 + 2 trunks), *P. cooki* (2 trunks), *P. defilippiana* (1), *Bulweria fallax* (1), and *B. bulwerii* (18). X-radiographs of the unique holotype of *Pterodroma* [*Bulweria* auct.] *macgillivrayi,* BMNH 1956.8.30.28.

Pterodroma jugabilis, new species
(Figs. 2A, C, 3A–B, E, G, 4A, C, E)

"*Pterodroma* sp.—curious undescribed species" Olson and James, 1982b:32.
"new extinct species of small *Pterodroma*" Olson and James, 1984:773.

Holotype: Complete cranium lacking rostrum and all palatal elements, USNM 395173 (Fig. 2A, C). Collected 4 or 5 August 1977 by Storrs L. Olson, Helen F. James, Aki Sinoto, and Eric Komori.
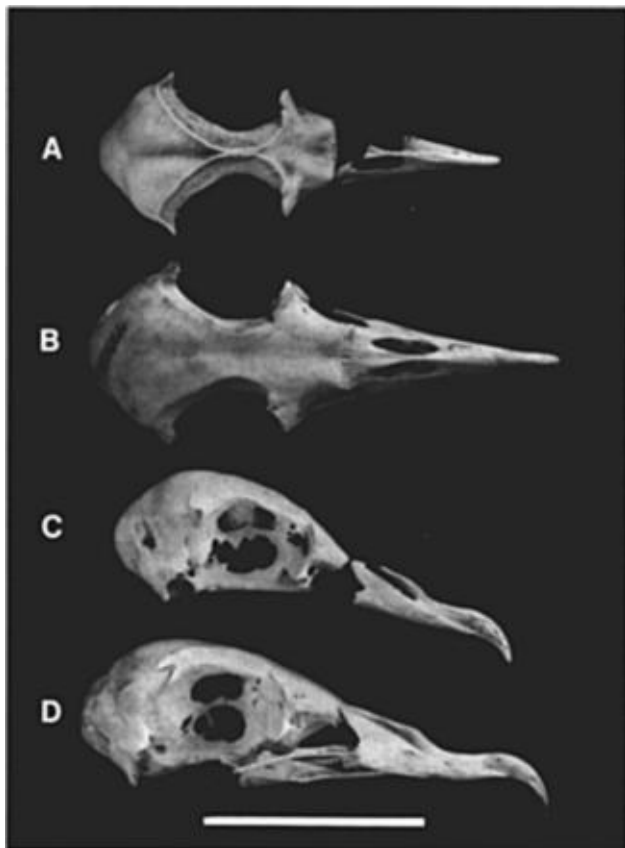
FIG. 2.   Cranial elements of *Pterodroma. A, P. jugabilis,* new species, cranium, holotype (USNM 395173), and rostrum (USNM 395174) in dorsal view; *C,* same in lateral view; *B, P. hypoleuca* (USNM 498091) skull in dorsal view; *D,* same in lateral view. Scale = 3 cm.

Type locality: Flooded cavern Site 50-Oa-B6-139, Barbers Point, Oahu, Hawaiian Islands.

Distribution: Oahu: Barbers Point. Hawaii: lava tubes in the North Kona District.

Etymology: Latin, *jugabilis,* that may be joined, in reference to the nearly conjoined supraorbital salt gland depressions.

Measurements (mm) of holotype: Length (from anterior point of left lacrimal), 31.7; width across lacrimals, 15.6; least width of interorbital bridge, 5.1; greatest width (across postorbital processes), 20.7; greatest depth, 16.8.

Paratypes: Oahu: Rostrum lacking part of the proximal portion of the left side, USNM 395174 (Fig. 2A, C); frontoparietal portion of skull including interorbital

→

FIG. 3.   Wing elements of *Pterodroma jugabilis,* new species (*A, B, E, G*), compared with *P. hypoleuca (C, D, F)* (USNM 498091). *A, B,* left humeri in anconal view (USNM 395181; USNM 395182); *E,* right ulna in internal view (USNM 395187); *G,* left radius in internal view (USNM 395188). Scale = 3 cm.
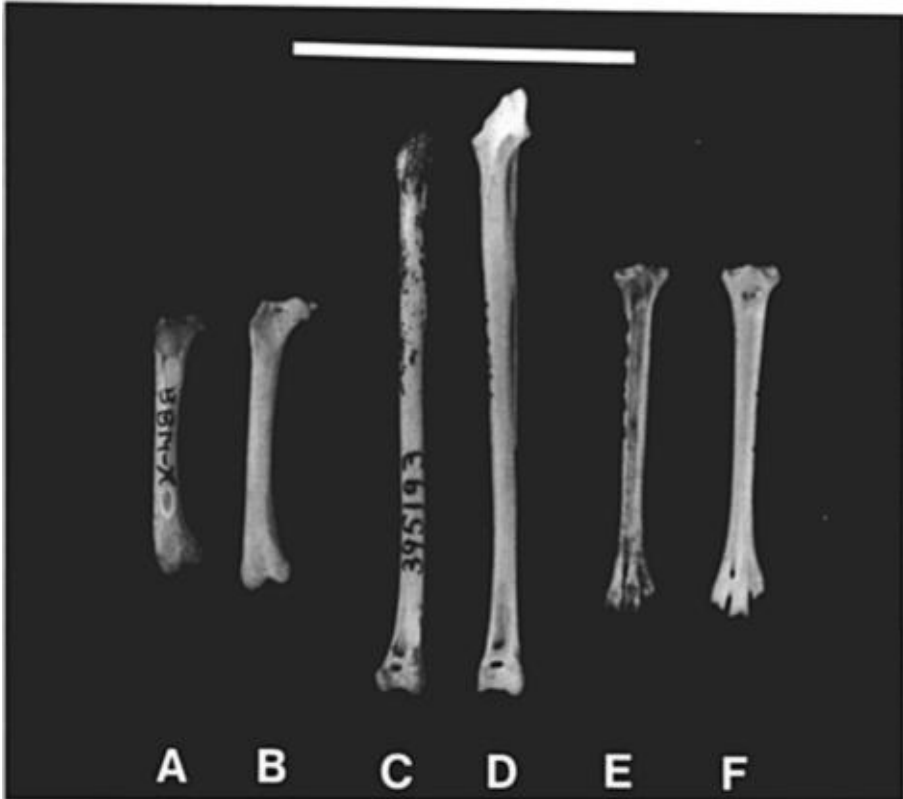
FIG. 4. Hindlimb elements of *Pterodroma jugabilis*, new species (*A, C, E*), compared with *P. hypoleuca* (*B, D, F*) (USNM 498091). *A*, right femur in anterior view (BBM-X 153690); *C*, left tibiotarsus in anterior view (USNM 395193); *E*, right tarsometatarsus in anterior view (USNM 395195). Scale = 3 cm.

bridge and left ectethmoid, BBM-X 157851; furcula, BBM-X 154921; right coracoid, USNM 395179; complete right humeri, USNM 395181 (Fig. 3A), USNM 395182 (Fig. 3B); distal portions of right humeri, USNM 395183, USNM 395184, USNM 395185; left radius, USNM 395188 (Fig. 3G); right ulna, USNM 395187 (Fig. 3E); left ulna, USNM 395186; left carpometacarpi, USNM 395191, USNM 395144; right femur, BBM-X 153690 (Fig. 4A); left femora, USNM 395231, USNM 395255; right tibiotarsus lacking cnemial crests and outer condyle, USNM 395146; left tibiotarsus, USNM 395193 (Fig. 4C); right tarsometatarsi, USNM 395160; USNM 395195 (Fig. 4E); left tarsometatarsi, USNM 395147, USNM 395194.

Hawaii: Associated skeleton consisting of all the major long bones (except right carpometacarpus), portions of the skull, mandible, sternum, pelvis, and various phalanges, vertebrae, and ribs, USNM 435164.

Measurements (mm) of paratypes: Oahu (in same sequence as above): Rostrum: length from nasofrontal hinge, 24.2; length of nostril, 7.5; length of premaxillary symphysis from anterior margin of nostril, 14.9; least depth of symphysis, 3.1. Cranium: least width of interorbital bridge, 5.5. Furcula: length, 26.0. Coracoid:

length (with sternal end flat on calipers), 17.6; least width of shaft, 3.1. Humerus: total length, 64.7, 72.2, —, —, —; length from distal end of pectoral crest, 50.6, 56.2, 57.7, —, —; width and depth of shaft at midpoint, 3.1 × 2.8, 3.6 × 3.2, 3.5 × 3.0, —, —; distal width, 7.9, 8.5, 8.7, 8.3, 8.3. Ulna: length, 76.4, 76.2. Radius: length, 73.3. Carpometacarpus: length, 33.4, 34.4; proximal depth, 8.3, 8.1. Femur: length, 22.1, 22.5, 21.5; proximal width, 4.3, 4.6, 4.2; width and depth of shaft at midpoint, 1.8 × 1.7, 1.6 × 1.8, 1.6 × 1.6; distal width, 3.8, 3.9, 3.6. Tibiotarsus: length (from proximal articular surface), 42.7, 43.9; distal width, —, 3.8. Tarsometatarsus: length, 28.8, 29.5, 28.8, 27.7; proximal width, 4.3, 4.5, 4.4, 4.1; width and depth of shaft at midpoint, 1.7 × 1.4, 1.9 × 1.3, 1.7 × 1.4; 1.7 × 1.2; distal width, —, 4.3, 4.0, 4.1.

Hawaii (associated skeleton USNM 435164): Rostrum: length from nasofrontal hinge, ca. 22; length of premaxillary symphysis from anterior margin of nostril, 13.8; least depth of symphysis, 3.1. Cranium: least width of interorbital bridge, 7.2. Coracoid: length (with sternal end flat on calipers), 16.2; least width of shaft, 3.2. Humerus: total length, 65.8; length from distal end of pectoral crest, 51.1; width and depth of shaft at midpoint, 3.7 × 3.2; distal width, 8.2. Ulna: length, 70.6. Radius: length, 68.9. Carpometacarpus: length, 33.0; proximal depth, 7.6. Phalanx 1 of major alar digit: length, 15.2. Synsacrum: length along midline, 25.7. Femur: length, 22.2; proximal width, 4.4; width and depth of shaft at midpoint, 1.8 × 1.8; distal width, 3.9. Tibiotarsus: length (from proximal articular surface), 41.5; distal width, 3.7. Tarsometatarsus: length, 28.0; proximal width, 4.5; width and depth of shaft at midpoint, 1.9 × 1.5; distal width, 4.2.

Diagnosis: A very small species of *Pterodroma*, skeletal elements always more gracile than in congeners of comparable size when overlap occurs in length; larger than *Bulweria bulwerii*. Cranium in dorsal view slender and elongate, very distinctive in having the supraorbital impressions for the salt glands nearly contiguous, separated only by a narrow ridge; postorbital processes reduced (Fig. 2A). Compared with *P. hypoleuca*: rostrum shorter, with tip not as strongly hooked; humerus much more gracile, bicipital crest not as pronounced, ventral tuberosity in ventral view shorter, ectepicondylar spur more slender and markedly more distally situated, brachial depression smaller and not extending as far proximally; ulna, radius, and major hindlimb elements much more gracile, and the trochleae of the tarsometatarsus markedly smaller and narrower.

Remarks: This is a most curious small petrel, with no obvious close relatives among living species of *Pterodroma*. The only petrel in the Hawaiian archipelago of roughly similar size is *Pterodroma hypoleuca,* a species that now occurs only in the Northwestern Hawaiian Islands but that was also in the main islands into the period of Polynesian settlement (Olson and James 1982b:43). Although there is some overlap in the length measurements of some of the elements of these two species, many of the bones referable to *P. jugabilis* are decidedly smaller than in *P. hypoleuca,* so that it was perhaps the smallest species of the genus. It is not closely related to the enigmatic *P. macgillivrayi,* of Ngau, Fiji, known only from the type and one other specimen, plus another that was captured, measured, and released (Watling and Lewanavanua 1985; Watling 1987). This is a considerably larger species (tarsus 35.3–37 mm; Watling and Lewanavanua 1985:232) related to the *Pterodroma rostrata* group, which has its own distinctive features (Olson 1975b) that are not shared with *P. jugabilis*.

The configuration of the salt gland depressions is unusual within the Procellariiformes, the only taxa that are somewhat similar being the Pelecanoididae and certain of the Oceanitidae, to which the Hawaiian bird is only very distantly related.

The true former distribution of *P. jugabilis* will probably be apparent only with further paleontological work. It is common at Barbers Point on Oahu, and in 1988 we recovered numerous bones of this species from a series of lava tubes in the North Kona District of Hawaii, 3.2–4.0 km (2–2.5 mi) SSE of Kiholo Bay, at an elevation of 244 to 305 m. A few individuals, such as the paratype listed above, were collected as associated skeletons found well into the lava tubes, beyond the light zone, where they surely arrived unaided. Most bones here, however, were in an archeological context, the birds almost certainly having been used as food by Hawaiians, so that the species must have persisted into relatively recent times. It probably bred elsewhere in the Hawaiian chain and it, or closely related forms, may have occurred in the other archipelagos in the Pacific as well. The possibility exists, of course, that the species still survives and has been overlooked. If it were an all-dark bird it might well be confused with *Bulweria bulwerii*.

Order CICONIIFORMES
Family PLATALEIDAE
Genus *Apteribis* Olson and Wetmore, 1976

Type species: Apteribis glenos Olson and Wetmore, 1976.

Included species: Apteribis glenos Olson and Wetmore, 1976; *A. brevis,* new species.

Distribution: Molokai and Maui.

Emended diagnosis: Two new fossil genera of insular ibises were discovered subsequent to the description of *Apteribis.* In *Xenicibis xympithecus* of Jamaica the calcaneal ridges of the hypotarsus are of unequal length (approximately equal in *Apteribis*) and the humerus is pneumatic (foramen lacking in *Apteribis*), with a much larger and deeper brachial depression and the shaft much more curved and not as robust as in *Apteribis* (Olson and Steadman 1977, 1979). Based on new, undescribed material from Jamaica, *Xenicibis* also had a much straighter ulna with the shaft more attenuated distally, and an elongated, swollen carpometacarpus quite unlike that of any other bird. *Borbonibis latipes* of Reunion Island in the Indian Ocean, was evidently a volant bird, with a normally developed carpometacarpus and coracoid and a relatively longer and more slender tarsometatarsus (Mourer-Chauviré and Moutou 1987). The species of *Xenicibis* and *Borbonibis* are both much larger than any of the species of *Apteribis.*

Comparative material examined: The new species described below needs comparison only with *Apteribis glenos.*

Remarks: Although postulating the absence of an organism may be risky, especially in the fossil record, we are increasingly confident that *Apteribis* occurred only on the islands that were connected at times during the Pleistocene to form the larger island of Maui Nui (see Fig. 1). Although we have as yet no meaningful fossil record from either Lanai or Kahoolawe, that from natural trap sites on Oahu is large and that from Hawaii is growing. As yet there is not a single scrap

of *Apteribis* bone from either of the islands that flank Maui Nui to the west and east.

Apteribis glenos Olson and Wetmore, 1976
(Fig. 5B, D, F, H, K)

Apteribis glenos Olson and Wetmore, 1976:252; Olson and James, 1982b:33; 1984:771.

Holotype: Complete right tarsometatarsus, BBM-X 147986 (Fig. 5B).
Type locality: Site 6, Moomomi dunes, Molokai, Hawaiian Islands.
Distribution: Molokai: Moomomi and Ilio Point dunes, and Kalaupapa Peninsula.
Emended diagnosis: See diagnosis of *Apteribis brevis.*
Material: In addition to the holotype and paratypes, the following specimens of *A. glenos* were examined: tip of premaxilla, USNM 426124; mandibular symphysis, USNM 426125 (Fig. 5K); mandible lacking left articulation and distal portion of symphysis, USNM 386135; incomplete sternum USNM 386139 (Fig. 5F); right coracoid, USNM 386119 (Fig. 5D); left humerus, USNM 386120; left ulnae, USNM 386121, BBM-X 152462.

Remarks: Olson and Wetmore (1976) described the fossil remains of a flightless ibis from Molokai as *Apteribis glenos,* a new genus and species, designating a tarsometatarsus from the Moomomi dunes as the holotype. Along with paratypes from Molokai, they also included the largely fragmentary remains of a single individual from the Lower Waihoi Valley Cave on Maui, which at the time was the only specimen of ibis known from that island.

Hundreds of bones of *Apteribis* have since been collected on Maui, whereas collecting on Molokai has been less productive, so that sample sizes from Maui are now much greater. Several qualitative characters distinguish the sample of *Apteribis* from Molokai from all individuals collected on Maui, so that recognition of at least one additional species is warranted. The geographic range of *A. glenos* may now be restricted to the island of Molokai.

Based on our analysis of size variation, there appear to have been two altitudinally separated populations (species) of *Apteribis* on Maui. If a second species in addition to *A. glenos* also occurred at higher elevations on Molokai, we would not have collected it because all fossil sites found so far on Molokai are near sea level.

Apteribis brevis, new species
(Fig. 5A, C, E, G, I)

Apteribis glenos (part) Olson and Wetmore, 1976.
"*Apteribis* sp." Olson and James, 1982b:33; James et al., 1987:2353.
"Maui *Apteribis* sp. A" Olson and James, 1984: 772.

Holotype: Nearly complete associated skeleton, USNM 378342 (Fig. 5A, C, E, G, I). Collected 8 September 1982 by Storrs L. Olson and Helen F. James. The specimen includes the skull (lacking right quadrate, pterygoids, and most of both quadratojugals), mandible, notarium, pelvis, all major elements of the wing, pec-
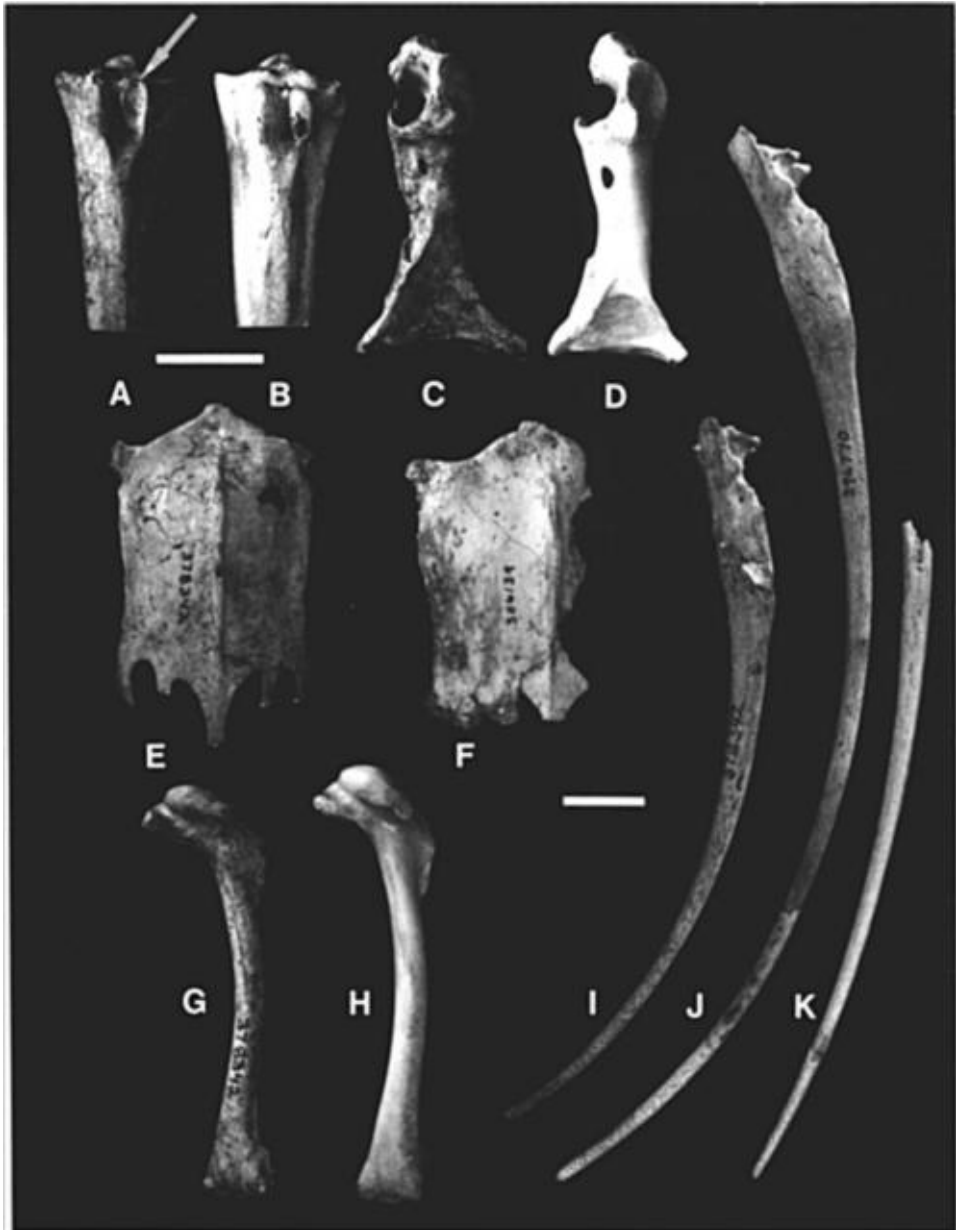
FIG. 5. Bones of *Apteribis* spp. from Maui (on left in each pair) compared with those of *A. glenos* from Molokai: *A, B* proximal ends of right tarsometatarsi in posterior view [*A, Apteribis brevis*, new species, holotype (USNM 378342), arrow indicates groove in external calcaneal ridge that is absent in *A. glenos*; *B, A. glenos*, holotype (BBM-X 147986)]; *C, D*, right coracoids in dorsal view [*C, Apteribis brevis*, holotype (USNM 378342); *D, A. glenos* (USNM 386119)]; *E, F*, sterna in ventral view [*E, Apteribis brevis*, holotype (USNM 378342); *F, A. glenos* (USNM 386139)]; *G, H*, right humeri in anconal view [*G, Apteribis brevis*, holotype (USNM 378342); *H, A. glenos* (BBM-X 147240)]; *I, J, K*, mandibles in right lateral view [*I, A. brevis*, holotype (USNM 378342); *J, Apteribis* sp., Maui (USNM 396770); *K, A. glenos* (USNM 426125)]. Scales = 1 cm (*A* and *B* are enlarged relative to the rest).

toral girdle and hindlimb (except right femur), various vertebrae, ribs, and phalanges of manus and pes.

Type locality: Auwahi Cave (1,145 m), Maui, Hawaiian Islands.

Distribution: Maui: from higher elevations on the southern slopes of Mt. Haleakala, including upper Kipahulu and possibly Lower Waihoi Valleys.

Etymology: Latin, *brevis,* short, from the short bill and small size that characterize this species.

Measurements (mm) of holotype: Skull: total length, 135.4; length of rostrum along midline from "forehead," 105.6; length and width of cranium, 36.5 × 31.6. Mandible: total length, 111.6; length of symphysis, 62.1; width of articulation, 10.9. Sternum: length along midline, 50.3; width through second costal facet, 29.2. Notarium: length of centra along midline, 26.4. Pelvis: length of synsacrum, 51.5; width through antitrochanters, 35.7. Coracoid: length, 29.8. Scapula: length, 42.2; width of articular end, 8.6. Furcula: length, 29.0. Humerus: length, 62.5; proximal width, 15.1; shaft width at midpoint, 5.0; distal width, 11.5. Ulna: length, 48.6; proximal depth, 8.5. Radius: length, 46.7. Carpometacarpus: length, 24.6; proximal depth, 8.5. Femur: length, 62.7; proximal width, 14.3; shaft width at midpoint, 6.1; distal width, 13.9. Tibiotarsus: length from cnemial crest, 94.0; shaft width at midpoint, 6.0; distal width, 11.2. Tarsometatarsus: length, 53.0; proximal width, 13.2; shaft width at midpoint, 6.8; distal width, 13.6.

Paratypes: A multitude of bones from many different individuals; virtually the entire skeleton is represented. The paratypes are not listed individually for economy of space. The incomplete associated skeleton from Lower Waihoi Valley Cave (BBM-X 147127–147175; see Olson and Wetmore 1976:248) is tentatively referred to this species based on size alone.

Measurements of paratypes: Certain measurements of long bones are incorporated into Tables 2 and 3 and Figures 5 and 6.

Diagnosis: Differs from *Apteribis glenos* as follows: tip of premaxilla and mandible not as narrow and pointed, mandible noticeably more decurved (Fig. 5I, K); sternum much more arched (concave dorsally), not broad and flattened as in *A. glenos* (Fig. 5E, F); coracoid with procoracoid foramen larger and situated closer to the medial margin of the bone, impression of M. sternocoracoideus extending farther up the shaft, not marked with a distinct semicircular lip, and decidedly more flattened at the sternal end, as opposed to concave (Fig. 5C, D); humerus (Fig. 5G, H) and ulna not as robust, humerus with head and pectoral crest less inflated; calcaneal ridges of tarsometatarsus more elongate, the lateral one invariably with a distinct tendinal groove that is absent in *A. glenos* (Fig. 5A, B).

Remarks: Ibises were probably comparatively abundant on Maui, where they were undoubtedly birds of the forest floor. Being flightless, they were highly susceptible to being trapped in lava tubes. Ibises (e.g., *Threskiornis aethiopicus,* pers. observ.) may at times feed heavily on snails. *Apteribis,* along with rails, may thus have exerted considerable predation pressure on the endemic land snails of Maui Nui, a factor that malacologists should recognize when assessing evolution in Hawaiian pulmonates. Unfortunately, the land snails of the Hawaiian Islands experienced much the same fate that befell so many of the birds and it may never be known if the snails of Maui Nui had evolved behavioral traits different from those on islands where ibises were absent.

TABLE 2

MEASUREMENTS (MM) OF THE SKELETON IN *Apteribis*.[1]

	Tarsometatarsus	Tibiotarsus	Femur
Molokai:			
Moomomi Dunes, (~9 m)	55.5, 55.5, 58.5, 58.6	98.2	65.9 ± 3.3 n = 6, 0.05
Maui:			
Kahawaihapapa Cave (15 m9	64.5	111.8	64.5, 69.9
Puu Naio Cave (305 m)	58.2 ± 4.0 n = 22, 0.07	105.1 ± 5.7 n = 13, 0.05	66.3 ± 2.9 n = 22, 0.04
Lower Waihoi Valley Cave (425 m)	—	101.0	63.8
Lua Lepo (808 m)	60.4 ± 3.8 n = 14, 0.06	107.5 ± 4.9 n = 12, 0.04	67.6 ± 3.0 n = 13, 0.04
Hukihuki (1,200 m) and Waihou Spring (1,463 m) Caves	—	100.0	64.0, 64.5
Auwahi Cave (1,145 m)	55.6 ± 2.7 n = 21, 0.05	99.4 ± 4.6 n = 17, 0.05	63.8 ± 2.4 n = 26, 0.04
Puu Makua Cave (1,463 m)	52.3 ± 1.9 n = 8, 0.04	95.7 ± 4.4 n = 6, 0.05	61.3 ± 1.2 n = 5, 0.02
Upper Kipahulu Valley Caves (~1,850 m)	58.8	95.8, 103.0	62.0, 64.0

[1] All measurements are lengths except for cranium width. Data are listed individually for samples of less than 5. For samples of 5 or more, mean ± standard deviation, sample size, and coefficient of variation are shown.

Apteribis sp., Maui
(Fig. 5J)

"Maui *Apteribis* sp. B" Olson and James, 1984:772.

Material: A multitude of bones from many individuals, including several nearly complete associated skeletons.

Distribution: Maui: tending to occur at lower elevations than *A. brevis* (see below).

Measurements: See Table 2 and Figs. 6 and 7.

Remarks: Bones of *Apteribis* from Maui originated in lava tubes that range from approximately 15 to 1,860 m in elevation, with the largest samples collected at approximately 305, 808, 1,145, and 1,463 m. These show great variation in robustness and in length (as much as 14 mm difference in the length of the tibiotarsus and 54 mm in the mandible). Although this might reflect sexual dimorphism within a single species (in many species of ibises males are larger and have longer bills than females), if this were the case one would not expect sexual size differences, particularly in a flightless bird, to be correlated with elevation.

To assess altitudinal variation, we measured the total length of the major long bones, synsacrum, and mandible, and the width of the cranium, for all reasonably complete specimens of *Apteribis*. These biometric data confirm our preliminary impression that the average size of these ibises varies from one locality to another (Table 2).

ANOVA statistics comparing long bone lengths among the four sites with the largest samples reveal a significant probability that at least one of the sample distributions is drawn from a distinct population ($P < 0.0001$ for each of four

TABLE 2

CONTINUED

Humerus	Ulna	Carpometacarpus	Synsacrum	Mandible	Cranium width
65.5	49.8, 3.9	25.5, 27.9	—	—	—
61.7	—	26.4, 28.2	60.7	—	—
68.3 ± 2.2	53.6 ± 2.2	26.4 ± 0.78	58.9 ± 4.0	137.7 ± 13.5	30.6, 32.0
n = 22, 0.03	n = 24, 0.04	n = 19, 0.03	n = 6, 0.07	n = 7, 0.10	—
—	—	—	—	—	—
68.9 ± 2.2	54.1 ± 1.5	26.5 ± 1.0	61.0 ± 2.3	157.0, 159.0,	32.9 ± 0.7
n = 15, 0.03	n = 10, 0.03	n = 8, 0.04	n = 6, 0.04	162.4, 166.0	n = 8, 0.02
66.0	—	—	63.7	—	—
64.9 ± 2.9	50.7 ± 2.2	24.4 ± 1.3	56.0 ± 3.5	112.0, 143.0,	31.0 ± 0.5
n = 25, 0.04	n = 22, 0.04	n = 16, 0.05	n = 6, 0.06	160.0	n = 6, 0.02
62.3 ± 3.1	47.0, 47.0,	24.0, 25.2	49.9, 50.0	116.0, 116.0,	30.0, 31.7
n = 6, 0.05	48.5, 49.4			117.0, 117.0	
67.1	—	—	—	—	—

tests). Independent *t*-tests for the same data suggest altitudinal differentiation (Table 3). Significant values ($P < 0.01$) were obtained for 17 out of 24 test statistics, including all twelve tests between sites separated by at least 650 m elevation. However, none of the four *t*-tests between the two sites that are lowest in elevation (Puu Naio and Lua Lepo) were significant, even though these sites are separated by 500 m elevation. The most abrupt size change appears to occur between Lua Lepo (808 m) and Auwahi Cave (1,145 m). All tests between these sites were significant, although they are separated by only 237 m. Because we compared four variables, we use $P < 0.01$ as the threshold for rejecting the null hypothesis. According to the Bonferroni method of correcting for multiple comparisons, this corresponds to a probability of about $P < 0.04$.

A trend toward smaller size above 808 m on the southern slope of Haleakala is illustrated graphically by the box plots in Figures 5 and 6. Thus we suspect that there were two partially sympatric species of ibis on Maui, with the smaller form (*Apteribis brevis*) being the predominant, if not the only, ibis at higher elevations on the southern slopes of Haleakala. These small ibises appear to have extended downslope as low as Puu Naio Cave (305 m) but perhaps not to sea level if their absence from Kahawaihapapa Cave is not an artifact. Larger birds appear to have ranged from sea level up certainly to Lua Lepo (808 m) and probably as far as Auwahi Cave (1,145 m).

A more detailed multivariate study, comparing inter- and intra-membral proportions in addition to bone lengths, may enable us to segregate the bones into two species, if such they were. For the time being, we have chosen to name only one of these forms, *Apteribis brevis,* with the holotype being a small individual from a site at relatively high elevation.

TABLE 3

SIGNIFICANCE LEVELS OF INDEPENDENT *T*-TESTS ON LENGTHS OF *Apteribis* LONG
BONES FROM FOUR MAUI CAVE LOCALITIES[1]

	PN (305 m)	LL (808 m)	AU (1,145 m)
Humerus, n = 68			
LL (808 m)	—		
AU (1,145 m)	*	*	
PM (1,463 m)	*	*	—
Ulna, n = 60			
LL (808 m)	—		
AU (1,145 m)	*	*	
PM (1,463 m)	*	*	+
Femur, n = 66			
LL (808 m)	—		
AU (1,145 m)	*	*	
PM (1,463 m)	*	*	*
Tibiotarsus, n = 48			
LL (808 m)	—		
AU (1,145 m)	*	*	
PM (1,463 m)	*	*	—

[1] —, not significant at the 0.05 level of probability; +, probability greater than 0.01 but less than 0.05; *, test significant, probability less than 0.01. PN—Puu Naio; AU—Auwahi; LL—Lua Lepo; PM—Puu Makua.

Order ANSERIFORMES
Family ANATIDAE
Moa-nalos (*Thambetochen* and Relatives)

The first of these extraordinary, flightless, goose-like ducks was described from Molokai as *Thambetochen chauliodous* (Olson and Wetmore 1976). Since then, species with similar adaptations have been found on all of the islands from which we have a reasonably good fossil record. It is now evident that the ancestor of these birds was not a true goose (Anserinae), as shown by the recovery on Maui of ossified syringeal bullae in association with bones of *Thambetochen* and a related genus. Such bullae do not occur in *Branta sandvicensis* (Humphrey 1958) or in any other Anserinae, but are characteristic of males of most genera of Anatinae, within which there is a great deal of variation in size and shape among the tribes and genera. The fossil bullae are very similar to those in the genus *Anas* (Fig. 8), but also resemble those in the Tadornini, a tribe that has not been recorded in the Hawaiian Islands, whereas species of *Anas* occur regularly as migrants and have given rise to two endemic forms. Thus the big flightless "goose-like" birds of the Hawaiian Islands may actually have been derived from something more like a Mallard (*Anas platyrhynchos*) and certainly were not derived from true geese, although in their terrestrial, herbivorous habits they were undeniably "goose-like."

Because of the proliferation of taxa and their derivation from something other than true geese, some short, convenient, collective term is needed for these flightless Hawaiian anatids. Otherwise we would be encumbered with such construc-
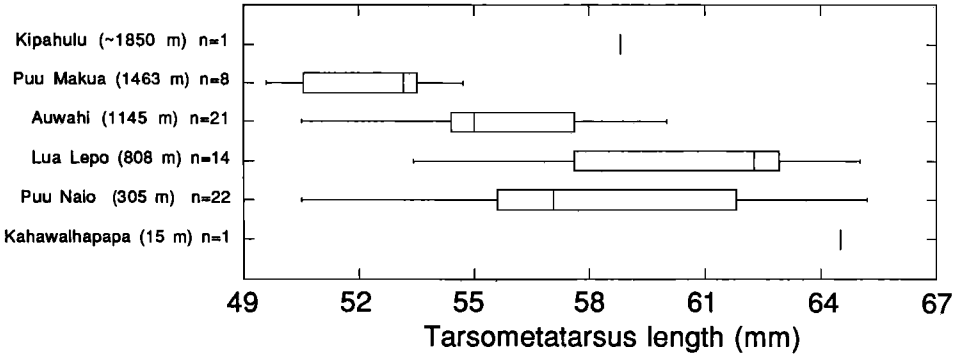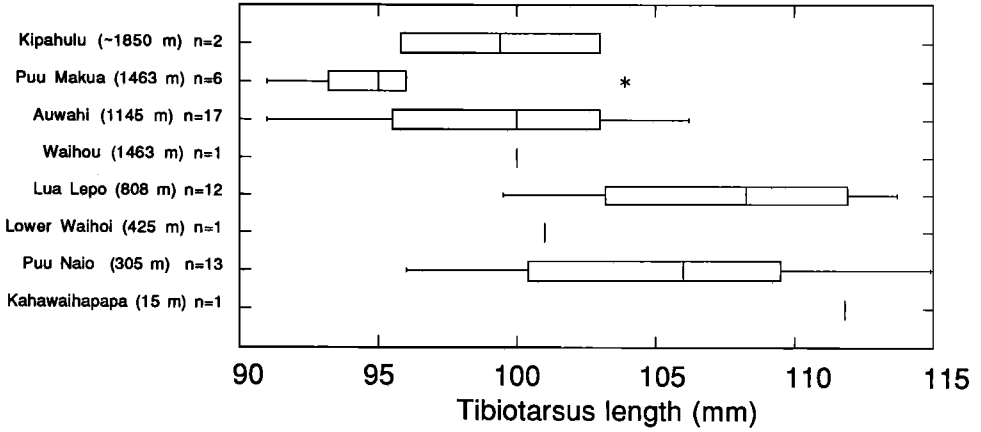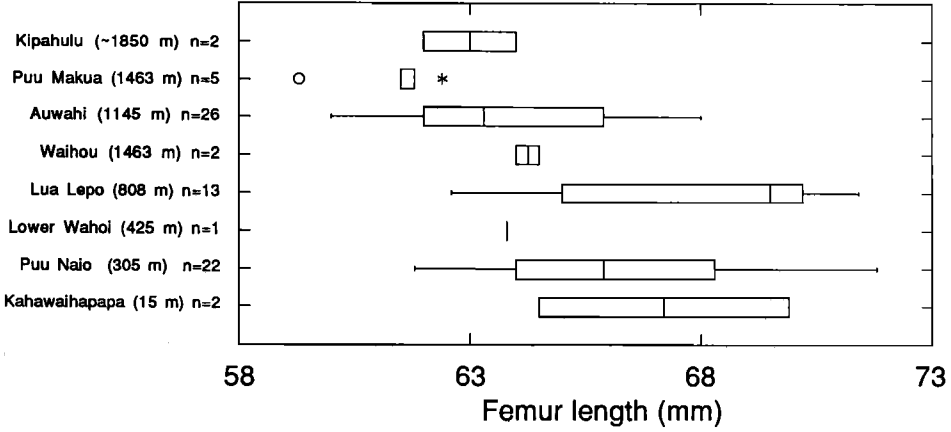
FIG. 6.   Box plots illustrating altitudinal variation in hindlimb bone lengths (mm) of *Apteribis* on Maui. Each box indicates 25% of the range of values on each side of the median, a horizontal line spans the range of values, the vertical line is the median, and outliers are indicated by an asterisk or circle.
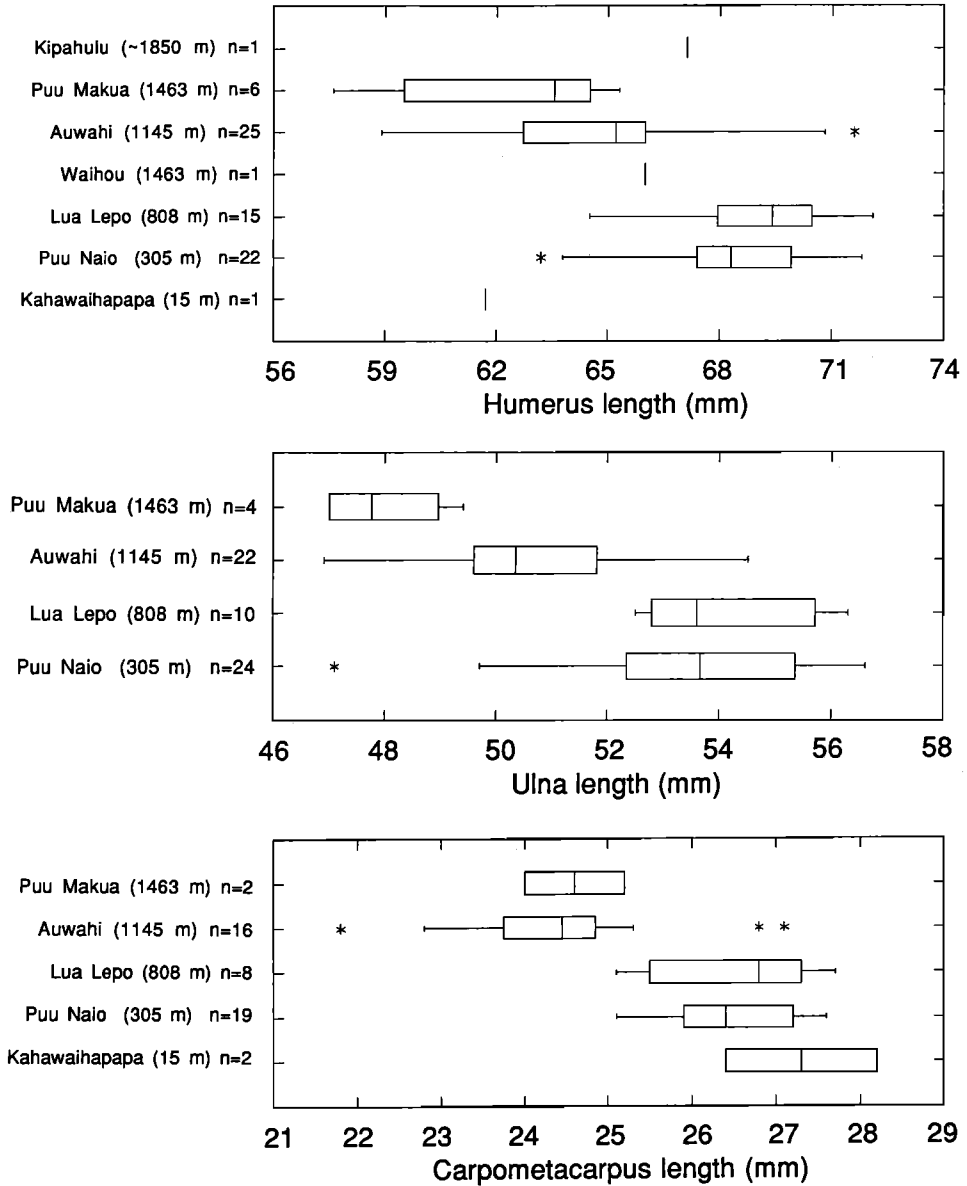
FIG. 7. Box plots illustrating altitudinal variation in the length of wing bones of *Apteribis* on Maui. For further explanation, see Figure 6.

tions as "*Thambetochen* and relatives" or "*Thambetochen*-like goose-like birds," which are as clumsy as the birds themselves were, and of which both writer and reader would soon become intolerant. Therefore we propose to coin a new word, "moa-nalo," from Hawaiian *moa,* fowl, and *nalo,* meaning lost, vanished, forgotten. Whereas *moa* in its most literal sense refers to the domestic fowl (*Gallus*), it also seems to convey a sense of edibility. Throughout Polynesia *moa* is applied, either alone or in combination with other words, to a variety of birds, such as the giant ratites of New Zealand ("Dinornithiformes"), or even to fruit bats (*Ptero-*
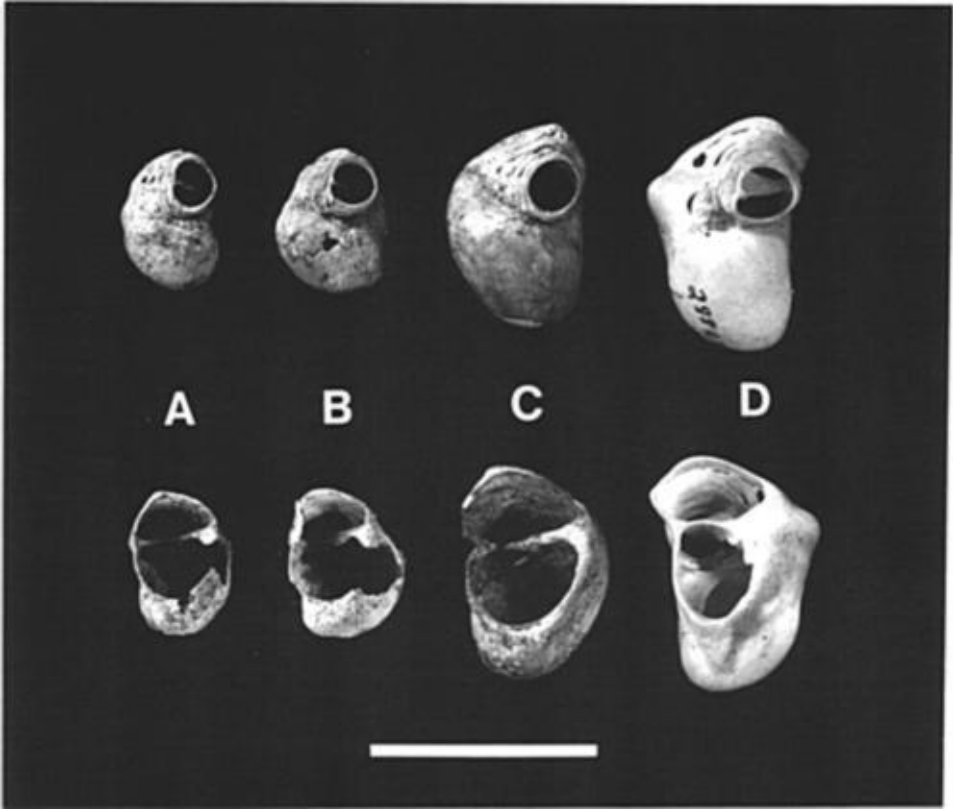
FIG. 8.   Syringeal bullae of moa-nalos compared with that of a Mallard; anterior view (top row) and posterior view (bottom row): *A–B, Thambetochen chauliodous* (USNM uncataloged); *C, Ptaiochen pau,* new genus and species (BPBM 158937); *D, Anas platyrhynchos* (USNM 288422). Scale = 3 cm.

pus), which in the Cook Islands are relished as food (D. W. Steadman, pers. comm.) and are known as *"moa-kirikiri"* (Savage 1962), meaning, in essence, "leather chicken." It is not at all unlikely that the word *moa,* in some form, was used by the early Hawaiians for the birds we shall now call the moa-nalos. The allusion to moas, in the New Zealand sense, is all the more appropriate for the Hawaiian birds, because both groups consist of a morphologically diverse assemblage of ponderous, flightless, extinct herbivores.

As far as known, all of the moa-nalos share the following distinctive morphological features that will not be repeated in the generic diagnoses. The pelvis and hindlimb elements are large and extremely robust, whereas the elements of the wing and pectoral girdle are excessively reduced, more so than in any other members of the Anseriformes, including the flightless "goose" *Cnemiornis* of New Zealand. The sternum totally lacks the carina and in the posterior half is unfused along the midline. The coracoid lacks the acrocoracoid and the long, strap-like scapula articulates with it nearly vertically, so that no acute angle is formed as in volant birds. Not infrequent individual variation results in fusion of the coracoid with the scapula or with the sternum. The furcula is weak, with widely divergent rami, and is possibly absent in one population. The wing elements are very small

for the size of the birds and are ill-formed, with the radius and ulna sometimes being fused. The intermetacarpal space of the carpometacarpus is partially or completely obliterated through fusion and the carpometacarpus may become fused with the first phalanx of the major digit. The premaxillae and dentaries are massive and always of a very peculiar appearance, usually with blunt tooth-like projections, except in the form from Kauai.

In their ecological role, the moa-nalos were probably very closely analogous to tortoises, such as those of the Galapagos and islands of the Indian Ocean, where there are no large herbivorous birds. The moas of New Zealand, and perhaps the elephantbirds of Madagascar, are the only obviously comparable avian assemblage of large insular herbivores, although the giant, extinct, flightless galliform *Sylviornis* of New Caledonia may have occupied a similar niche (Balouet 1984; Balouet and Olson 1989). Other birds may also have evolved similar adaptations on the larger archipelagos of the Pacific, such as Fiji or Samoa, only to be exterminated by prehistoric man.

Comparative material examined: Owing to the highly distinctive features of the moa-nalos, discussed above, for the purposes of generic and specific diagnoses the fossils need comparison only among themselves.

Chelychelynechen, new genus

Type species: Chelychelynechen quassus, new species.

Included species: Type-species only.

Distribution: Kauai, Makawehi dunes.

Etymology: "Turtle-jawed goose," from Greek, *chelys,* turtle, *chelyne* lip, jaw, and *chen,* goose; so named for the decidedly chelonian aspect of the rostrum and mandible. The gender is masculine.

Diagnosis: Postcranially a typical moa-nalo. Differs from *Thambetochen* and *Ptaiochen* in the unique shape of the rostrum, which is almost as high as it is long, with the palatal surface being much broader, especially so in the spaces between the two median ridges and the edge of the bill. The occlusal surface of the dentary is correspondingly broad and flat, and both jaws lack the bony tooth-like projections of *Thambetochen* and *Ptaiochen.* In *Chelychelynechen* the nostril is reduced and oriented almost vertically instead of horizontally. In lateral view of the mandible, the symphysis curves upward anteriorly, rather than being straight, the coronoid area is much higher and more expanded, with the coronoid process much better developed and more dorsally situated, and the retroarticular process markedly shorter and deeper.

Remarks: From what we know of the postcranial skeleton of *Chelychelynechen,* this genus has developed its flightless characters in a manner extraordinarily similar to that of *Thambetochen.* The structure of its feeding apparatus is so different, however, that we can only assume that *Chelychelynechen* developed from an ancestor similar to that of *Thambetochen,* rather than from some other kind of anatid. Material of the genus is still scant and we know nothing of the structure of the syringeal bulla, nor whether salt-gland impressions were present or absent, an important character distinguishing the other two genera of moa-nalos from each other.

Chelychelynechen quassus, new species
(Fig. 9) .

"Large Kauai goose" Olson and James, 1982b:34, 44; 1984:771.

Holotype: Associated rostrum, mandible, and os entoglossum, USNM 389743 (Fig. 9A–C). Collected 11 August 1976 by Storrs L. Olson. The rostrum lacks much of the surface of the right side and tip, and the mandible lacks most of the right ramus, although fragments of it may be included among the considerable amount of uncleaned scrap found at this site.

Type locality: Site K-1, Makawehi dunes, Kauai, Hawaiian Islands.

Distribution: Kauai: Makawehi dunes.

Etymology: Latin, *quassus,* broken, shattered, in reference to the regrettably fragmented condition of the type material, which was probably deposited as a complete skeleton but was unfortunately exposed in a jeep trail.

Measurements (mm) of holotype: Rostrum: length from vertical posterior border to tip as preserved, 45; posterior height as preserved, 42.8; posterior width of palatal surface, 37.7; greatest diameter of nostril, 9.4. Mandible: total length without retroarticular process, 91.2; symphysis length, ca. 27; greatest width of dentary, 10.2; height at coronoid process, 25. Os entoglossum: length and width, 20.3 × 7.9.

Paratypes: From Site K-1, all doubtless from the same individual as the holotype: left pterygoid, USNM 389750; 16 vertebrae or large fragments thereof, USNM 389767–79; right (Fig. 9E) and left coracoids, USNM 389762–3; left scapula, USNM 389764 (Fig. 9D); distal and proximal ends of right humerus USNM 389758–59; left humerus lacking head, USNM 389757 (Fig. 9G); proximal end of radius, USNM 389761; left carpometacarpus, 389760 (Fig. 9F); proximal end of left femur, USNM 389755; proximal end of left fibula, USNM 389756; two fragments of pedal phalanges, USNM 389765–6; plus many other fragments.

Site 303: anterior portion of a pelvis including about two-thirds of the sacrum and the right innominate extending far enough posteriorly to include the anterior third or more of the ilioischiatic fenestra, BBM-X 150095.

Measurements (mm) of paratypes: Coracoid (right): greatest length 34.2; depth through scapular end, 13.2; width and depth of shaft just below glenoid facet, 7.0 × 7.1; width at sternal end, 28.5. Scapula: length 82. Humerus: estimated length 56; shaft width and depth at midpoint, 6.9 × 6.8; distal width, 13.0. Carpometacarpus: length, 23.4. Pelvis: estimated width across antitrochanters, 76; greatest internal diameter of acetabulum, 13.8. Femur: greatest diameter of head, 16.8. Fibula: proximal width and depth, 5.8 × 20.0.

Diagnosis: As for the genus. Compared to *Thambetochen,* the shafts of the coracoid and humerus are more robust, the latter being very straight. The os entoglossum is shorter and wider than that in the holotype of *T. chauliodous,* but like it has a distinct fenestra in the proximal end.

Remarks: The rostrum and mandible of this species are remarkably convergent with tortoises. This might be due to the greater geological age of Kauai, which would allow for a longer period of evolution, in which case, given enough time the other moa-nalos might have evolved similar adaptations. On the other hand, the unique morphology of *Chelychelynechen* may have been a response to eco-
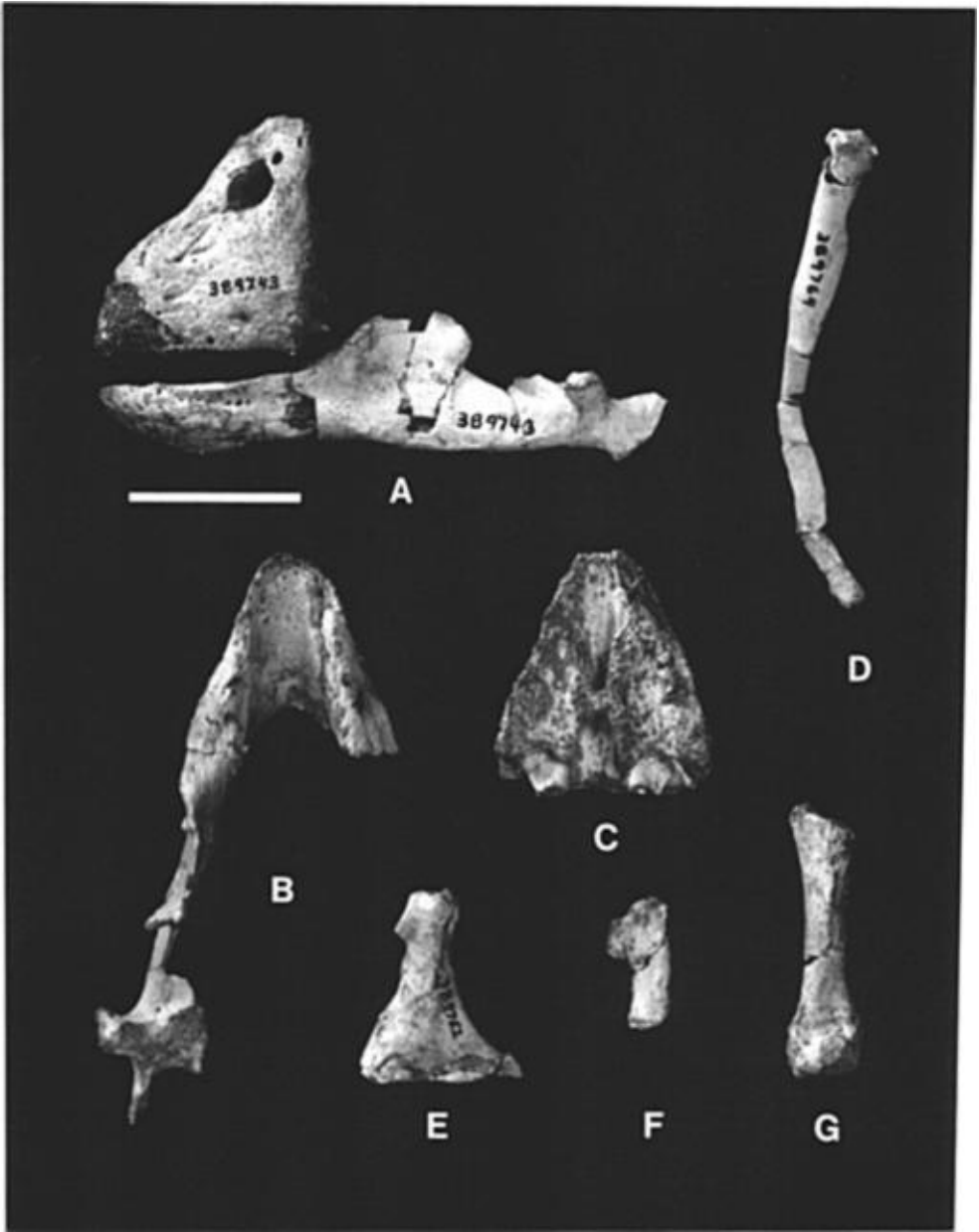
FIG. 9. Skeletal elements of *Chelychelynechen quassus*, new genus and species: *A*, rostrum and mandible in left lateral view (USNM 389743, holotype); *B*, mandible in dorsal view (USNM 389743, holotype); *C*, rostrum in ventral view (USNM 389743, holotype); *D*, left scapula in ventral view (USNM 389764); *E*, right coracoid in ventral view (USNM 389762); *F*, left carpometacarpus in external view (USNM 389760); *G*, left humerus (lacking head) in palmar view (USNM 389757). Scale = 3 cm.

logical conditions unique to Kauai, such as the predominance of some vegetation type that was rare or absent on the other islands.

Genus *Thambetochen* Olson and Wetmore, 1976

Type species: Thambetochen chauliodous Olson and Wetmore, 1976; by original designation.

Included species: T. chauliodous Olson and Wetmore, 1976; *T. xanion,* new species.

Distribution: Oahu, Molokai, and Maui.

Emended diagnosis: Moa-nalos differing from *Chelychelynechen* in that the rostrum is not greatly vaulted and widened, and the occlusal surfaces of the dentaries are not flattened but are ridged and bear well developed "teeth." Nostril comparatively large, longer than high. Mandibular symphysis straight, coronoid area not greatly expanded, lateral protuberance of coronoid reduced and more ventrally situated, retroarticular process long and narrow.

Compared with *Ptaiochen,* the nostrils are situated farther posteriorly, with the rostral tip anterior to the nostril being longer; the midline groove on the palatal surface of the rostrum is deeper and wider; the prefrontals (lacrimals) are much smaller; the roof of the orbits is expanded laterally and contains deep impressions for the salt glands on the ventral surface; the temporal fossae and the scars for attachment of the dorsal neck musculature are much more extensive, whereas the scar for M. depressor mandibulae has become more elongate and narrow; the overall outline of the cranium in lateral view is more flattened dorsally and in posterior view is squared. The coracoid is proportionately shorter, more robust, and has the sternal end much more expanded (not differing greatly from *Chely-chelynechen* in this respect). The head of the femur is not angled as much proximally and is more nearly on a level with the trochanter, and the fibula lacks a distinct, squared crest on the anterior margin. The syringeal bulla is smaller and differs in several qualitative features.

Thambetochen xanion, new species
(Fig. 10A, C)

"*Thambetochen* sp." Olson and James, 1982b:34, 44; James, 1987:225, 226.
"Oahu *Thambetochen* sp." Olson and James, 1984:771.

Holotype: Complete rostrum, USNM 389293 (Fig. 10A, C). Collected 3 April 1980 by Storrs L. Olson, Helen F. James, Aki Sinoto, and Eric Komori.

Type locality: Site 50-Oa-B6-22, Barbers Point, Oahu, Hawaiian Islands.

Distribution: Oahu: Barbers Point and Ulupau Head.

Etymology: Greek, *xanion,* a comb, in reference to the appearance conveyed by the bony tooth-like projections of the jaws. The name is a neuter noun in apposition.

Measurements (mm) of holotype: Length from nasofrontal hinge to tip, 61.2; height and width at posterior margin of nostril, 26.6 × 26.3; length of nostril, 15.2; least width of internarial bar, 5.3; length from anterior margin of nostril to tip, 36.3.

Paratypes: Rostrum, USNM 426094; mandible, USNM 426095; cranium, BPBM 158859; right coracoids, USNM 426096, USNM 426097, BBM-X 156342; right
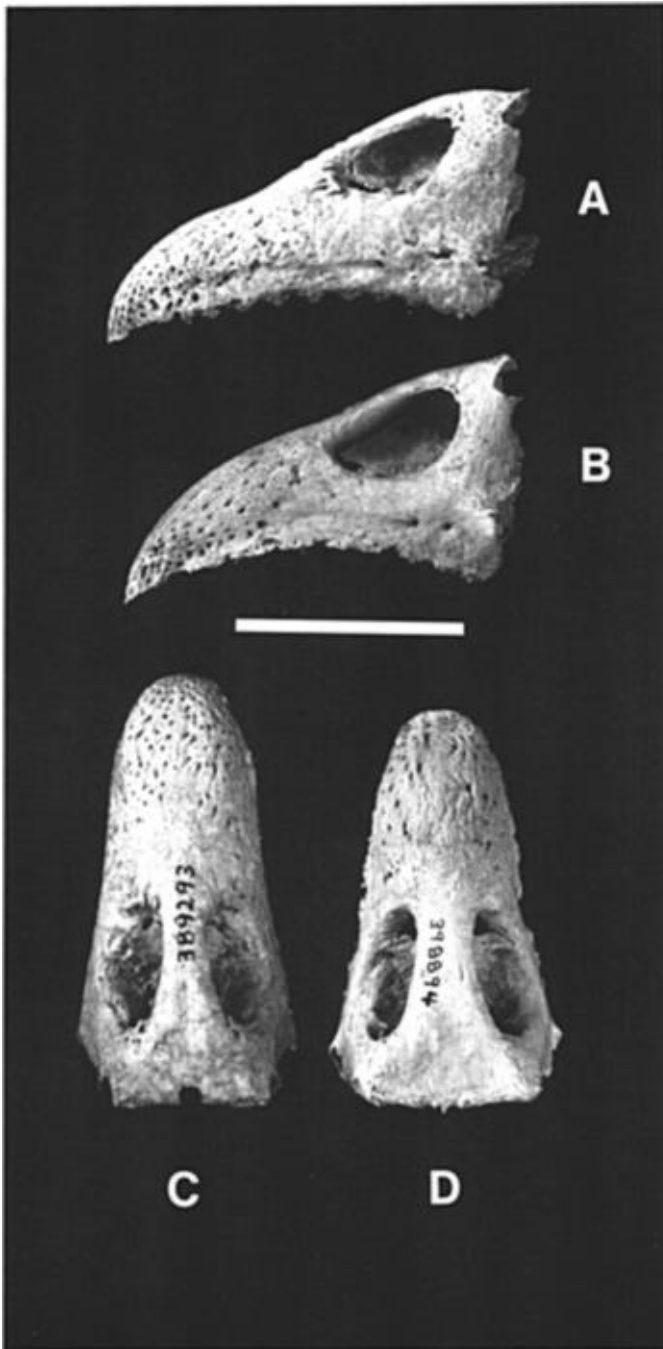
FIG. 10. Rostra of *Thambetochen*: *A, T. xanion*, new species, in left lateral view (USNM 389293, holotype); *C,* same, dorsal view; *B, T. chauliodous* in left lateral view (USNM 398894, Maui); *D,* same, dorsal view. Scale = 3 cm.

femora, USNM 426098, BBM-X 156365, BBM-X 156366; right tibiotarsi, BBM-X 156379, BBM-X 156381; left tibiotarsus, BBM-X 156380; right tarsometatarsus, USNM 426099; right and left tarsometatarsi, USNM 389295.

Measurements (mm) of paratypes: (These are in the same sequence as above.) Rostrum: length from nasofrontal hinge to tip, 59.8; height and width at posterior margin of nostril, 29.6 × 28.5; length of nostril, 15.5; least width of internarial bar, 5.0; length from anterior margin of nostril to tip, 36.1. Cranium: length from nasofrontal hinge, 61.5; greatest width (across postorbital processes), 46.6; width across squamosals, 41.8; greatest horizontal diameter of orbit, 27.1. Mandible: total length without retroarticular, 87.7; symphysis length, 22.9; greatest width of dentary, 5.8; height at coronoid process, 17.0. Coracoid: length with sternal end flat on calipers, 27.9, 26.7, 26.9; depth of proximal end, 10.2, 9.3, 10.0; width and depth of shaft just distal to glenoid facet, 5.3 × 5.2, 5.8 × 5.0, 5.3 × 4.8; width at sternal end, 23.8, 22.6+, 19.1. Femur: length, 92.0, 93.3, 98.7; proximal width and depth, 25.7 × 22.2, 25.4 × 21.9, 26.3 × 23.3; greatest diameter of head, 12.2, 11.4, 12.5; shaft width and depth at midpoint, 10.2 × 8.8, 10.5 × 10.1, 10.2 × 10.3; distal width and depth, 27.5 × 19.6, 26.8 × —, 28.8 × 20.9. Tibiotarsus: length, 160, 151.5, —; length from proximal articular surface, 154.0, 146.5, 153.2; width of proximal articular surface, 22.7, 22.6, 23.6; length of fibular crest, 24.3, 29.5, 24.0; width and depth of shaft at midpoint, 9.9 × 8.2, 9.1 × 8.1, 10.3 × 8.7; distal width and depth, 22.0 × 22.7, 21.2 × 21.9, 22.4 × 22.5. Tarsometatarsus: length, 85.1, 84.6, 85.8; proximal width, 22.6, 22.0, 22.9; width and depth of shaft at midpoint, 12.1 × 8.2, 10.2 × 6.8, 11.5 × 8.0; distal width, 24.9, 24.5, 23.7; depth of middle trochlea, 13.0, 13.5, 12.6.

Diagnosis: Generally smaller and less robust than *T. chauliodous,* especially in the hindlimb and coracoids. The rostrum anterior to the nostril is proportionately longer and straighter (less decurved), the nostril smaller, the internarial bar narrower and the lateral nasal bar wider than in *T. chauliodous.*

Remarks: Although *T. xanion* is certainly distinct from *T. chauliodous,* the degree of differentiation between these two species seems rather slight given that there has been no land connection between Oahu and Maui Nui.

Thambetochen chauliodous Olson and Wetmore, 1976
(Figs. 10B, D, 11A, C, E, G, 12A, C, D)

Thambetochen chauliodous Olson and Wetmore, 1976: 252.
"Maui *Thambetochen* sp. A" Olson and James, 1984:772.
"*Thambetochen* sp." James et al., 1987:2351.

Holotype: Nearly complete associated skeleton, BBM-X 146029.
Type locality: Site 1, Moomomi dunes, Molokai, Hawaiian Islands.
Distribution: Molokai: Moomomi dunes and Ilio Point. Maui: lava tubes on the southern slope of Mt. Haleakala.
Emended diagnosis: Differs from *T. xanion* in larger size, shorter, more decurved tip of rostrum, larger nostril, wider internarial bar and narrower lateral nasal bar.
Remarks: The considerable amount of material of *Thambetochen* from the dunes of Molokai pales by comparison with the hundreds of beautifully preserved

bones that are now available from the lava tubes of Maui. On Maui, *Thambetochen* is less common at higher elevations than *Ptaiochen,* which in turn is much less abundant in the lowlands.

Given the amount of variation in the populations from Maui and Molokai, we have not been able to detect any certain differences between them. For the time being we would refer the Maui population to *T. chauliodous,* which was originally described from Molokai. There is one possible difference, however, that we are unable to assess without better-associated individual skeletons, particularly from Molokai. The holotype of *T. chauliodous* was a complete articulated skeleton with the pectoral girdle in place. The specimen was very carefully prepared, so that it is certain that this individual did not possess a furcula. Nor have we encountered any furculae or fragments thereof among the material of *T. chauliodous* from Molokai. On the other hand, there are three distinct types of anatid furculae in the Maui deposits that we assume to correspond with *Branta* and the two moa-nalos found there. The furculae of the moa-nalos are weak, with widely divergent rami, those belonging to *Ptaiochen* being markedly flattened antero-posteriorly. Although it appears that the population of *Thambetochen* on Molokai may have lacked the furcula and that the population on Maui retained it, it is also possible that this condition varied individually.

Ptaiochen, new genus

Type species: Ptaiochen pau, new species.

Included species: Type species only.

Distribution: Maui.

Etymology: Greek, *ptaio,* stumble, and *chen,* goose; so named for the propensity of the species to fall into holes. The gender is masculine.

Diagnosis: Similar to *Thambetochen* in having both jaws with bony toothlike projections, while lacking the very deep rostrum of *Chelychelynechen.* Differs from *Thambetochen* in having the rostrum proportionately shorter, the nostrils situated farther anteriorly, with the rostral tip anterior to the nostril being much shorter. The midline groove on the palatal surface of the rostrum is deeper and wider. The prefrontals (lacrimals) are much better developed, extending ventrally and posteriorly towards the equally well developed postorbital processes so as to come much closer to encircling the orbit than in *Thambetochen.* The roof of the orbits is not expanded laterally and the ventral surfaces do not contain impressions for salt glands as in *Thambetochen.* The temporal fossae and the scars for attachment of the dorsal neck musculature are much less extensive than in *Thambetochen,* whereas the scar for M. depressor mandibulae is deeper and wider. The overall outline of the cranium in lateral and posterior views is more rounded, rather than being flattened dorsally and squared in posterior view as in *Thambetochen.*

The mandible has a much shorter symphysis, with the dorsal surface of the dentary flattened and expanded, though not nearly to the extent as in *Chelychelynechen,* and the tooth-like projections along the inner margins of the dentary are very reduced compared with *Thambetochen.* The lateral protuberance of the coronoid process is better developed and more dorsally situated than in *Thambetochen,* although again not to the degree that it is in *Chelychelynechen.*

The coracoid is proportionately longer, straighter, and has the sternal end much less expanded than in either *Thambetochen* or *Chelychelynechen*. The head of the femur is angled much more proximally, well above the level of the trochanter, than in *Thambetochen*. The fibula has a distinct squared crest on the anterior margin. The syringeal bulla is larger, more inflated, and differs in shape from that of *Thambetochen* (Fig. 8).

Remarks: Although clearly related to *Thambetochen* on the basis of bill morphology, the differences shown by *Ptaiochen* are consistent with recognizing this moa-nalo as a distinct genus. Some of the characters of the mandible in particular suggest that *Chelychelynechen* may have been derived from an ancestor more similar to *Ptaiochen* than *Thambetochen*. On the other hand, the coracoid in *Chelychelynechen* is more like that of *Thambetochen* and dissimilar to that of *Ptaiochen*.

Ptaiochen pau, new species
(Figs. 11B, D, F, H, 12B, E, F)

"Maui *Thambetochen* sp. B" Olson and James, 1984:772.

Holotype: Associated cranium, rostrum, and mandible lacking the right postdentary portion, USNM 384776 (Figs. 11B, 12B, E, F). Collected in September 1982 by Storrs L. Olson, Helen F. James and others.

Type locality: Auwahi Cave (1,145 m), Maui, Hawaiian Islands.

Distribution: Maui, southern slopes of Mt. Haleakala at upper elevations, from 1,145 m (Auwahi Cave) to 1,860 m (Kipahulu Valley).

Etymology: Hawaiian, *pau*, finished, ended, destroyed; in reference to the lamentable extinction of the species.

Measurements (mm) of holotype: Rostrum: length from nasofrontal hinge to tip, 48.7; height and width at posterior margin of nostril, 22.2 × 24.4; length of nostril, 14.6, least width of internarial bar, 4.0; length from anterior margin of nostril to tip, 22.9. Cranium: length from nasofrontal hinge, 55.0; greatest width (across postorbital processes), 44.4; width across squamosals, 39.5; greatest horizontal diameter of orbit, 22.7. Mandible: total length without retroarticular process, 65.6; symphysis length, 13.7; greatest width of dentary, 6.2; height at coronoid process, 15.0.

Paratype: Associated incomplete skeleton from the type locality, USNM 322649; very eroded cranium in two pieces; 5 presacral and 5 caudal vertebrae plus pygostyle; eroded pelvis lacking most of the postacetabular ilia; right coracoid (Fig. 11F); right and left scapulae (incomplete); right and left humeri (distal ends incomplete); right and left radii and ulnae; right carpometacarpus; right (Fig. 11H) and left femora, tibiotarsi, fibulae (Fig. 11D), and tarsometatarsi; 16 pedal phalanges plus 5 unguals; a few ribs and other fragments.

Measurements (mm) of paratype: Coracoid: greatest length, 30.2; depth through scapular end, 10.4; width and depth of shaft just below glenoid facet, 4.6 × 4.6; width at sternal end, 13.6. Scapula: proximal width, 10.2. Humerus: length, 50.9; shaft width and depth at midpoint, 5.3 × 5.0. Ulna: length, 33.1. Radius: length, 31.3. Carpometacarpus: length, 18.5. Pelvis: length of sacrum, ca. 110; width across antitrochanters, ca. 51; greatest internal diameter of acetabulum, 10.4.

FIG. 11. Comparison of bones of the two genera of "toothed" moa-nalos: *A*, skull and mandible of *Thambetochen chauliodous* in left lateral view (one individual with composite number BPBM 159001 and USNM 384749); *B*, skull and mandible of *Ptaiochen pau*, new genus and species, (USNM 384776, holotype) in left lateral view; *C*, left fibula of *T. chauliodous* (BBM-X 146029, holotype) in lateral view; *D*, left fibula of *P. pau* (USNM 322649) in lateral view; *E*, right coracoid of *T. chauliodous* (BBM-X 146029, holotype) in ventral view; *F*, right coracoid of *P. pau* (USNM 322649) in ventral view; *G*, right femur of *T. chauliodous* (USNM 384034) in anterior view; *H*, right femur of *P. pau* (USNM 322649) in anterior view. Scale = 3 cm.
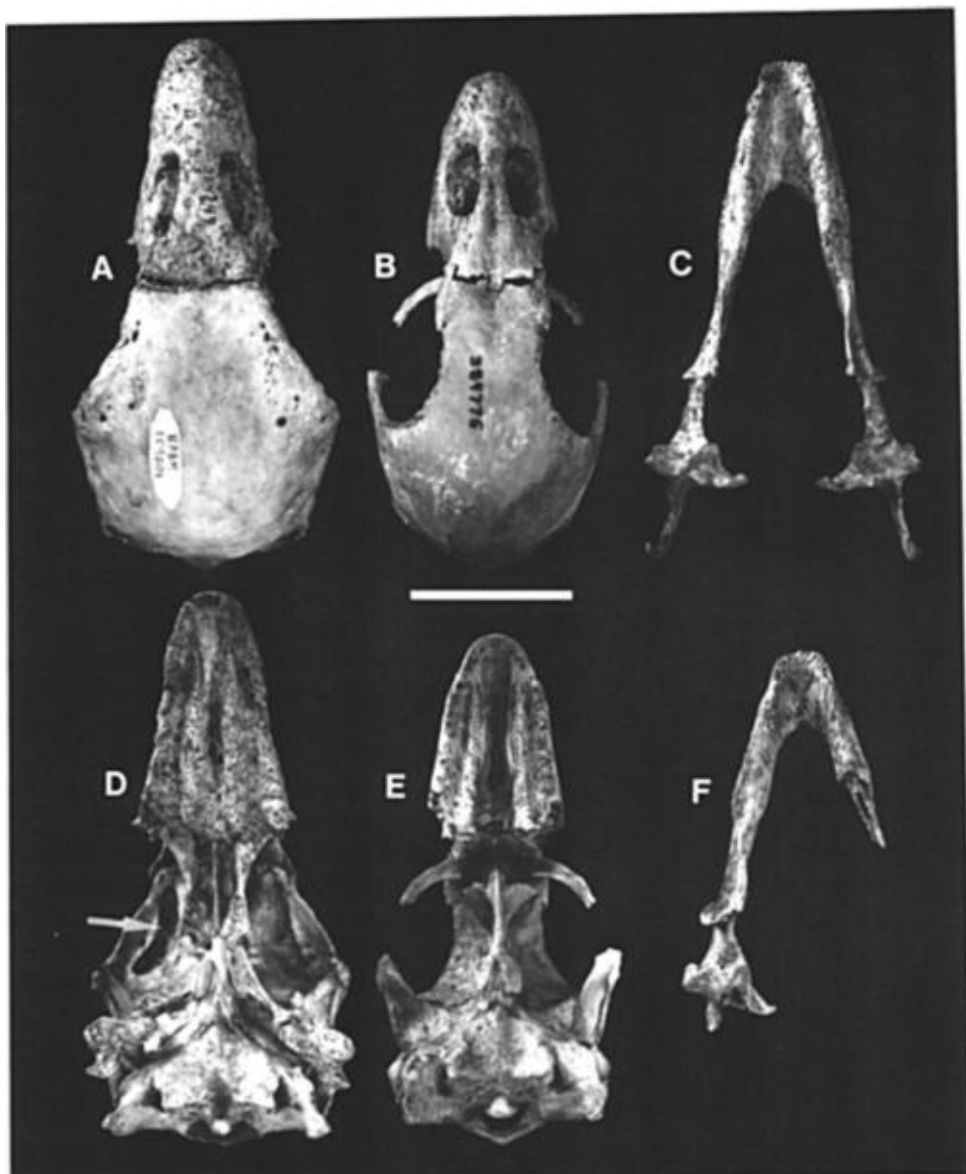
FIG. 12. Comparison of skulls (*A–B, D–E*) and mandibles (*C–F*) of the two genera of "toothed" moa-nalos: *A, Thambetochen chauliodous* (one individual with composite number BPBM 159001 and USNM 384749), dorsal view; *D,* same, ventral view (arrow indicates impression of salt gland); *B, Ptaiochen pau,* new genus and species (USNM 384776, holotype), dorsal view; *E,* same, ventral view; *C, T. chauliodous* (USNM 384749), dorsal view; *F, P. pau* (USNM 384776, holotype), dorsal view. Scale = 3 cm.

Femur: length, 89.3; proximal width and depth, 25.6 × 26.1; greatest diameter of head, 11.4, shaft width and depth at midpoint, 10.5 × 9.9; distal width and depth, 20.8 × 20.8. Fibula: proximal width and depth, 5.3 × 14.5. Tibiotarsus: length from cnemial crest, 146; length from proximal articular surface, 138.8; width of proximal articular surface, 21.9; length of fibular crest, 22.1; width and

depth of shaft at midpoint, 9.3 × 8.2; distal width and depth, 18.7 × 20.5. Tarsometatarsus: length, 80.2; proximal width, 21.5; width and depth of shaft at midpoint, 10.9 × 7.1; distal width, 22.4; depth of middle trochlea, 13.1.

Diagnosis: As for the genus.

Remarks: Ptaiochen pau appears to have been restricted to higher elevations. Its lowest occurrence is at the type locality, Auwahi Cave (1,145 m), where it is decidedly less abundant than *Thambetochen.* At sites at higher elevations, *Ptaiochen* is the most common if not the only moa-nalo. At Puu Makua (1,463 m) *Thambetochen* is rare by comparison, and in the Kipahulu Valley caves (1,860 m) *Ptaiochen* is the only mao-nalo identified. Altitudinal differences in the relative abundances of anatids on a given island might explain the great rarity of the "supernumerary goose" on Oahu, and the lack of a second species of moa-nalo on Molokai, on both of which islands all fossil localities are just above sea level.

True Geese (The Nene and Relatives)
Genus *Branta* Scopoli, 1769

The sole goose now resident in the Hawaiian Islands is the Nene, *Branta sandvicensis* (Vigors), the only certain historical records of which are from the island of Hawaii. Fossils, however, show that the distribution and diversity of *Branta* in the islands was formerly much greater, although the systematic problems attendant upon these fossils are so complex that we are unable at this time to establish species' limits with any confidence.

The true geese of the subfamily Anserinae (nominal genera *Anser, Eulabeia, Cygnopsis, Chen, Philacte, Branta, Nesochen*) are closely interrelated and are osteologically rather uniform. After analyzing the postcranial skeleton, Woolfenden (1961) recognized only three genera, *Anser, Branta,* and *Nesochen,* the last for *B. sandvicensis* alone. The characters given for separating *Branta* from *Anser* are rather weak and variable, with the most striking difference being the considerable pneumaticity of the furcula in *Anser,* which is not pneumatized in *Branta* (including *Nesochen*). Even this must show some variation, however, as Woolfenden (1961:104) says that pneumatic foramina "are almost always present" in *Anser.* Nevertheless, it is not questioned that the species of *Branta* form a natural group within the true geese, characterized externally by darker plumage and black legs and feet (Kear and Berger 1980:35). Humphrey (1958) also noted differences in the trachea between *Anser* and *Branta,* and found that the Nene did not differ from *Branta,* for which reason he questioned the validity of *Nesochen.* Furthermore, *Branta* appears to have differentiated from *Anser* at least by the late Miocene, about 5.5 million years ago (Bickart 1990), so it does seem expedient to continue to recognize the genus *Branta,* despite the difficulty of providing it with a rigorous osteological diagnosis.

Although the Nene is derived from the *Branta* group of geese, its specializations for terrestrial life and more sedentary existence (increase in relative size of hindlimb, reduced webbing, reduction of forelimb) have caused some authors to segregate the species in its own genus, *Nesochen* (e.g., Miller 1937; Woolfenden 1961; American Ornithologists' Union 1983). Of the characters given by Woolfenden (1961:105), most appear to be correlated with the preceding specializations and several are too variable within geese to be of generic value (e.g., configuration of the ventral manubrial spine of the sternum; size of pneumatic foramen of sternum).

Some of the characters of "*Nesochen*" are consistent, although we would not accord them generic weight. These are: the narrow sternum, the broad dorsal manubrial spine, the overall shape and proportions of the bill and mandible, and the degree of inflation of the frontal bones. These characters are shared by *B. sandvicensis* and the various extinct, fossil populations of *Branta* from the Hawaiian islands. This suggests that these geese constitute a monophyletic assemblage derived from a single colonization of the archipelago. Although they have diverged somewhat from their mainland ancestor in response to the Hawaiian environment, the degree of divergence is not sufficient, in our opinion, to necessitate separate generic status for the Hawaiian birds, whose relationships are best reflected by retaining them in the genus *Branta.*

The Nene is known in historical times only from the island of Hawaii, with old reports of the species from Maui in the 19th century being based only on unverifiable hearsay evidence (Kear and Berger 1980). The place name Puunene (Nene Hill) on east Maui, contrary to J. Pratt (1972), does not constitute evidence for the existence of *B. sandvicensis,* per se, on Maui, as the name "nene" may have been used by Hawaiians to refer to the larger extinct forms of *Branta* as well.

Bones of *B. sandvicensis* are found regularly in lava tubes in various parts of the island of Hawaii, mostly, but not always, in archeological contexts. We have also examined bones that are inseparable from those of *Branta sandvicensis* from dune and archeological deposits on Molokai, from dune deposits on Lanai and Kauai, and from lava tubes on the east slope of Haleakala on east Maui, where this form of *Branta* is decidedly rare. Apparently, the Nene once occurred naturally throughout the main Hawaiian islands, although as yet we have not identified remains of it from Oahu, where all fossils of *Branta* found so far appear to be from an extinct form with reduced wings.

A similar extinct form of *Branta* is abundant in the lava tubes of Maui, and is also known from a single incomplete skeleton from Kauai. The tremendous variation in these fossils, particularly in the bones of the wing, makes the interpretation of species-level systematics exceedingly difficult. Basically, compared with *Branta sandvicensis,* most of these birds are larger and more robust, but with smaller wings and pectoral apparatus (Fig. 13). Other seemingly consistent qualitative differences may be discerned, particularly in more complete and better-preserved specimens. On Maui, variation in reduction of the wing elements ranges from individual bones that are inseparable from those of *B. sandvicensis,* a species that is capable of strong flight, to those from birds that were without doubt flightless. However, some of the individuals with the most reduced wings are also quite small, the size of *B. sandvicensis* or perhaps a bit smaller, and the possibility exists that more than one extinct species of *Branta* is represented on Maui. There is also apparent variation from island to island, with specimens from Oahu appearing more gracile than the majority of Maui birds. The single specimen from Kauai is robust, more like the birds from Maui than those from Oahu.

It appears that various populations of *Branta* in the Hawaiian Islands were at a stage in the evolution of flightlessness that has rarely if ever been observed in modern birds. These populations probably included both volant and flightless individuals and may have been variously affected by introgression with *B. sandvicensis.* Analysis of Hawaiian fossil *Branta* may provide us with some of our
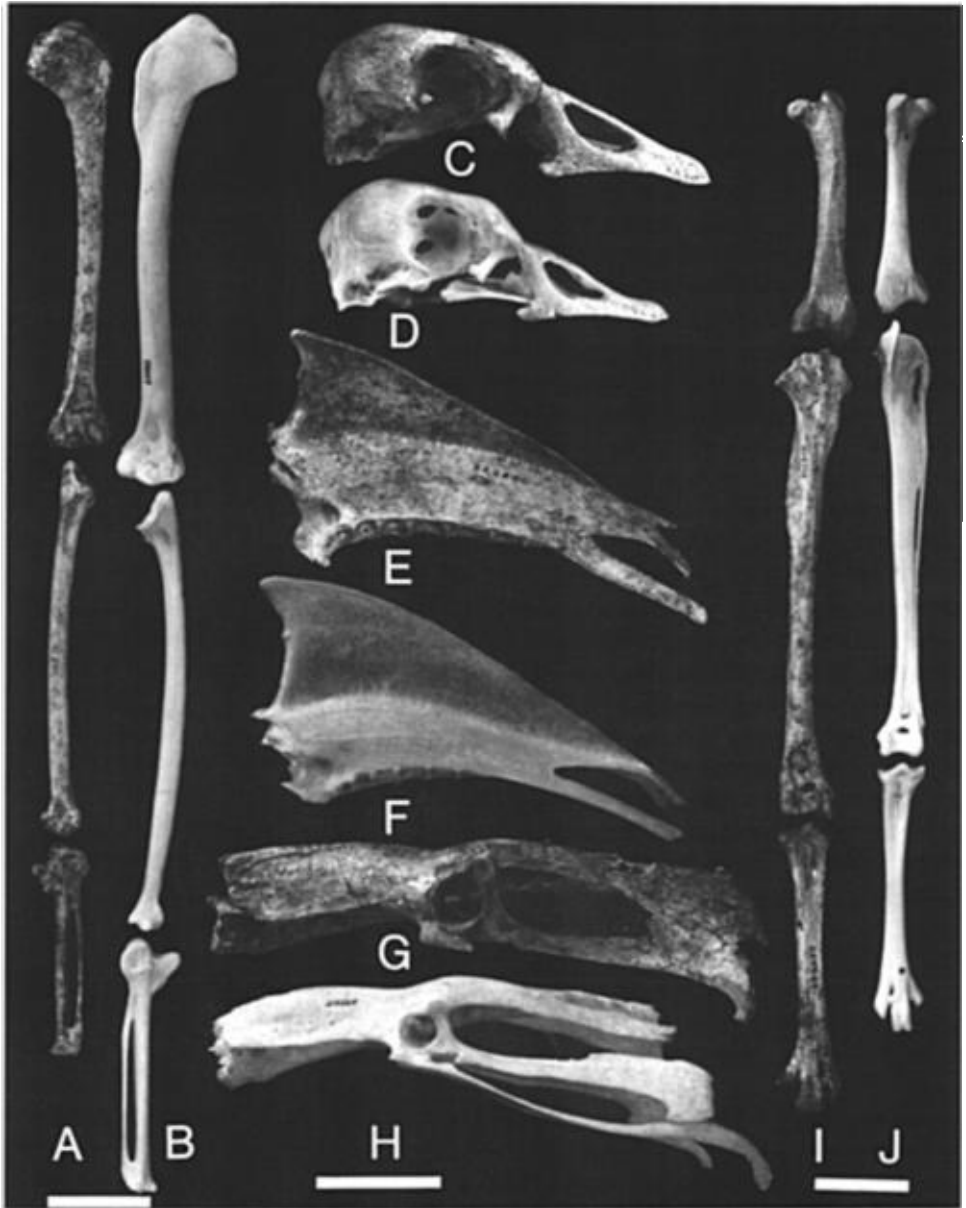
FIG. 13. Bones of the wing, axial skeleton, and hindlimb of *Branta hylobadistes*, new species, compared with bones of the extant Nene Goose *Branta sandvicensis*: *A*, wing elements of *Branta hylobadistes* (USNM 322600); *B*, wing elements of *B. sandvicensis* (USNM 553679); *C*, skull of *Branta hylobadistes* (USNM 373443); *D*, skull of *B. sandvicensis* (USNM 344617); *E*, sternum of *Branta hylobadistes* (USNM 322600); *F*, sternum of *B. sandvicensis* (USNM 344617); *G*, pelvis of *Branta hylobadistes* (USNM 322600); *H*, pelvis of *B. sandvicensis* (USNM 344617); *I*, hindlimb elements of *Branta hylobadistes* (femur, USNM 384066; tibiotarsus, USNM 322600; tarsometatarsus, USNM 384069); *J*, hindlimb elements of *B. sandvicensis* (USNM 553679). Note the large size of the skull and pelvic elements and the reduced wing and sternal carina. Each group of figures is at slightly different magnification; scales = 3 cm.

best insights into "intermediate" stages of evolution in the development of flight-lessness and be particularly instructive in showing how species that are ultimately completely flightless may develop striking parallel similarities on different islands.

Although we will not attempt to resolve inter-island species differences at this time, it is expedient to name the best represented of the extinct populations (that from Maui) for convenience in discussing this distinctive assemblage of endemic "non-Nene" populations of *Branta*.

Comparative material examined: Branta sandvicensis, 8 skeletons and 2 trunks (USNM 291307, 320211, 344617, 500352, 553079, 553800, 557918, 575094, 567522, 576674); *B. canadensis minima* (USNM 429115); *B. canadensis interior* (USNM 429868, 488763); *B. bernicla* (USNM 501615); *Anser caerulescens* (USNM 488571); *A. albifrons* (USNM 488577); *A. rossi* (USNM 430473).

Branta aff. *hylobadistes,* Kauai

"Medium Kauai goose" Olson and James, 1982b:44; 1984:771.

Material: Much of an associated skeleton of one individual, USNM 389723–41, including cranium, partial sternum and all the major elements of wing and leg.

Distribution: Kauai: Makawehi dunes.

Remarks: This specimen is more robust than those from Oahu and is thus more similar to the birds from Maui.

Branta aff. *hylobadistes,* Oahu

"*Branta* sp." Olson and James, 1982b:44; 1984:771.

Material: Many bones of most parts of the skeleton.

Distribution: Oahu, Barbers Point.

Remarks: This population of *Branta* from Oahu was very similar to *B. hylobadistes* but the hindlimb elements are generally longer and more gracile and the cranium shorter. As on Maui, there is a great deal of individual variation in size, especially of the wing elements. Pending detailed statistical study of the large forms of *Branta,* we consider that it would be premature to name either the Oahu or Kauai populations at this time.

Branta hylobadistes, new species
(Fig. 13A, C, E, G, I)

"Maui *Branta* sp. A" Olson and James, 1984:772.
"Maui *Branta* sp. B" Olson and James, 1984:772.
Branta sp. James et al., 1987:2353.

Holotype: Incomplete associated skeleton, USNM 322600 (Fig. 13A, E, G, I—tibiotarsus only). Collected August or September 1982 by Storrs L. Olson and Helen F. James. The specimen includes a complete rostrum with palatines and vomer, a portion of basicranium including foramen magnum, mandible, left quadrate, incomplete atlas and 9 other vertebrae, left coracoid, right and left scapulae, sternum, left humerus, left ulna, right carpometacarpus, left carpometacarpus lacking proximal end, pelvis, right tibiotarsus, ribs, syrinx.

Type locality: Auwahi Cave (1,145 m), Maui, Hawaiian Islands.

Distribution: Maui: lava tubes on the southern slope of Mt. Haleakala.

Etymology: "Woods-walker," from Greek, *hyle,* wood, forest, and *badistes,* a walker, from the obvious abundance of the species in formerly forested areas and its dependence on foot power as evidenced by the reduced wings and pectoral girdle. The name is a masculine noun in apposition.

Measurements (mm) of holotype: (For paired elements, measurements are from the right side only.) Rostrum: length along midline from nasofrontal hinge to tip, ca. 49; nostril length, 19.0; length from anterior margin of nostril to tip, 22.8; proximal width (ventral) and height, 25.7 × 22.2. Mandible: total length without retroarticular process, 79.9; symphysis length, 10.6. Sternum: length of carina from apex, 84.4; depth of carina from apex to sternal plate, 25.3; width across anterior lateral processes, 54.1; width at third costal facet, 49.9. Coracoid: greatest length, 56.6. Scapula: length, 78.8; articular width, 13.1; width at neck, 6.6. Humerus: length, 126.1; proximal width, 27.1; shaft width at midpoint, 7.2; distal width, 18.3. Ulna: length, 108.6. Carpometacarpus: length, 63.9; proximal depth, 16.9. Pelvis: length along midline (sacral vertebrae), 133.1; width across antitrochanters, 50.1; greatest diameter of acetabulum, 9.9. Tibiotarsus: total length, 152.7; length from distal end of fibular crest, 96.5; shaft width at midpoint, 9.0; distal width, 17.6.

Paratypes: Incomplete associated skeleton, USNM 322632, including rostrum, left palatine, quadratojugals, mandible, right quadrate, right coracoid, right scapula, furcula, left humerus lacking distal end, right ulna, right and left radii, right and left cubitals, right carpometacarpus, left carpometacarpus lacking distal end, right femur, right and left tibiotarsi, right and left fibulae, right and left tarsometatarsi, atlas, axis, and 19 other vertebrae, ribs, 7 pedal phalanges.

Cranium with rostrum and left palatine, USNM 373443 (Fig. 13C); three left femora, USNM 384064–384066 (Fig. 13I, part); three left tarsometatarsi, USNM 384068–384070 (Fig. 13I, part).

Thousands more bones from dozens of individuals were available for the comparisons but have not been listed for economy of time and space.

Measurements (mm) of paratypes: Associated incomplete skeleton USNM 322632 (for paired elements, measurements are from the right side only). Rostrum: length along midline from nasofrontal hinge to tip, 45.8; nostril length, 19.7; length from anterior margin of nostril to tip, 19.8; proximal width (ventral) and height, 23.8 × 20.7. Mandible: length without retroarticular process, 72.7; symphysis length, 8.9. Coracoid: greatest length, 50.0. Scapula: length, 75.3; articular width, 15.3; width at neck, 6.3. Furcula: length, 55.9. Humerus: length, ca. 112; proximal width, 22.6; shaft width at midpoint, 7.0. Ulna: length, 103.4. Radius: length, 98.4. Carpometacarpus: length, 59.7; proximal depth, 15.2. Femur: length, 75.2; proximal width, ca. 20; shaft width at midpoint, 9.3; distal width, 20.2. Fibula: length, 77.7; proximal depth, 11.3. Tibiotarsus: total length, 143.3; length from distal end of fibular crest, 87.8; shaft width at midpoint, 9.0; distal width, 17.2. Tarsometatarsus: length, 85.8; proximal width, 17; shaft width at midpoint, 7.2; distal width, 18.8.

Skull, USNM 373443: total length, 97.6; cranium length from nasofrontal hinge, 54.2; cranium width at postorbital processes, 35.5; length of rostrum along midline from nasofrontal hinge to tip, 47.3; nostril length, 20.1; length from anterior

margin of nostril to tip, 20.9; proximal width (ventral) and height of rostrum, 24.0 × 21.0.

Femora, USNM 384064–384066: length, 79.6, 79.0, 83.6; proximal width, 20.2, 20.0, 22.0; depth of head, 10.1, 9.6, 10.0; shaft width at midpoint, 9.6, 8.6, 9.2; distal width, 20.7, 21.4, 22.5.

Tarsometatarsi, USNM 384068–384070: length, 90.5, 95.6, 93.5; proximal width, 18.1, 18.7, 18.7; shaft width at midpoint, 8.1, 8.5, 7.5; distal width 20.7, 21.6, 20.3.

Diagnosis: Larger and more robust than *Branta sandvicensis* but with reduced wing and pectoral girdle. Dorsal surface of premaxilla in lateral view not as distinctly depressed posterior to tip, ventral surface of rostrum more concave. Sternal carina much reduced in depth and in posterior extent. Furcular facet of coracoid not as undercut, usually not pneumatic. Scapula with dorsal pneumatic foramen usually absent or greatly reduced. Pelvis with acetabulum and antitrochanter absolutely and relatively much larger, preacetabular portion relatively longer and postacetabular portion shorter than in *B. sandvicensis*; broad posterior fusion between ilium and ischium as typical of Anatidae, unlike the unique condition in *B. sandvicensis* in which there is little or no fusion (Miller 1937; Olson 1985b). Wing elements extremely variable in size, usually smaller, sometimes much more so, than in *B. sandvicensis.* Pneumatic opening of humerus with lesser distal extent, shaft more gracile, brachial depression larger and deeper. Femur much more robust, head much larger, trochanter higher, rotular groove much deeper, anterior margins of condyles more elevated. Tibiotarsus more robust, outer cnemial crest broader, thicker, and rotated markedly more posteriad. Tarsometatarsus more robust, trochleae more divergent.

Remarks: The absence of any fossils of *Branta* similar to *B. hylobadistes* on Molokai, where bones of *B. sandvicensis* occur rather commonly, may reflect the paleoenvironment of the fossil sites, which are situated in the arid western end of the island where only dry scrubby forest and strand vegetation would have been present. Fossils of *B. sandvicensis* and those of the *B. hylobadistes* type have been found sympatrically on Maui and Kauai.

Goose-like Birds of Uncertain Affinity

At least three probable species of goose-like birds are known only from very fragmentary remains sufficient to show only that they are different from any of the species described thus far. These may perhaps be unrelated to either of the two known stocks of goose-like birds in the archipelago (*Branta* and the moanalos). We mention them here only to call attention to further diversity among the Anatidae of the Hawaiian Islands. Better fossil material is needed before more definitive conclusions can be reached.

Supernumerary Oahu Goose

"Supernumerary Oahu goose" Olson and James, 1982b: 34, 44; 1984:771.

Material: Premaxillary symphysis, USNM 426100; left pterygoid, USNM 426101.

Distribution: Barbers Point, Oahu, Hawaiian Islands.

Measurements (mm): Pterygoid: length, 21.2.

Remarks: The premaxillary symphysis is heavy and swollen, unlike the more delicate element in *Branta*. It lacks any evidence of tooth-like projections and the median groove on the ventral surface is much shallower than in any of the known moa-nalos. Although distinctive, it will not be possible to determine the affinities of this species until additional material is discovered.

Genus *Geochen* Wetmore, 1943

Type species: Geochen rhuax Wetmore, 1943; by monotypy and "new genus and species" convention.
Included species: Type species only.
Distribution: Hawaii: Kau District.
Emended diagnosis: Larger and more robust than Hawaiian populations of *Branta,* including the robust fossil forms. Differs from *Branta* and from the moa-nalos in having the proximal articular surface of the tibiotarsus oriented latero-medially, rather than having its long axis in an antero-posterior plane, and also in having the head and trochanter of the femur more sharply set off by a groove. Differs further from the moa-nalos in having a shorter neck of the femur and a more sharply rising trochanter.

Geochen rhuax Wetmore, 1943

Geochen rhuax Wetmore, 1943:146.

Holotype: Very imperfect right tibiotarsus, USNM 16740.
Type locality: Near Kaumaikeohu, above Pahala, Kau District, Island of Hawaii.
Distribution: Known only from the type locality.
Paratypes: Very fragmentary remains of right and left femora, fibula, and pelvis associated directly with the holotype and doubtless belonging to the same individual.
Remarks: This was the first fossil bird to be described from the Hawaiian Islands, the type material having been found in 1926 in the course of a public works excavation, at a depth of 25 m under a lava flow (Wetmore 1943). From their very friable and warped appearance, the bones were almost certainly heated until glowing, with all organic material in the bone having been combusted. Although Wetmore (1943) considered *Geochen* to be more closely related to the Australian genus *Cereopsis* than to *Branta* or other goose-like anatids, we regard the material as being much too imperfect for determining the affinities of the bird. We can only hope that additional specimens will be found that can unambiguously be identified with the type. Otherwise, this will simply have to be regarded as a form of doubtful relationships.

Very Large Hawaii Goose

"Large Hawaii goose" Olson and James, 1982b:35; 1984:772.

Material: Associated fragmentary material consisting of the proximal end of a right ulna, posterior portion of a sacrum and other pelvic fragments, a vertebra, 9 pedal phalanges, and other unidentified scraps, USNM 389448–389469. Incomplete cranium lacking most of the right side and basioccipital, BPBM 158620;

fragment of proximal end of right femur, BPBM 158621. Six uncataloged lots of various very poorly preserved bones, probably representing six individuals.

Distribution: Hawaii: western side of the island. The first specimens were from two lava tubes in the vicinity of Kailua, North Kona District. The uncataloged lots are from a lava tube on Kahua Ranch, North Kohala District, at an elevation of about 1,133 m.

Measurements (mm): Cranium: approximate width at nasofrontal hinge, 30. Tibiotarsus: length from proximal articular surface, 205. Tarsometatarsus: length, ca. 110.

Remarks: There are scarcely any comparable elements among these samples of fragmentary bone, but all the material comes from a very large goose, larger than any of the moa-nalos or the various forms of *Branta,* so we assume that they represent one and the same species. The wing was reduced, but not nearly to the extent as in the moa-nalos.

<div style="text-align:center">

Order GRUIFORMES
Family RALLIDAE
Genus *Porzana* Vieillot, 1816

</div>

Historically, the only endemic species of Rallidae known from the Hawaiian archipelago are *"Porzanula" palmeri* of Laysan, and *"Pennula" sandwichensis* from the island of Hawaii. Both were flightless, are now extinct, and are properly referred to the widespread mainland genus *Porzana* (Olson 1973a). The history and synonymy of *Porzana sandwichensis* is rather complex and will be dealt with elsewhere.

The fossil record now shows that flightless rails were distributed throughout the archipelago, one or more species doubtless occurring on each of the islands. We have been able to document the existence of 9 or 10 species in addition to the two known historically. These were all short-billed "crakes" and were presumably derived from multiple invasions by species of *Porzana,* in which genus we have provisionally placed all of them. Determining the closest mainland relatives of each species and the total number of invasions involved will be very difficult given the incomplete representation of some of the species, the rather extreme degree of modification that accompanies flightlessness, and the osteological homogeneity of the extant, volant, mainland forms of *Porzana* from which the Hawaiian birds were derived.

Diagnosing so many closely related species has been a difficult task, the single most useful character being size (Fig. 14). Size alone may not necessarily permit the identification of certain disassociated elements on a given island, however, because of the differing degrees of reduction of the pectoral apparatus that accompanies flightlessness. For example, a large species may have the wing elements proportionately much more reduced than in a smaller species. We have named the five new species for which we consider the material at hand to be sufficiently diagnostic, although perhaps as many as five additional species are represented.

All of the extinct fossil rails in the Hawaiian Archipelago were flightless, so that dispersal of species from one island to another would have been unlikely, with the exception of those islands of the Maui Nui group that were united during periods of lowered sea level. Therefore, the characteristics associated with flightlessness are assumed to have been derived independently within any given insular
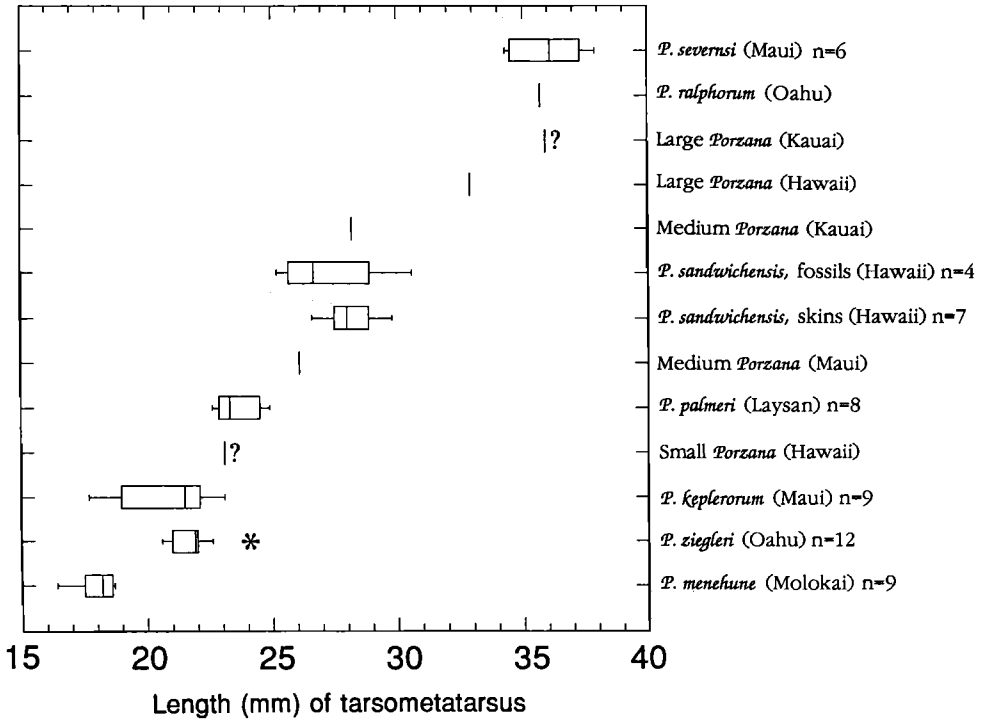
FIG. 14. Box plots of relative sizes of Hawaiian species of *Porzana* as shown by length of tarso-metatarsus. Where not otherwise indicated, n = 1. Queried points were estimated from width measurements. Skin measurements of *P. sandwichensis* were adjusted by subtracting 0.8 mm, the difference between the tarsus measurement made from a skin and the length of the actual tarsometatarsus after removal from the same specimen. The asterisk indicates a single exceptionally large specimen. For further explanation see Figure 6.

population. None of the flightless populations of the Hawaiian Archipelago are likely to be conspecific with flightless species occurring elsewhere in the Pacific, so we have limited our comparisons to flightless Hawaiian rails.

Comparative material examined: Extensive comparisons throughout the Rallidae or even within *Porzana* were not made, for reasons given above, and are reserved for future studies of the origin and relationships of the various Hawaiian rails. The following skeletons were consulted when writing the descriptions: *Porzana palmeri*, USNM 289241; *P. pusilla*, USNM 291705; *P. fusca bakeri*, USNM 344361; *P. albicollis*, USNM 345125; *P. carolina*, USNM 501051; *P. paykulli* (PIN); *Gallinula chloropus sandvicensis*, USNM 502535. Also, a radius, ulna, carpometacarpus, tarsometatarsus, and partial humerus and tibiotarsus from a skin of *Porzana sandwichensis*, AMNH 546232 was used. In addition, we obtained measurements from 7 other skeletons of *Porzana palmeri* (USNM) and from all 7 extant skin specimens of *Porzana sandwichensis* (AMNH, BMNH, BBM, NMHW, RMNH, UMZC).

GROUP 1—THE SMALLEST RAILS

This group consists of three, perhaps four, closely related species of extremely small flightless rails known so far from Oahu, Molokai, Maui, and possibly Hawaii.

All are smaller than *Porzana palmeri* (Fig. 14). They differ from one another mainly in body size, degree of reduction of the wing elements, and in details of the bill. These rails may have been derived from a single invasion of the archipelago, quite possibly by the same ancestor that gave rise to *P. palmeri*. This ancestor is hypothesized to have been the widespread Eurasian species *P. pusilla* (Olson 1973a, b; 1975b).

Porzana ziegleri, new species
(Figs. 15C, G, 16A)

"small Oahu rail" Olson and James, 1982b:36; 1984:771; James, 1987:225.
"*Porzana* sp., small flightless rail" James, 1987:227.

Holotype: Right tarsometatarsus, USNM 385877 (Fig. 15G). Collected 4 April 1980 by Storrs L. Olson, Helen F. James, Aki Sinoto, and Eric Komori.

Type locality: Site 50-Oa-B6-22, Barbers Point, Oahu, Hawaiian Islands.

Distribution: Oahu: Barbers Point (including some sites that are purely archeological), Ulupau Head.

Etymology: To Alan C. Ziegler, whose hospitality and assistance to our Hawaiian researches have been unbounded.

Measurements (mm) of holotype: Length, 21.5; proximal width, 3.4; shaft width at midpoint, 1.6; distal width, 3.3.

Paratypes: Cranium and associated mandible (Fig. 15C), BBM-X 153681; premaxillary symphysis and part of dorsal bar, USNM 426102; pelvis lacking posterior part of right innominate, USNM 426103; right humeri, USNM 385867 (Fig. 16A), 385868; left humeri, USNM 385843, 426104, BBM-X 158072; right ulnae, USNM 385874, 385878 (Fig. 16A); left ulnae, USNM 426105, BBM-X 157787; right carpometacarpus, USNM 426106 (Fig. 16A); left carpometacarpi, USNM 426107, 426108; right femora, USNM 385850, 385864, 426109, BBM-X 157790; left femora, USNM 385844, 385849, 385871; proximal end of right tibiotarsus, USNM 385851, distal end of right tibiotarsus, USNM 385854; left tibiotarsus, USNM 426110; left tibiotarsus lacking proximal end, USNM 385862; distal end of left tibiotarsus, USNM 385853; right tarsometatarsi, USNM 385856, 385863, 385865, 385870, 426111, 426112, 426113, BBM-X 157797, 157798; left tarsometatarsi, USNM 385861; BBM-X 158074.

Measurements (mm) of paratypes: (These are in the same sequence as the preceding.)—Premaxillary symphysis: length, 7.8. Cranium: length from nasofrontal hinge, 21.8; width, 13.1. Mandible: overall length, 33.2; length of symphysis, 6.0. Pelvis: length of synsacrum, 19.2; width across antitrochanters, 10.6. Humerus: length, 18.9, 17.7, 17.9, 18.2. Ulna: length, 12.6, 13.2, 12.9, 12.7. Carpometacarpus: length, 8.3, 8.3, 8.5. Femur: length, 23.1, 23.3, 24.6, 25.9, 24.2, 23.8, 23.3; proximal width, 3.9, 4.2, 3.7, —, 3.9, —, —; shaft width at midpoint, 1.5, 1.6, 1.5, 1.6, 1.5, 1.5, 1.5; distal width, —, —, 3.7, 4.1, 3.9, 3.8, 4.0. Tibiotarsus: length, 33.3; distal width, 3.2, 3.4, 3.3, 3.3. Tarsometatarsus: length, 22.3, 22.6, 21.3, 22.0, 20.6, 21.0, 21.0, 23.6, 21.9, 20.9, 22.0; proximal width, 3.2, 3.4, 3.4, 3.6, 3.4, 3.3, 3.5, 3.7, 3.5, 3.3, 3.5; shaft width at midpoint, 1.8, 1.8, 1.9, 1.8, 1.7, 1.7, 1.6, 1.7, 1.8, 1.6, 1.6; distal width, —, 3.7, 3.6, 3.6, 3.5, 3.6, 3.6, 3.8, 3.6, 3.5, 3.5.

Diagnosis: Larger than *P. menehune* but smaller than any other species of
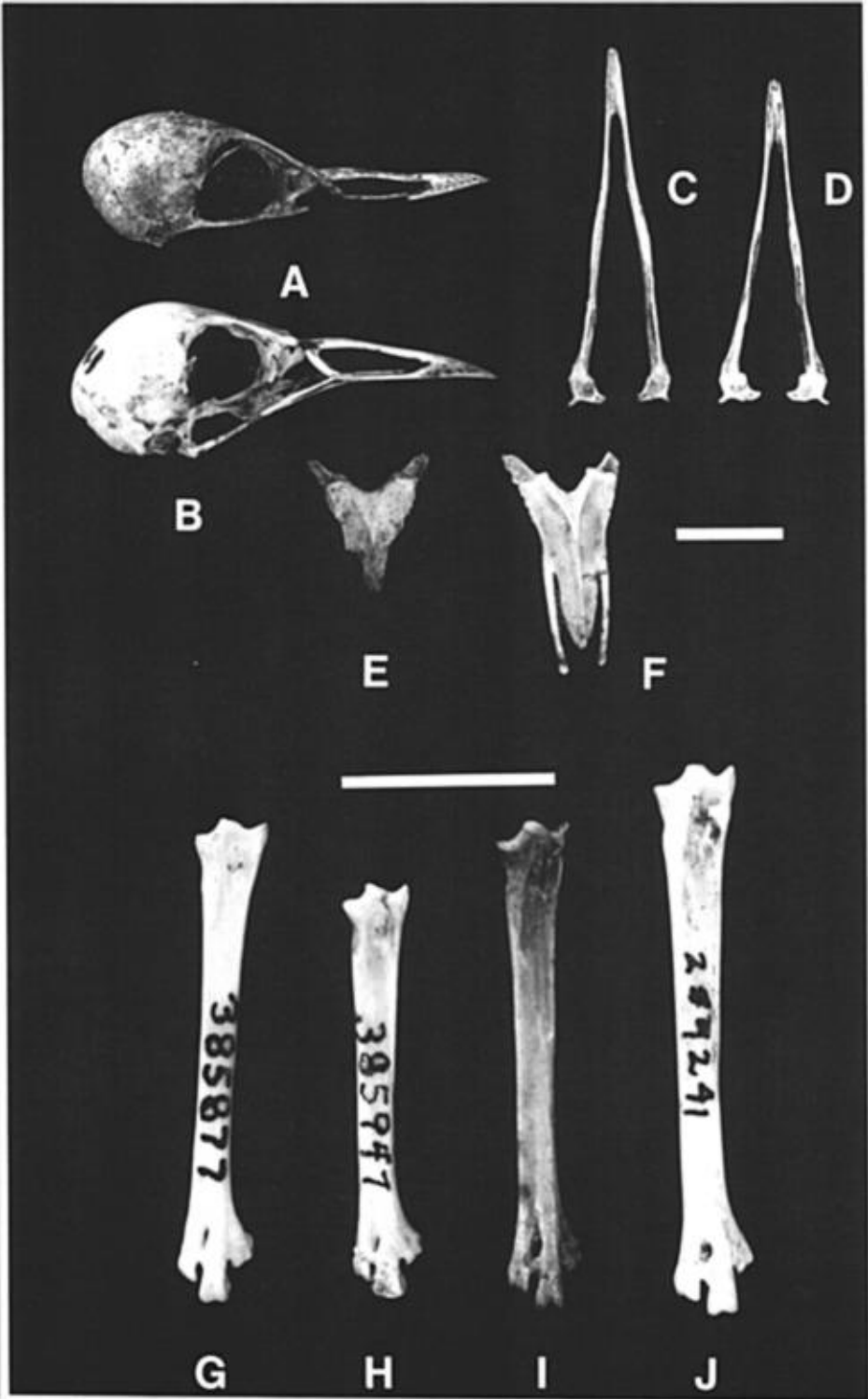
Hawaiian Rallidae except *P. keplerorum.* Extremely similar in size and morphology to *P. keplerorum* except the premaxillary symphysis is longer and more slender and the wing elements are markedly less reduced, the humerus being larger, with the distal end more expanded; also, the proximo-anterior surface of the tarsometatarsus is not as excavated and the distal foramen is smaller.

Remarks: See *P. keplerorum.* A single right tarsometatarsus (USNM 426114) is considerably larger than any in the type series (length, 24.1; proximal width, 3.7; shaft width at midpoint, 1.9; distal width, 3.8), but otherwise shows no distinguishing features. This may be from an unrecognized medium-sized species of rail that inhabited Oahu or it could be from a very large individual of *P. ziegleri.* There appear to be exceptionally large or small individuals in the series of *P. menehune* and *P. keplerorum* as well.

Porzana menehune, new species
(Figs. 15H, 16B)

"very small Molokai rail" Olson and James, 1982b:36; 1984:772.

Holotype: Right tarsometatarsus, USNM 385947 (Fig. 15H). Collected July or August 1976 by Storrs L. Olson and others.

Type locality: Site 20, Ilio Point, Molokai, Hawaiian Islands.

Distribution: Molokai: Moomomi and Ilio Point dunes.

Etymology: From contemporary Hawaiian, *menehune,* the legendary leprechaun-like little people of the Hawaiian Islands, in reference to the size of this, the smallest known species of rail, living or extinct. The *menehune* legend is probably mostly a post-European invention incorporating much of non-Polynesian tradition. The best explanation of the origin of the word seems to be in *manahune,* a term used elsewhere in Polynesia for certain lower classes of people. It is not difficult to envision a change in meaning from people of low social status to those of low physical stature. For more and diverse opinions on the subject, however, see Luomala (1951), whose seemingly jocular tone, whether intended or not, certainly befits the subject. The name is a noun in apposition.

Measurements (mm) of holotype: Length, 18.6; proximal width, 3.1; shaft width at midpoint, 1.6; distal width, 3.2.

Paratypes: Premaxillary symphysis and most of dorsal bar, USNM 386069; right mandibular articulations, USNM 386070, 386071; right humeri, USNM 385963, 385966; left humeri, USNM 385965 (Fig. 16B), 386038, 386039; right ulnae, USNM 385976 (Fig. 16B), 385977, 386051, 386059; left ulnae, USNM 385975, 385978, 385979, 386053, 386054, 386056; right carpometacarpi, USNM 385983 (Fig. 16B), 385988; left carpometacarpi, USNM 385986, 385987, 385989;

←

FIG. 15. Cranial elements, sterna, and tarsometatarsi of the group of smallest Hawaiian species of *Porzana* compared with *P. palmeri. A,* skull (lateral view, bill angle affected by warping) of *P. keplerorum,* new species (USNM 384309, associated with holotype); *B,* skull of *P. palmeri* (USNM 289241); *C,* mandible (dorsal view) of *P. ziegleri,* new species (BBM-X 153681); *D,* mandible of *P. palmeri* (USNM 289241); *E,* incomplete sternum (ventral view) of *P. keplerorum* (USNM 378081); *F,* sternum of *P. palmeri* (USNM 289241); *G–J,* tarsometatarsi in anterior view; *G, P. ziegleri,* holotype (USNM 385877); *H, P. menehune,* new species, holotype (USNM 385947); *I, P. keplerorum,* holotype (USNM 378377); *J, P. palmeri* (USNM 289241). Scales = 1 cm.

FIG. 16.   Major wing elements (humeri in anconal view, ulnae and carpometacarpi in palmar view) of the group of smallest Hawaiian species of *Porzana* compared with *P. palmeri. A, P. ziegleri,* new species (humerus, USNM 385867; ulna, USNM 385878; carpometacarpus, USNM 426106); *B, P. menehune,* new species (humerus, USNM 385965; ulna, USNM 385976; carpometacarpus, USNM 385983); *C, P. keplerorum,* new species (humerus, USNM 397669; ulna, USNM 398587; carpometacarpus, USNM 398138); *D, P. palmeri* (USNM 289241). Scale = 1 cm.

left femora, USNM 385956, 385990, 386072; left tibiotarsi, USNM 385923, 386091; right tarsometatarsi, USNM 385946, 385948, 385949, 385951, 386073; left tarsometatarsi, USNM 385950, 385952, 386074.

Measurements (mm) of paratypes: (These are in the same sequence as the preceding.)—Premaxillary symphysis: length, 5.0. Humerus: length, 13.0, 13.5, 14.0, 13.5, 13.4. Ulna: length, 9.3, 9.1, 9.2, 9.1, 9.1, 9.1, 9.3, 8.8, 8.9, 8.4. Carpometacarpus: length, 6.3, 6.4, 6.5, 6.3, 6.2. Femur: length, 21.7, 22.2, 21.5; proximal width 3.5, 3.7, 3.6; shaft width at midpoint, 1.3, 1.3, 1.3; distal width, 3.3, 3.6, 3.5. Tibiotarsus: length, 29.0, 31.4; distal width 2.8, 2.9. Tarsometatarsus: length, 17.1, 18.7, 16.4, 18.4, 18.2, 18.7, 18.0, 17.5; proximal width, 2.9, 3.1, 2.8, 2.8, 3.1, 3.1, 3.0, 3.0; shaft width at midpoint, 1.5, 1.6, 1.7, 1.7, 1.6, 1.5, 1.6, 1.6; distal width, 3.1, 3.2, 2.9, 3.1, 3.1, 3.2, 3.2.

Diagnosis: Smaller than *P. ziegleri, P. keplerorum,* or any other known species of Rallidae. Humerus with the shaft relatively straighter and more robust than in *P. ziegleri* or *P. keplerorum.* The carpometacarpus differs from that of *P. ziegleri* or *P. keplerorum* in having a deep notch proximal to the alular metacarpal on the dorsal edge of the external trochlea, giving the latter a hooked appearance (Fig. 16B).

Remarks: See *P. keplerorum.* That this is the only flightless species of Rallidae known so far from Molokai may be a result of ecological bias as the collecting sites are situated in the driest part of the island (Olson and James 1982b).

Porzana keplerorum, new species
(Figs. 15A, E, I, 16C)

"smallest Maui rail" Olson and James, 1984:772.
"small flightless rail" James et al., 1987:2353.

Holotype: Right tarsometatarsus, USNM 378377 (Fig. 15I). Collected September 1982 by Storrs L. Olson, Helen F. James, and others.

Type locality: Auwahi Cave (1,145 m), Maui, Hawaiian Islands.

Distribution: Maui: lava tubes on the southern slopes of Mt. Haleakala.

Etymology: To Cameron B. Kepler and Angela K. Kepler, who have in many ways aided our field investigations in the Hawaiian Islands, especially on Maui, and assisted in collecting some of the type material of this species.

Measurements (mm) of holotype: Length, 21.9; proximal width, 3.3; shaft width at midpoint, 1.7; distal width, 3.5.

Paratypes: Skull (Fig. 15A) with associated right palatine and quadratojugal bar, USNM 384309; right humerus, USNM 378375; right and left tibiotarsi, USNM 378376—these were found in close association with the holotype and are probably from the same individual; sternum lacking posterolateral portions, USNM 378081 (Fig. 15E); right humeri, USNM 397379, 397668, 397669 (Fig. 16C), 398712, 398713, 399876; left humerus, USNM 399861; right ulnae, USNM 398586, 398587 (Fig. 16C); left carpometacarpus, USNM 398138 (Fig. 16C); right femora, USNM 378226, 384275, 397280; left femora, USNM 384454, 396319, 399000; right tibiotarsi, USNM 373459, 378230, 397559; left tibiotarsi, 378227, 378230; right tarsometatarsi, USNM 378231, 378233, 397880, 397935, 397241; left tarsometatarsi, USNM 378232, 384600, 397176.

Measurements (mm) of paratypes: (These are in the same sequence as the preceding.)—Skull: premaxillary symphysis length, 5.9; nostril length, 8.8; rostrum length from nasofrontal hinge, 18.1; cranium length from nasofrontal hinge, 20.3; cranium width, 13.7. Sternum: width across tips of anterolateral processes, 11.7; width at level of posteriormost costal facet, 7.1. Humerus: length, 16.1, 14.5, 14.0, 14.9, 15.1, 15.0, 15.7, 14.4. Ulna: length, 12.5, 10.1. Carpometacarpus: length, 6.6. Femur: length, 25.9, 23.9, 22.0, 23.8, 21.4, 21.2; proximal width, 4.1, 3.9, 3.3, 3.8, 3.7, 3.6; shaft width at midpoint, 1.7, 1.5, 1.4, 1.6, 1.4, 1.4; distal width, 4.2, 3.9, 3.4, 3.8, 3.6, 3.5. Tibiotarsus: length, 35.3, 35.4, 34.5, 38.0, 30.4, 35.1, 37.7; distal width, 3.3, 3.3, 3.2, 3.5, 2.9, 3.2, 3.2. Tarsometatarsus: length, 22.1, 23.1, 17.7, 20.0, 21.5, 22.7, 18.5, 19.0; proximal width, 3.2, 3.7, 2.6, 3.2, 3.4, 3.7, —, 2.9; shaft width at midpoint, 1.7, 1.9, 1.6, 1.6, 1.6, 1.7, 1.6, 1.6; distal width, 3.4, 3.7, 3.0, 3.4, 3.4, 3.7, 3.0, —.

Diagnosis: Larger than *P. menehune* but smaller than any other known species of Hawaiian Rallidae except *P. ziegleri.* Differs from *P. ziegleri* in having the wing elements much more reduced, the premaxillary symphysis shorter and stouter, and the distal end of the humerus less expanded. The proximo-anterior surface of the tarsometatarsus is more excavated, producing a narrower, better defined external ridge, and the distal foramen is larger.

Remarks: Porzana ziegleri, P. menehune, and *P. keplerorum* are all likely to be descendants of a single colonization of the archipelago from the mainland. In size, *P. menehune* of Molokai is the most divergent, being smaller than the two species found on islands on either side of it, although there is slight overlap with *P. keplerorum* in a few specimens.

The species from Oahu and Maui are extremely similar, the crania, for example, being inseparable. The more reduced wing elements of *P. keplerorum* are diagnostic, as, apparently, are differences in the bill. The single available premaxillary symphysis of *P. ziegleri* is much longer and more slender than in the one available for *P. keplerorum.* The lengthened bill of the former is also reflected in the fact that the mandible assigned to *P. ziegleri* is absolutely longer than in the otherwise larger species *P. palmeri* (Fig. 15C, D). The premaxilla of *P. menehune* is similar to that of *P. keplerorum* but is smaller and possibly proportionately shorter, especially in the symphysis.

In these smallest of Hawaiian rails, the only sternum yet known is that of *P. keplerorum.* This is clearly from a completely flightless bird and differs from that of *P. palmeri* in the much broader and shallower notch between the coracoidal articulations, the markedly smaller carina, and the much less pronounced ridge anterior to the carina (Fig. 15E, F).

<center>*Porzana* sp., small Hawaii rail</center>

Porzana sandwichensis.—Olson and James, 1982b:35.

Material: Possibly associated hindlimb elements (BBM-X 151708–15): right femur, proximal and distal ends of left femur and left tibiotarsus, proximal half of left tarsometatarsus [cataloged with these are the proximal portions of right and left tibiotarsi of a larger individual, possibly of a different species].

Distribution: Hawaii: archeological site 50-Ha-D24-22, about 18 km west-southwest of Pohakuloa Ranger Station, 1,540 m, Mauna Kea.

Measurements (mm): Femur: length 24.5, proximal width 4.2, shaft width at midpoint 1.6, distal width 4.2. Tarsometatarsus: proximal width 3.7.

Remarks: We mentioned this site previously and tentatively referred these bones to *P. sandwichensis* (Olson and James 1982b:14, 35). With additional fossil material that is more likely to be referable to *P. sandwichensis,* as well as bones removed from a skin of that species, we now see that the present specimens are probably too small for *P. sandwichensis* and fall within the range of the smallest size-class of rails in the archipelago.

GROUP 2—MEDIUM-SIZED RAILS

This is a confusing assemblage, all populations of which are still represented by inadequate material for proper diagnosis. As a consequence, we do not know how many species are involved. Most are similar in size to the historically known species *Porzana sandwichensis* of Hawaii, and may be descended from an ancestral stock related to the Asian species *Porzana fusca* (Olson 1973a, b).

Porzana sp., medium Kauai rail

"medium Kauai rail" (part) Olson and James, 1982b:36, 44; 1984:771.

Material: Premaxillary symphysis, USNM 385884; left femur lacking distal end, USNM 385887; distal two-thirds of shaft of left humerus preserving part of the brachial depression, USNM 385886; right and left tarsometatarsi, USNM 385879–80 (of identical size and probably from the same individual).

Distribution: Kauai: Makawehi dunes.

Measurements (mm): Femur: estimated length, 30 mm; proximal width, 4.7, shaft width at midpoint, 2.0. Tarsometatarsus: length, 28.2, proximal width, 4.6, width of shaft at midpoint, 2.3, distal width, 4.7.

Remarks: This bird would probably have been about the size of *Porzana sandwichensis,* perhaps slightly larger. The femur is longer and straighter than in *P. palmeri* and is somewhat larger than in the medium-sized rail of Maui. The tarsometatarsi are slightly larger than in *P. sandwichensis* and considerably more robust. The premaxillary symphysis can only tentatively be referred to this species, as it could belong to the larger rail from Kauai.

Porzana sp., medium Maui rail

"small Maui rail" Olson and James, 1982b:35,44; 1984:772.

Material: Partial associated skeleton (BBM-X 147179–147187) consisting of right and left humeri, incomplete right and left femora, right and left tibiotarsi and tarsometatarsi, all very soft and friable. Right femur, USNM 399863.

Distribution: Maui: Puu Naio and Lower Waihoi Valley caves.

Measurements (mm): Humerus: length, 19.6. Femur (USNM specimen only): length, 27.4; proximal width, 4.4; width of shaft at midpoint, 1.7; distal width, 4.6. Tibiotarsus: length, 42.5; distal width, 3.8. Tarsometatarsus: length, 26.1; proximal width, 3.8; width of shaft at midpoint, 2.3; distal width, 4.0.

Remarks: This is an enigmatic form, the distribution and rarity of which are most puzzling. The one individual from Lower Waihoi Valley Cave occurred with at least two individuals of the large species *P. severnsi,* yet *P. keplerorum* was

FIG. 17. Skeletal elements of the group of largest Hawaiian species of *Porzana* compared to *P. albicollis* (USNM 345125), a volant South American species of similar size. *A*, skull of *P. severnsi*, new species, in lateral view, holotype (USNM 378344); *B*, premaxilla of *P. ralphorum*, new species,

evidently absent at this site. The size of the specimens, particularly the individual from Lower Waihoi Valley, would seem to preclude their being at the large end of variation in *P. keplerorum*. The bones of the medium Maui rail are about the size of those of *P. sandwichensis,* but are somewhat smaller and less robust.

GROUP 3—THE LARGEST RAILS

Several taxa of Hawaiian flightless rails are considerably larger than any of the preceding species, being about the size of the living South American rail *Porzana albicollis*. The two that are best represented, from Oahu and Maui, are distinctive in having a short, wide premaxillary symphysis. At least these two probably resulted from a single colonization by a different species of rail from those giving rise to Groups 1 and 2. Because there are no species of *Porzana* in this size range in North America, and because the two historically known flightless rails from the Hawaiian Archipelago, *P. palmeri* and *P. sandwichensis,* both appear to have been derived from Palearctic forms (*P. pusilla* and *P. fusca,* respectively, see Olson 1973b), it is likely that the larger flightless rails described below originated in Asia as well. Examination of a skeleton of one possible Old World relative, *Porzana paykulli,* showed it to have somewhat larger and more slender hindlimb elements and, more importantly, a narrow premaxillary symphysis, unlike the Hawaiian forms.

Porzana sp., large Kauai rail

"medium Kauai rail" (part) Olson and James, 1982b:36, 44; 1984:771.

Material: Distal end of left femur, USNM 385881.
Distribution: Kauai: Makawehi dunes.
Measurements (mm): Femur: distal width, 6.0; shaft width at break, 2.5.
Remarks: We had previously included this specimen with material of the medium Kauai rail but it is from a much larger bird (Fig. 14), the distal width being nearly as great as in *P. ralphorum* or *P. severnsi.*

Porzana ralphorum, new species
(Fig. 17B, D, F, M)

"medium-large Oahu rail" Olson and James, 1982b:36, 44; 1984:771; James, 1987.
"*Porzana*" sp., medium flightless rail" James, 1987: 227.

Holotype: Right tarsometatarsus, USNM 426114 (Fig. 17M). Collected 10 July 1981 by Storrs L. Olson, Helen F. James, James and Emilee Mead, Patrick McCoy, and Virgil Meeker.
Type locality: Site 50-Oa-B6-22, Barbers Point, Oahu, Hawaiian Islands.
Distribution: Oahu: Barbers Point, Kuliouou shelter, and Ulupau Head.

←
in lateral view (USNM 426116); *C,* mandible of *P. severnsi* in dorsal view, holotype (USNM 378344); *D,* mandibular symphysis of *P. ralphorum* in dorsal view (USNM 426120). *E,* humerus (anconal view) of *P. albicollis*; *F,* humerus of *P. ralphorum* (USNM 426121); *G–K, P. severnsi* holotype; *G,* humerus (USNM 378350); *H,* ulna in palmar view (USNM 378354); *I,* carpometacarpus in palmar view (USNM 378352); *J,* coracoid in ventral view (USNM 378348); *K,* sternum in ventral view (USNM 378356); *L–N,* tarsometatarsi in anterior view; *L, P. albicollis*; *M, P. ralphorum* holotype (USNM 426115); *N, P. severnsi* holotype (USNM 378360). Scale = 1 cm.

Etymology: To our friends C. J. Ralph and Carol Pearson Ralph, who assisted our research in the islands in many ways and whose hospitality is deeply appreciated.

Measurements (mm) of holotype: Length, 35.7; proximal width, 5.0; shaft width at midpoint, 2.2; distal width, 4.9.

Paratypes: Premaxillary symphyses, USNM 426116 (Fig. 17B), 426117–426119; mandibular symphysis, USNM 426120 (Fig. 17D); right humerus, USNM 426121 (Fig. 17F); proximal end of left femur, USNM 426122; right tibiotarsus lacking proximal end, BBM-X 153139; distal end of right tibiotarsus, USNM 426123; distal end of left tibiotarsus, USNM 385876.

Measurements (mm) of paratypes: (These are in the same sequence as the preceding.)—Premaxillary symphysis: length from anterior margin of nostril, 7.3, 5.5, 5.5, 6.7. Mandibular symphysis: length, 2.5. Humerus: length, 26.7; proximal width, 4.9; shaft width at midpoint, 1.3; distal width, 3.9. Femur: proximal width, 6.8. Tibiotarsus: length from distal end of fibular crest, 40.9; shaft width at midpoint, 2.2; distal width, 4.9, 4.9, 4.8.

Diagnosis: Larger than any of the flightless Rallidae known so far from the Hawaiian Islands except *Porzana severnsi*. Differs from *P. severnsi* as follows: premaxillary and mandibular symphyses shorter and wider; humerus larger and more robust, especially the shaft, and bicipital crest more rounded, not as angular; distal tendinal opening of tibiotarsus smaller and more rounded, not longer in its transverse diameter; tarsometatarsus with distal foramen situated farther distally.

Remarks: This species is much scarcer as a fossil than the tiny species *P. ziegleri*, with which it was sympatric. The premaxillary symphysis is even shorter than in *P. severnsi*, in which the symphysis is shorter than in most species of *Porzana*. The paratypical mandibular symphysis, if correctly assigned, is extremely short, unlike the rather lengthened, troughlike symphysis of *P. severnsi*. It is curious that the two species of *Porzana* from Oahu each differ from their relative on Maui in having the wing elements less reduced.

Porzana severnsi, new species
(Fig. 17A, C, G–K, N)

"larger Maui rail" Olson and James, 1982b:36; 1984:772.

Holotype: Associated nearly complete skeleton with elements numbered separately under USNM 378344–378363. Collected 9 September 1983 by Helen F. James and Storrs L. Olson. The specimen consists of the skull and mandible (Fig. 17A, C), both palatines, right pterygoid, both quadrates, lacrimals, sternum (Fig. 17K), both coracoids (Fig. 17J), scapulae, humeri (Fig. 17G), ulnae (Fig. 17H), right radius, both carpometacarpi (Fig. 17I), pelvis, both femora, tibiotarsi, fibulae, and tarsometatarsi (Fig. 17N), 11 vertebrae, 3 pedal phalanges, and an assortment of ribs and ossified tendons.

Type locality: Auwahi Cave (1,145 m), Maui, Hawaiian Islands.

Distribution: Maui: known from various caves on the southern slopes of Mt. Haleakala and from the Lower Waihoi Valley Cave near Hana.

Etymology: To R. Michael Severns, who discovered most of the important fossil localities on Maui and shared his discoveries with us. Through his efforts,

Maui has been changed from one of the paleontologically poorest known islands to one of the best known.

Measurements (mm) of holotype: (For paired elements, measurements are from the right side only.)—Skull: total length, 51.2; cranium length from nasofrontal hinge, 26.4; cranium width at postorbital processes, 18.6; nostril length, 13.4; premaxillary symphysis length, 8.1. Mandible: total length, 40.0; symphysis length, 8.3. Sternum: length from anterior lateral processes to posterior margin, 23.8; length along midline (from notch between coracoidal articulations), 17.0; width through anterior lateral processes, 18.4; width at last costal facet, 10.6. Coracoid: greatest length, 12.2. Scapula: length, 22.2. Humerus: length, 25.3; proximal width, 4.5; shaft width at midpoint, 1.2; distal width, 3.6. Ulna: length, 17.8. Carpometacarpus: length, 11.6; proximal depth, 3.3. Pelvis: total length, 35.2; length along midline (sacral vertebrae), 28.9; width across antitrochanters, 15.5. Femur: length, 35.9; proximal width, 6.9; shaft width at midpoint, 2.4; distal width, 6.3. Fibula: length, 31.8. Tibiotarsus: length, 55.4; length from distal end of fibular crest, 41.5; shaft width at midpoint, 2.3; distal width, 5.2. Tarsometatarsus: length, 37.3; proximal width, 5.3; shaft width at midpoint, 2.3; distal width, 5.3.

Paratypes: Complete mandibles, USNM 384372, 384264; mandible lacking right articulation, USNM 384373; right humeri, USNM 384258, 384259; left humeri, 384015, 384017; right femora, USNM 378585, 384583; left femora, USNM 384584, 384585; right tibiotarsi, USNM 384021, 384023, 384024; left tibiotarsi, USNM 378585, 384591; right tarsometatarsus, USNM 378585; left tarsometatarsus, USNM 378585, 384280, 384594, 384595.

Measurements (mm) of paratypes: (These are in the same sequence as the preceding.)—Mandible: total length, 39.2, 40.7, 41.0; symphysis length, 7.7, 7.8, 8.2. Humerus: length, 24.6, 24.9, 23.7, 24.1; proximal width, 4.4, 4.5, 4.1, 4.4; shaft width at midpoint, 1.2, 1.1, 1.2, 1.1; distal width, 3.5, 3.3, 3.3, 3.2. Femur: length, 36.3, 33.9, 35.1, 36.1; proximal width, 6.5, 5.9, 6.2, 5.5; shaft width at midpoint, 2.4, 2.2, 2.4, 2.3; distal width, 6.2, 5.6, 5.8, 6.5. Tibiotarsus: length, 55.5, 53.9, 57.8, 53.3, 52.5; length from distal end of fibular crest, 41.9, 40.4, 44.0, 40.6, 40.5; shaft width at midpoint, 2.3, 2.2, 2.3, 2.1, 2.2; distal width, 5.2, 5.0, 5.2, 4.6, 4.9. Tarsometatarsus: length, 34.5, 34.3, 35.5, 37.9, 36.7; proximal width, 5.1, 4.8, 5.1, 5.8, 5.7; shaft width at midpoint, 2.1, 2.1, 2.1, 2.5, 2.4; distal width, 5.2, 5.0, 4.9, 5.5, 5.2.

Diagnosis: Larger than any of the known flightless rails from the Hawaiian Islands except *P. ralphorum* of Oahu. Differs from *P. ralphorum* in the longer premaxillary and much longer mandibular symphyses; more reduced humerus with more angular bicipital crest; tibiotarsus with distal tendinal opening widest in its transverse dimension, not rounded; tarsometatarsus with distal foramen situated more proximally.

Remarks: This is the most abundant rail in the deposits from Maui. Many more specimens were available than are included in the paratypical series, which was selected only to provide sufficient material for comparison with *P. ralphorum.* The pectoral girdle and wings in *P. severnsi* are very reduced compared with the overall size of the bird. The sternum (Fig. 17K) is extremely degenerate, with the coracoidal sulci widely separated by a deep, rounded notch and the carina reduced to a short flattened ridge. In the holotype, the sternum is so poorly ossified that there is a series of three paired fenestrae on either side of the carina, but this

appears to be an individually variable condition, as most other specimens lack these openings.

Porzana sp., large Hawaii rail

"larger Hawaii rail" Olson and James, 1982b:35, 44.

Material: Distal end of left femur, BBM-X 152040; left tibiotarsus, BPBM 162024; left tibiotarsus lacking proximal end, BBM-X 152063; right tarsometatarsus BBM-X 152006.

Distribution: Hawaii: archeological sites at Kailua, Kona, and the Mauna Kea Adz Quarry. Bones at the latter site, which is above the treeline between 3,355 and 3,780 m, are almost certainly the remains of food brought from lower elevations.

Measurements (mm): (Those in parentheses are from fossils tentatively identified as *P. sandwichensis* and from a tarsometatarsus taken from a modern specimen (AMNH 546232) [italicized].)—Femur: distal width, 6.0 (5.0). Tibiotarsus: length, 54.0, —; distal width, 4.6, 5.2 (*4.2,* 3.5, 3.7). Tarsometatarsus: length, 32.9 (*27.0,* 27.2, 30.6, 25.2, 26.1); width of shaft at midpoint, 2.6 (*2.0*); distal width, 5.1 (*4.5,* 4.3, 4.5, 4.1, 4.3, 4.4).

Remarks: This material seems too large and robust to be encompassed within the range of individual variation of *P. sandwichensis* (Fig. 14). The tarsus length in the 7 existing skins of *P. sandwichensis* ranges from 27.3 to 30.4 mm (our data), although this is subject to some error due to the difficulty of taking this measurement in mounted specimens. Additional rallid material will need to be collected from the island of Hawaii before any new species of rails can be diagnosed from there.

Order FALCONIFORMES
Family ACCIPITRIDAE
Genus *Haliaeetus* Savigny, 1809

Fossils from the Hawaiian Islands belonging to a species of eagle are certainly referable to the genus *Haliaeetus* as shown by the fusion of the phalanges of pedal digit II. These elements were found as fossils from three different individuals. This condition does not occur in any other genus of Accipitridae of comparable size except *Ichthyophaga* (Olson 1982). The Hawaiian eagle agrees with *Haliaeetus* and differs from *Ichthyophaga* in the characters outlined by Olson (1984).

Comparative material examined: (All USNM.)—*Haliaeetus leucocephalus* (20 skeletons, including individuals from Alaska, Minnesota, Pennsylvania, West Virginia, Virginia, North Carolina, and Florida, although the majority were unsexed and many were captive birds with no locality data); *H. albicilla* (2 complete and 1 partial); *H. leucoryphus* (1 partial); *H. leucogaster* (4); *H. vocifer* (2); *H. pelagicus* (2, and 2 partials).

Haliaeetus sp., aff. *H. leucocephalus/H. albicilla*

"*Haliaeetus* sp." Olson and James, 1982b:35, 44; 1984:771; James, 1987:225.

Material: Oahu: distal portion of right ulna, USNM 386099; proximal end of left radius, USNM 386100; distal end of left radius, BBM-X 150270; right femur, BBM-X 150208; fused phalanges 1 and 2 of pedal digit II, USNM 386101.

Molokai (most specimens considerably worn): thoracic vertebra, BBM-X 146667; right coracoid, BBM-X 148187; anterior half of right scapula, USNM 386103; 2 fragments of right carpometacarpus, BBM-X 146267–8; left carpometacarpus, BBM-X 146272; phalanges 1 and 2 of major alar digit, BBM-X 146295, 147417; proximal end of left femur, BBM-X 152519; shaft of tibiotarsus, BBM-X 146271; proximal ends of left fibulae, USNM 386104; BBM-X 147413; right tarsometatarsus, BBM-X 146290; metatarsal 1, BBM-X 146289; phalanx 1 digit I, BBM-X 146293; fused phalanges 1 and 2 of digit II, USNM 386105; phalanx 1 digit III, USNM 386107; phalanges 2 and 4 of digit IV, BBM-X 147423, 146294; ungual phalanges, BBM-X 146291, 146292, 147424, 148185.

Maui: A nearly complete associated skeleton, USNM 431238.

Distribution: Oahu: Barbers Point (a single site, possibly one individual). Molokai: Moomomi dunes (from three well separated sites representing at least three individuals). Maui: Puu Makua Cave (a single nearly complete skeleton).

Measurements (mm): Oahu and Molokai specimens. Coracoid: length from head to internal distal angle, 68.6; least shaft width, 13.4. Radius: greatest proximal and distal diameters, 11.1 and 15.6. Carpometacarpus: length, 102.4; distal depth, 20.5. Femur: length, 115.8; proximal width, 24.0; width and depth of shaft at midpoint, 11.9 × 10.9. Tarsometatarsus: length (from internal cotyla), 90.4; width and depth of shaft at midpoint, 12.9 × 9.9; distal width, 25.2. Fused phalanges of digit II: length, 39.3, 37.5.

Associated individual from Maui. Cranium: length from nasofrontal hinge, 69.4; least width through temporal fossae, 40.9; depth through occipital condyle, 43.1. Mandible: length, 90.4; articular width including internal process, 22.9. Coracoid: length from head to internal distal angle, 66.4; least shaft width, 12.8. Ulna: length, 227.7; proximal width and depth, 15.8 × 22.3; distal depth, 15.2. Radius: length, 218.8, greatest proximal and distal diameters, 10.4 and 14.6. Carpometacarpus: length, 106.0; proximal depth, 24.7. Pelvis: length of synsacrum, 96.1. Femur: length, 112.6; proximal width, 23.5; width and depth of shaft at midpoint, 11.9 × 11.4; distal width, 26.0. Tibiotarsus: length, 154.1; length of fibular crest, 36.5; distal width, 20.3. Tarsometatarsus: length (from internal cotyla), 90.6; proximal width, 21.4; width and depth of shaft at midpoint, 12.4 × 11.3; distal width, 24.2. Digit I, phalanx 1: length, 32.9. Fused phalanges of digit II: length, 35.7.

Remarks: This species is too small to be either *H. pelagicus* or its close relative *H. australis,* which is known only from subfossil material from the Chatham Islands (Olson 1984). It differs from *H. leucogaster* in the same way that *H. australis* does (Olson 1984). The Hawaiian eagle is clearly most closely related to the "superspecies" comprising *H. leucocephalus* of North America and *H. albicilla* of Eurasia. There was a great deal of individual and sexual variation in size and relative robustness of skeletal elements in the series of *H. leucocephalus* we examined. There is also considerable variation among the Hawaiian fossils. Given this, we could find no consistent osteological characters by which to distinguish *H. leucocephalus* and *H. albicilla* from each other or from the Hawaiian eagle. The Hawaiian bird could therefore belong to either of the continental species. On the other hand, because *H. leucocephalus* and *H. albicilla* are recognizable as different species yet seem to be inseparable osteologically, it remains possible that the Hawaiian bird was a distinct species that likewise had not differentiated
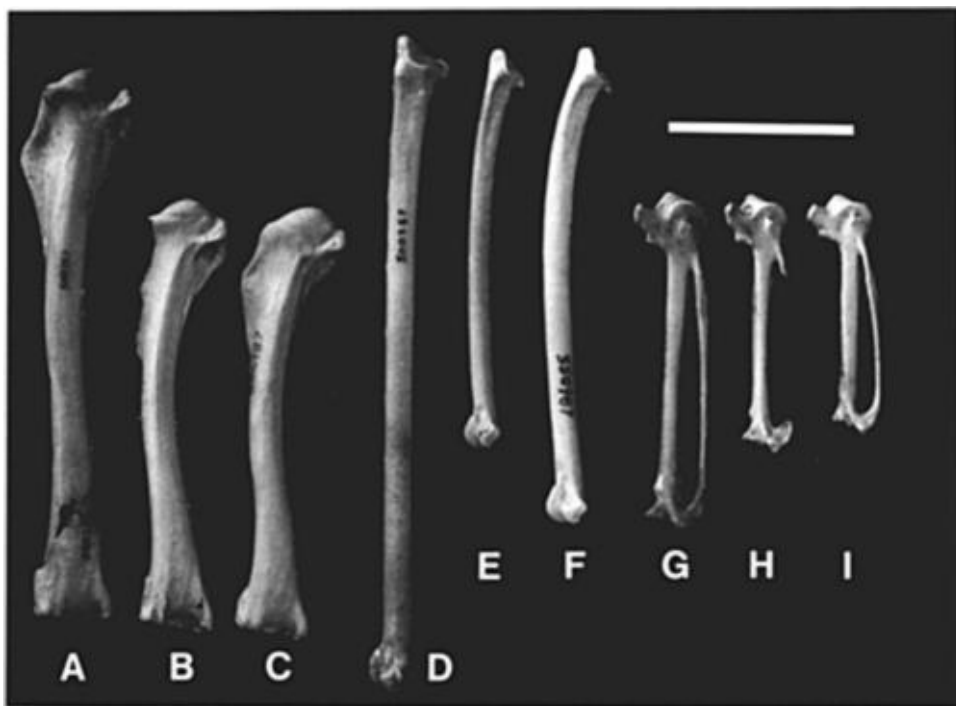
FIG. 18. Comparison of wing elements of *Circus* and *Accipiter*. Left humeri in anconal view (*A–C*), left ulnae in internal view (*D–F*), and right carpometacarpi in internal view (*G–I*): *A, D, G, C. melanoleucos* (male, USNM 500257); *B, C. dossenus*, new species, holotype (BPBM 175709); *E, C. dossenus* (USNM 426127); *H, C. dossenus* (BPBM 175710); *C, F, I, A. henicogrammus* (female, USNM 556987). Scale = 3 cm.

osteologically, although one would expect an insular endemic to show some differences. We recognize that it would be highly desirable to have better resolution of the nomenclature of the Hawaiian eagle, but none is possible at this time.

This species was surely resident in the Hawaiian Islands, given the discovery of several different individuals on three different islands and at elevations ranging from sea level to 1,463 m. The presence of one of these eagles in the formerly forested area at Puu Makua on the east slope of Haleakala on Maui suggests that these birds, which must have subsisted to a considerable extent on flightless ibises, geese, and moa-nalos, were not confined to scavenging in coastal areas. That the Hawaiian eagle had differentiated so little (or not at all) from its mainland progenitors may indicate that it was a relatively recent colonizer of the archipelago, so that predation pressure on some of the flightless birds may have been greater in the recent past than during their initial period of evolution and adaptation.

Genus *Circus* Lacépède, 1799

We originally reported the following as a species of *Accipiter* (Olson and James 1982b:35, 44; 1984:771), a misidentification based on the very scant material from Oahu indicating a small hawk that lacked a procoracoid foramen. *Accipiter* is the only known genus of hawks in which the procoracoid foramen is invariably

absent, whereas in *Circus* the condition is variable, with the foramen lacking in certain individuals or species (Olson 1988).

The Hawaiian fossils differ from *Accipiter* and agree with *Circus* as follows. Humerus: bicipital surface more elongate, not rounded; bicipital crest in palmar view indistinct, tapering gradually into the shaft; pectoral crest larger, extending farther distally; ventral condyle in ventral view deeper, in anconal view oriented more nearly parallel with shaft; ectepicondylar process more proximally situated; area of tricipital grooves more excavated and flattened. Ulna: olecranon not as prominent, angled ventrally rather than projecting straight proximally. Femur: much more slender and gracile; proximal end in lateral view markedly narrower, with trochanter less expanded anteriorly; head proportionately smaller; distal end in anterior view not as expanded laterally; rotular groove narrower; in lateral view the external condyle does not project as far beyond the fibular condyle. Tibiotarsus: in posterior view the rim of the internal condyle angles strongly laterally to expose more of the internal surface of the shaft. Tarsometatarsus: proximal end relatively narrower.

Comparative material examined: Skeletons (USNM unless otherwise noted) of most of the genera of Accipitridae, including a wide variety of species of *Accipiter* (see Olson 1982, 1988). *Circus cyaneus hudsonius* (12, plus 10 trunks); *C. melanoleucos* (1); *C. assimilis* (1 trunk); *C. cinereus* (1, plus 2 trunks; 2 incomplete KU); *C. maurus* (1); *C. approximans gouldi* (1); *C. buffoni* (1 trunk); *C. aeruginosus* (2). Also, particular use was made of a skeleton of *Accipiter henicogrammus* (USNM 556987) because of its similarity in length of the humerus and femur to the Hawaiian bird.

Circus dossenus, new species
(Figs. 18B, E, H, 19B)

"*Accipiter* sp." Olson and James, 1982b:35, 44; 1984:771; James, 1987:225.

Holotype: Left humerus lacking only parts of the pectoral crest, BPBM 175709 (Fig. 18B). Collected in 1983 by Joan Aidem.

Type locality: Site 10, Moomomi dunes, Molokai, Hawaiian Islands.

Distribution: Molokai: Moomomi dunes. Oahu: Barbers Point.

Etymology: Latin, *dossenus,* a clown or jester, without which one cannot have a circus; especially applicable here because the species initially fooled us as to its generic placement. The name is a masculine noun in apposition.

Measurements (mm) of holotype: Length, 67.9; proximal depth through ventral tubercle, 8.3; width and depth of shaft at midpoint, 5.1 × 4.5; distal width, 2.1.

Paratypes: Molokai (all from the type locality and almost certainly from the same individual as the holotype): right coracoid, BPBM 162394; left scapula lacking posterior third, BPBM 162393; right carpometacarpus lacking minor metacarpal, BPBM 175710 (Fig. 18H); complete left femur, BPBM 162395 (Fig. 19B); proximal and distal ends of right tibiotarsus, BPBM 162396, BPBM 162397.

Oahu (Barbers Point, two sites representing at least two individuals): premaxillary symphysis, USNM 426126; right coracoid lacking head, USNM 386098; left ulna, USNM 426127 (Fig. 18E); proximal end of left carpometacarpus, USNM 386097; proximal and distal halves of left tibiotarsus, BBM-X 150678, 150679;
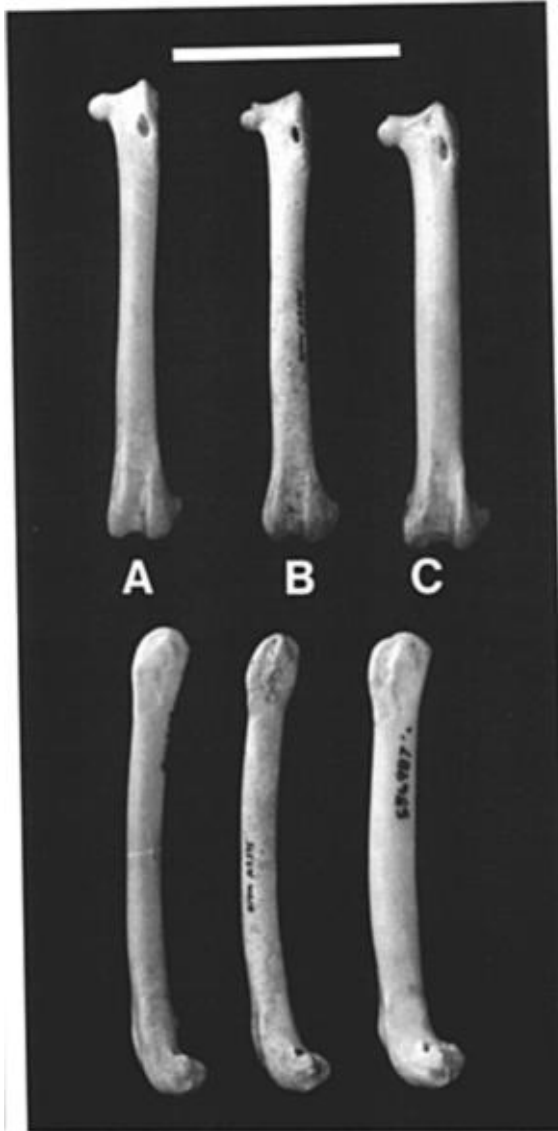
FIG. 19. Comparison of left femora of *Circus* and *Accipiter* in anterior view (top row) and lateral view (bottom row): *A, C. melanoleucos,* male (USNM 500257); *B, C. dossenus,* new species (BPBM 162395); *C, A. henicogrammus,* female (USNM 556987). Scale = 3 cm.

juvenile right tarsometatarsus lacking distal end, BPBM 158687; distal end of right tarsometatarsus, USNM 426128.

Measurements (mm) of paratypes: Coracoid: length (with sternal end flat on calipers), 28.7, 24 (estimated); width and depth of shaft at midpoint, 3.1 × 3.2, 2.7 × 2.9; width of sternal end, 13.2, 11.0. Scapula: width of articular end, 8.0. Ulna: length 64.4, proximal depth, 7.2; distal width, 5.3. Carpometacarpus: length, 40.7, —; proximal depth, 9.8, 8.4. Femur: length, 58.4; proximal width, 9.3; width and depth of shaft at midpoint, 4.3 × 4.3; distal width, 10.3. Tibiotarsus: length

(estimated from Oahu specimen), 77.5; distal width, 7.7, 7.2. Tarsometatarsus: proximal width, 7.6; distal width, 6.9.

Diagnosis: Smaller than any known species of *Circus,* though approached in size of femur by *C. cinereus* and *C. melanoleucos.* Wing and pectoral elements greatly shortened, so that the proportions are essentially those of an *Accipiter.* Premaxillary symphysis more laterally compressed than in other species of *Circus* and rather deeply channeled.

Remarks: The fragmentary material from Oahu is assigned to this species only tentatively, as it is insufficient for determining whether the same or a different species is involved.

Circus dossenus is remarkable in the proportions of its wing elements, which are much more like those of an *Accipiter* than any species of *Circus* (Fig. 18). Within the latter genus there is some variation in the relative length and robustness of the humerus; *C. cinerus,* for example, has a shorter, heavier humerus than in *C. melanoleucos,* a species of similar size. None approaches the condition in *C. dossenus,* however. The premaxillary symphysis is narrower, more laterally compressed, in *Circus* than in *Accipiter,* and in *C. dossenus* is more compressed still. It differs from any of the species of *Circus* examined in that the ventral surface bears a rather deep groove rather than being flat.

The species of *Circus* are characteristically long-winged birds of open marshes, prairies, steppes, and savannas, that hunt by coursing back and forth low to the ground. Such habitats would have been much scarcer in the Hawaiian Islands prior to the arrival of humans. To judge by the proportions of the wing elements, *Circus dossenus* may have adapted to conditions in the Hawaiian Islands by assuming the habits of an *Accipiter,* as there would have been little for it to feed on besides birds and insects. It was therefore in all likelihood a forest inhabitant.

Although we were at first surprised to discover that the small Hawaiian hawk was a species of *Circus,* the characters separating that genus from *Accipiter* are distinctive and are well developed in the Hawaiian bird, despite its different proportions. Furthermore, long-winged gliding harriers of the genus *Circus* would be more likely colonizers of the remote Hawaiian islands than the short-winged hawks of the genus *Accipiter,* which have a fast, flapping flight. Indeed, the Holarctic species *Circus cyaneus* has been taken or observed in the Hawaiian Islands on several occasions (Wilson and Evans 1891; Pyle 1977), whereas no species of *Accipiter* has ever been recorded (Pyle 1988). In the historic avifauna of the Pacific, *Accipiter* occurs eastward only to Fiji, whereas *Circus approximans* extends naturally as far as Tonga (Pratt et al. 1987).

Order STRIGIFORMES
Family STRIGIDAE

Fossils of an extinct endemic genus of strigid owl have been recovered from four of the main Hawaiian Islands. In the following comparisons, the dissertation of Ford (1967) on the osteology of the Strigiformes proved useful. Ford found that postcranial differences between the various subgroups and genera of Strigidae were very slight or nonexistent, for which reason we have based our determination of the relationships of the new genus of Hawaiian owls mainly on characters of the skull. The generic groups are those of Ford (1967), with whom we found ourselves in agreement wherever we had appropriate material.

The new genus differs from the Tytonidae in possessing an ossified loop (retinaculum extensorii) on the anteroproximal face of the tarsometatarsus. Whereas this is not always ossified in the Strigidae, it is invariably unossified in the Tytonidae, from which there are numerous other differences as well.

Within the Strigidae, the skull in the *Asio* group has a distinctive shape caused partly by the "extensive vertical flattened area over the orbit" (Ford 1967:56–57). Another character of the *Asio* group not mentioned by Ford is the extremely long, slender zygomatic process. In *Aegolius* the auditory area is characterized by the extreme asymmetry of the tympanic wings. In the *Ninox* group and the *Surnia* group there is a distinctive dorsal process on the posterior portion of the quadratojugal bar and in the latter group the skull is very short and rounded, with a long, pointed supraorbital process (except in *Micrathene*), and a posteriorly directed ectethmoid. Because all of the preceding characters are lacking in the new Hawaiian owl, it is assumed that it was not derived from any of these groups.

The resemblances of the new genus are closest to the core of "typical" owls represented by the *Otus, Bubo,* and *Strix* groups. In size it is considerably larger than any of the *Otus* group except *Lophostrix,* and much smaller than any of the *Bubo* group. In *Otus* the interorbital septum is thin and fenestrate anteriorly. In *Bubo* the flattened area on the lateral surface of the frontals between the prefrontal bone and the supraorbital process is short and wide, and the rims of the middle trochlea of the tarsometatarsus are not equally developed (Ford 1967). In these respects, the new Hawaiian owl differs from the *Otus* and *Bubo* groups and resembles the *Strix* group. Within the *Strix* group, it differs from *Pulsatrix,* in which the rostrum is much deeper and wider and the frontal area is inflated so that the cranial roof is horizontal. The resemblance of the new Hawaiian owl is thus closest to *Strix* (including *Ciccaba*), particularly in the narrower, shallower, and more elongate rostrum, in which it differs from all other owls to which it could possibly be related.

Comparative material examined: Tytonidae. *Tyto glaucops* USNM 288593; *Phodilus badius,* USNM 20310.

Strigidae. *Otus* group: *Otus asio,* USNM 556918; *Otus* ("*Gymnoglaux*") *lawrencii,* USNM 554287. *Bubo* group: *Bubo virginianus,* USNM 553903; *Nyctea scandiaca,* USNM 491639; *Ketupa zeylonensis,* USNM 18999 [the differences between genera in this group are very slight]. *Strix* group: *Strix varia,* USNM 556919; *S. nebulosa,* USNM 556948; *S. aluco,* USNM 559072; *S. occidentalis* (skulls only), USNM 206148, USNM 221672; *S. uralensis,* 500252; *Ciccaba woodfordi,* USNM 291790; *Pulsatrix perspicillata,* USNM 18350. *Surnia* group: *Surnia ulula,* USNM 290337; *Glaucidium siju,* USNM 555176; *Micrathene whitneyi,* USNM 502286; *Athene noctua,* USNM 490358; *Athene* ("*Speotyto*") *cunicularia,* USNM 553670. *Aegolius* group: *Aegolius acadicus,* USNM 556838. *Ninox* group: *Ninox novaeseelandiae,* USNM 492457; *N. scutulata,* USNM 343047. *Asio* group: *Asio otus,* USNM 553816; *Asio flammeus,* USNM 553816; *Pseudoscops grammicus,* USNM 559185.

Grallistrix, new genus

Type species: Grallistrix geleches, new species.

Included species: Grallistrix auceps, new species; *G. orion,* new species; *G. geleches,* new species; *G. erdmani,* new species.

Distribution: Kauai, Oahu, Molokai, and Maui.

FIG. 20. Skull of *Grallistrix geleches*, new genus and species, holotype USNM 386140 (*A–C*), compared with *Strix aluco*, USNM 559072 (*D–F*): left lateral (*A, D*), dorsal (*B, E*), and ventral (*C, F*) views. Scale = 3 cm.

FIG. 21. Wing and pectoral elements of *Grallistrix geleches*, new genus and species (*A–D*), compared with *Strix aluco*, USNM 559072 (*E–H*): *A, E*, humerus (*A*, holotype USNM 386140); *B, F*, ulna (*B*, BBM-X 152434); *C, G*, carpometacarpus (*C*, USNM 386164); *D, H*, coracoid (*D*, BBM-X 147983). Scale = 3 cm.

Etymology: Latin, *gralla*, stilt, plus *strix*, owl, in reference to the extremely long legs that characterize the genus. The gender is feminine.

Diagnosis: Strigidae similar to *Strix* and different from other genera of owls in possessing the following combination of characters: narrow, elongate skull and rostrum (Fig. 20); posterior margin of orbit not vertically flattened; zygomatic process very short; interorbital septum thick, lacking fenestrae; flattened lateral portion of frontals long and thin; supraorbital processes short and triangular; ectethmoid directed straight ventrally; quadratojugal bar without dorsal process; tympanic wings not greatly asymmetrical; rims of middle trochlea of tarsometatarsus in distal view of about equal extent.

Differs from *Strix* in having the wing elements relatively much shorter (Fig. 21), but with the tibiotarsus and tarsometatarsus greatly elongated and slender (Fig. 22). The pedal phalanges are much wider and more robust (Fig. 23). The cranium is relatively narrower, the skull roof and maxillopalatines are markedly less inflated, the tympanic wing is deeper and less anteriorly projecting so that the space between the tympanic wing and postorbital process is greater (Fig. 20). In accordance with the narrower skull, the mandibular rami are less divergent; also the mandibular symphysis is relatively longer. The calcaneal ridge of the hypotarsus is shorter and wider.

Remarks: Grallistrix is so divergent from *Strix* that it was not possible to identify any of the living species of that genus as being more closely related to the insular derivative. In size, *Grallistrix* is rather small compared to most species of *Strix*.
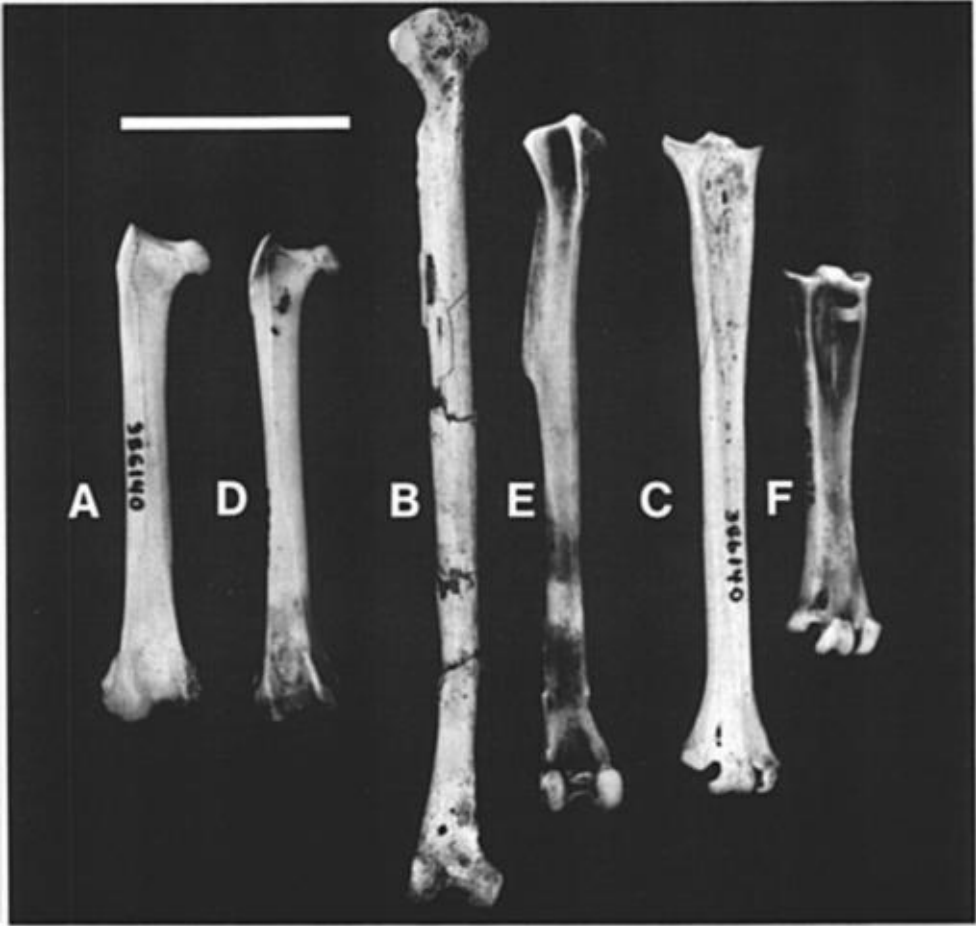
FIG. 22. Hindlimb elements of *Grallistrix geleches*, new genus and species (*A–C*), compared with *Strix aluco*, USNM 559072 (*D–F*): *A, D*, femur (*A*, holotype USNM 386140); *B, E*, tibiotarsus (*B*, BBM-X 147928); *C, F*, tarsometatarsus (*C*, holotype USNM 386140). Scale = 3 cm.

In the type species, *G. geleches,* the skull, mandible, coracoid, furcula, and sternum are all about the same size as in the specimen of *Strix aluco* used in the comparisons, so the overall body size was similar to that species. The pelvis, however, is somewhat larger, whereas the femur is similar in size to that of *S. aluco,* possibly indicating that the femur is relatively shorter in *Grallistrix.* In contrast, the tibiotarsus and tarsometatarsus of *Grallistrix* are extremely elongated, whereas the humerus, radius, ulna, and carpometacarpus are very much smaller than in *Strix aluco* (Figs. 21, 22). The pedal phalanges are quite strong, being relatively more robust even than in such a large owl as *Strix nebulosa.*

We have documented fossil pellets showing that the species of *Grallistrix* fed on birds (Olson and James 1982b), and indeed there was little else in the Hawaiian Islands upon which they could have fed, other than insects. The elongated legs and shortened wings of *Grallistrix* may thus be specializations for bird-catching that parallel the skeletal proportions in the bird-eating hawks of the genus *Accipiter.*
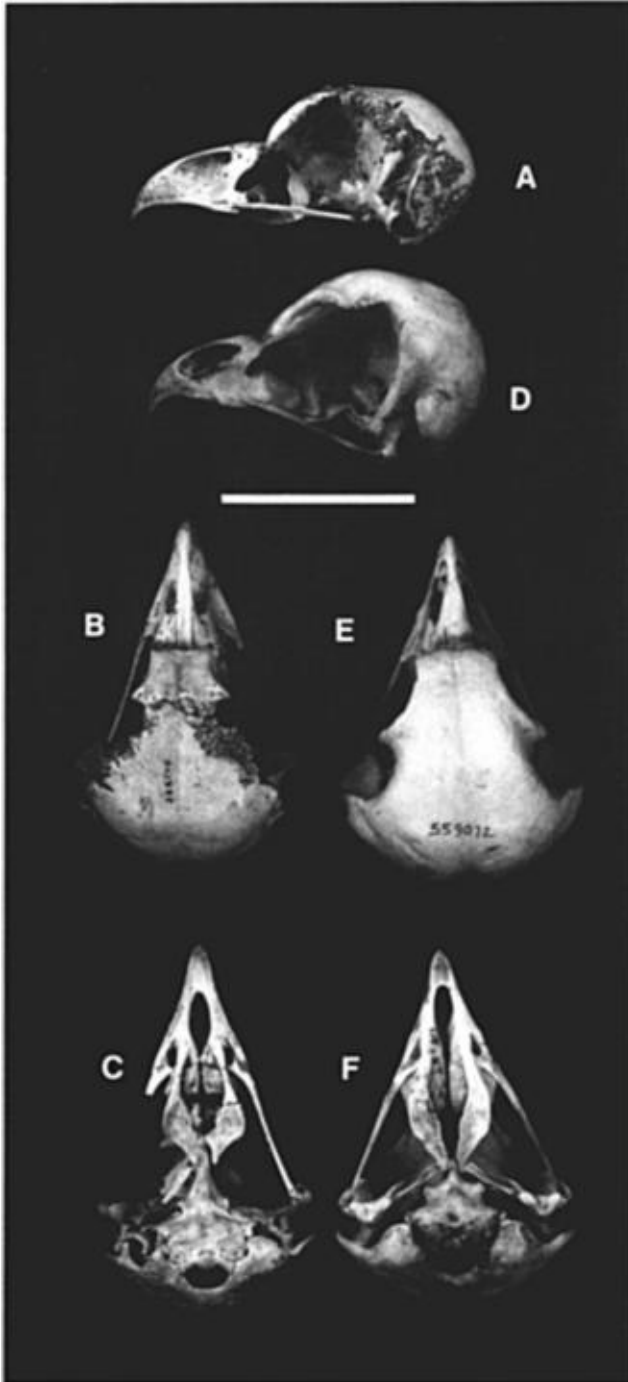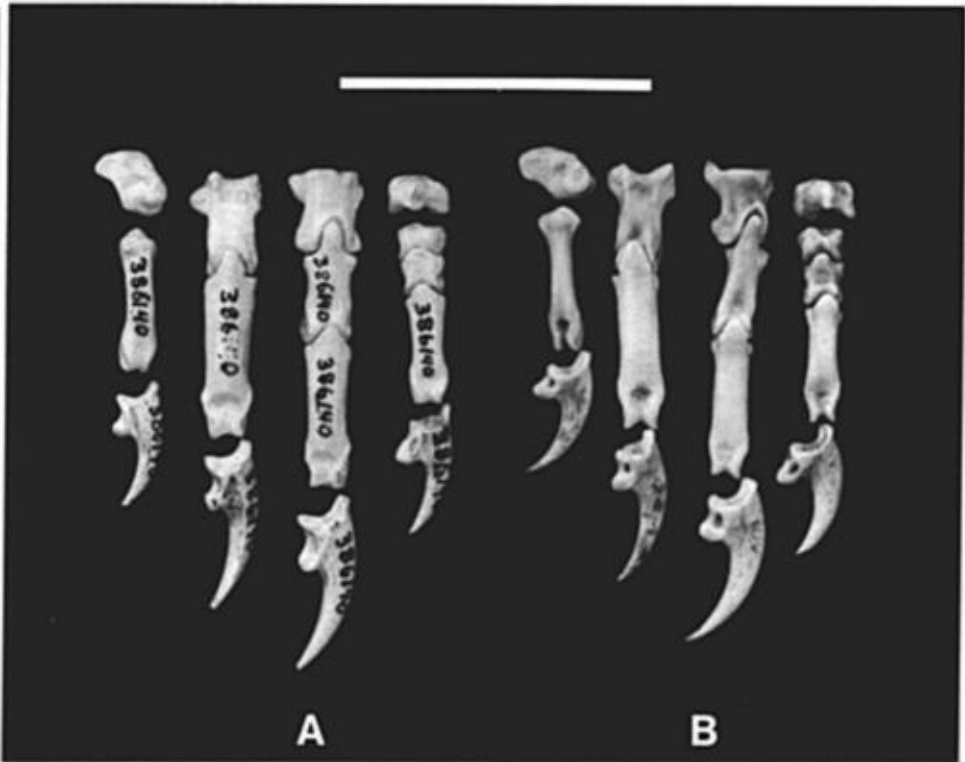
FIG. 23. Pedal phalanges in dorsal view (except ungues in lateral view) of *Grallistrix geleches,* new genus and species, holotype USNM 386140 (*A*), compared with *Strix aluco,* USNM 559072 (*B*). Scale = 3 cm.

Grallistrix auceps, new species
(Figs. 24B, 25B, D, 26A, 27A)

"long-legged Kauai owl" Olson and James, 1982b:38, 44; 1984:771.

Holotype: Associated partial skeleton, BBM-X 150202. Collected 19 November 1976 by Joan Aidem, Stephen L. Montgomery, and others. The specimen consists of: sternum (Fig. 25B, D), left scapula, nearly complete pelvis in several pieces (including portions numbered BBM-X 150109 and BBM-X 150159), seven vertebrae, right and left humeri (Figs. 24B, 26A), left radius, distal two-thirds of left ulna, right and left femora, left tibiotarsus including a portion numbered BBM-X 150162 (Fig. 27A), various rib and other fragments.

Type locality: Site 303, Makawehi dunes, Kauai, Hawaiian Islands.

Distribution: Kauai: Makawehi dunes.

Etymology: Latin, *auceps,* a bird-catcher, from the ornithophagous habits of this and the other species of the genus. The name is a common noun in apposition.

Measurements (mm) of holotype: Sternum: length along midline, 40.5; width across second costal facet, 26; depth through apex of carina, 16.0. Scapula: length, ca. 46. Pelvis: length of sacrum along midline, 40.9; width through antitrochanters, ca. 33.5; greatest diameter of acetabulum, 6.1; greatest diameter of ilioischiatic fenestra, 9.2. Humerus: length, 80.7; proximal width, 15.6; shaft width at mid-

Fig. 24. Humeri of *Grallistrix*, new genus, in ventral view: (*A*) *G. geleches*, new species, holotype USNM 386140; (*B*) *G. auceps*, new species, holotype BBM-X 150202; (*C*) *G. orion*, new species, USNM 386182. Scale = 3 cm.

point, 5.4; distal width, 14.5. Radius: length, 83.3. Ulna: width and depth of shaft at approximate midpoint, 3.3 × 3.6; distal width and depth, 6.4 × 7.2. Femur: length, 66.7; proximal width, 11.6; shaft width at midpoint, 4.9; distal width, 12.5. Tibiotarsus: length, 109.1; proximal width, 11.5; shaft width at midpoint, 5.0; distal width, 12.1.

Paratypes: Measurements (mm) follow in parentheses when available. Rostrum, BBM-X 152741 (length of premaxillary symphysis from anterior margin of nasal fossa, 15.8; width at juncture of quadratojugals, ca. 18.5); left carpometacarpus, BBM-X 512894 (length, 43.1), left tibiotarsus, USNM 386228 (length, 110.6).

The following are from the same locality as the holotype and are very likely from the same individual: distal end of right radius BBM-X 152824; proximal end of left carpometacarpus BBM-X 150148; right tibiotarsus lacking condyles, BBM-X 150163; right fibula BBM-X 150160; five pedal phalanges BBM-X 150094, BBM-X 150170, BBM-X 150171, BBM-X 152833, BBM-X 152834.

Measurements of paratypes: See above.
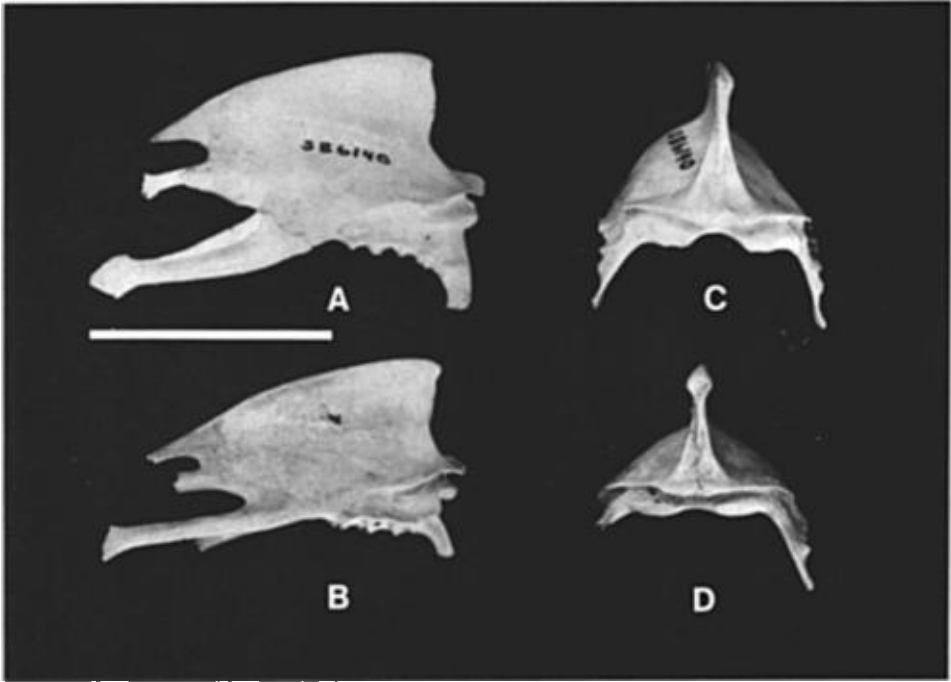
FIG. 25. Sterna of *Grallistrix geleches*, new genus and species, holotype USNM 386140 (*A, C*) and *G. auceps*, new species, holotype BBM-X 150202 (*B, D*). Left lateral view (*A, B*); anterior view (*C, D*). Scale = 3 cm.

Diagnosis: Larger than *Grallistrix orion* or *G. erdmani* (Table 4); nearly identical in size to *G. geleches* but differing qualitatively as follows: humerus in ventral view (Fig. 24B) with ventral tubercle displaced proximo-dorsally so as to expose most of the pneumatic foramen, this foramen being partially obscured in *G. geleches*; brachial depression of humerus more extensive, extending farther proximally; carina of sternum lower (Fig. 25D), with anterior margin not markedly set back from manubrium, dorsal intercoracoidal notch shallow and indistinct; rostrum apparently deeper.

Remarks: There may be some proportional differences as well between *G. auceps* and *G. geleches*, with the limited material in *G. auceps* seeming to indicate a somewhat smaller and more gracile hindlimb combined with a wing as large or larger than in *G. geleches*. Given the degree of isolation of Kauai and the fact that the smaller species *G. orion* of Oahu intervenes geographically between *G. auceps* and *G. geleches*, it is unlikely that the similarity in size between the last two species is indicative of their being more closely related to one another than to other members of the genus.

Grallistrix orion, new species
(Figs. 24C, 26C, 27C, 28E–H, 29B, D, F)

"long-legged Oahu owl" Olson and James, 1982b:38, 44; 1984:771; James, 1987:225.

Holotype: Right tarsometatarsus, USNM 386170 (Figs. 28E, 29F). Collected July 1981 by Storrs L. Olson, Helen F. James and others.

FIG. 26. Humeri of *Grallistrix*, new genus, in palmar view: (*A*) *G. auceps*, new species, holotype BBM-X 150202; (*B*) *G. geleches*, new species, holotype USNM 386140; (*C*) *G. orion*, new species, USNM 386182; (*D*) *G. erdmani*, new species, USNM 384403. Scale = 3 cm.

Type locality: Site 50-Oa-B6-22, Barbers Point, Oahu, Hawaiian Islands.

Distribution: Oahu: Barbers Point and Ulupau Head.

Etymology: Latin, *Orion,* the fabled hunter of mythology who was turned into a constellation, from the inferred hunting prowess of the owl. The name is a masculine noun in apposition.

Measurements (mm) of holotype: Length, 66.1; proximal width, 10.2; width and depth of shaft at midpoint, 4.2 × 3.3; distal width, 10.6.

Paratypes: Measurements (mm) follow in parentheses when available and are lengths unless otherwise stated. Rostrum, BBM-X 155515 (length of premaxillary symphysis from anterior margin of nasal fossa, 12.3); anterior portion of sternum, USNM 386192; left coracoids, BBM-X 155087 (33.8), BBM-X 155564 (33.4), BBM-X 155565 (33.4); right humeri, USNM 386181 (73.5), USNM 386209 (69.9), USNM 435153 (68.1); left humerus, USNM 386182 (74.6) (Figs. 24C, 26C); right radius, USNM 386187 (72.4); right ulnae, USNM 386207 (76.0), BBM-X 150234 (81.7); left ulna, USNM 368219 (78.7); right carpometacarpi, BBM-X 155095 (37.8), BBM-X 155571 (36.3); left carpometacarpi, USNM 386220 (37.4), BBM-X 155570 (39.7); right femora, BBM-X 155098 (56.5), BBM-X 156313 (57.0), USNM 435154 (57.8); left femora, BBM-X 155517 (56.3) (Fig.

TABLE 4

COMPARISON OF LENGTH MEASUREMENTS (MM) OF SELECTED ELEMENTS OF
Grallistrix, BASED ON HOLOTYPICAL AND PARATYPICAL SPECIMENS ONLY. FOR
EACH MEASUREMENT THE FIGURES GIVEN ARE THE MEAN, RANGE, AND NUMBER
OF SPECIMENS WHEN GREATER THAN 1

	G. auceps (Kauai)	G. orion (Oahu)	G. geleches (Molokai)	G. erdmani (Maui)
Coracoid	—	33.5 33.4–33.8 n = 3	39.8	33.3 31.6–34.6 n = 4
Humerus	80.7	71.5 68.1–74.6 n = 4	80.2	71.3 70.2–73.0 n = 3
Ulna	83.3*	78.8 76.0–81.7 n = 3	85.5 84.4–87.0 n = 3	76.3 76.1–76.6 n = 2
Carpometacarpus	43.1	37.8 36.3–39.7 n = 4	41.0 40.8–41.3 n = 2	36.8 35.6–37.4 n = 3
Femur	66.7	57.0 56.3–57.8 n = 6	64.1 62.5–65.0 n = 4	54.7 54.5–55.0 n = 2
Tibiotarsus	109.8 109.1–110.6 n = 2	100.5 97.0–104.4 n = 8	116	98.0 96.7–99.1 n = 3
Tarsometatarsus	—	65.7 64.4–66.9 n = 4	80.5 76.4–85.0 n = 4	69.3 68.6–70.1 n = 2

* Measurement is of a radius; no ulna was available.

29B), USNM 435155 (56.7), USNM 143156 (57.8); right tibiotarsi, USNM 435157 (102.2), USNM 435158 (98.9), USNM 435159 (98.2), USNM 435161 (102.6); left tibiotarsi, USNM 386123 (ca. 97), USNM 386175 (104.4) (Figs. 27C, 29D), USNM 435160 (98.0), USNM 435162 (102.4); right tarsometatarsi, BBM-X 155106 (66.0) (Fig. 28F), USNM 435163 (66.9); left tarsometatarsi, USNM 386225 (64.4) (Fig. 28G), BBM-X 155105 (65.5) (Fig. 28H).

Measurements of paratypes: See above.

Diagnosis: Decidedly smaller than *Grallistrix auceps* or *G. geleches* (Table 4). Similar in size to *G. erdmani* but limb elements more robust; tarsometatarsus shorter whereas the femur is longer than in *G. erdmani*. In the characters that distinguish *G. auceps* from *G. geleches, G. orion* is more similar to the latter. The carina in the one available sternum of *G. orion* is more reduced than in either of those two species.

Remarks: See *G. erdmani*.

Grallistrix geleches, new species
(Figs. 20A–C, 21A–D, 22A–C, 23A, 24A, 25A, C, 26B, 27B, 28A–D)

"long-legged Molokai owl" Olson and James, 1982b:37, 44; 1984:772.

Holotype: Associated partial skeleton, USNM 386140. Collected 9 and 12 July 1976 by Storrs L. Olson and Joan Aidem. The specimen consists of a nearly complete skull (Fig. 20A–C), partial sclerotic rings, right pterygoid, right and left

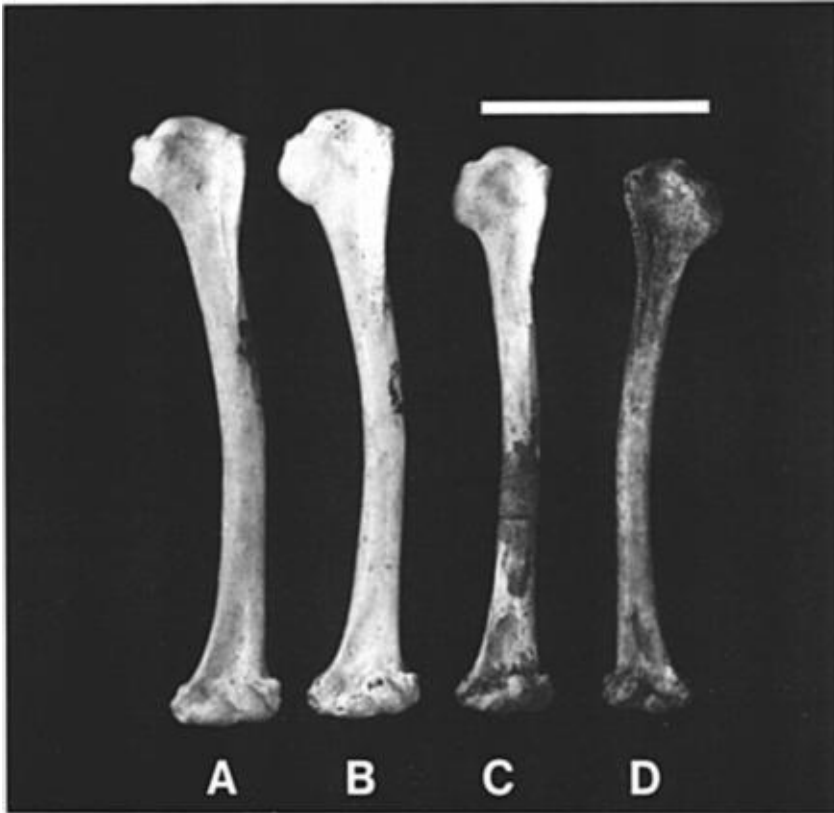FIG. 27. Tibiotarsi of *Grallistrix*, new genus, in anterior view: (*A*) *G. auceps*, new species, holotype BBM-X 150202; (*B*) *G. geleches*, new species, BBM-X 147928; (*C*) *G. orion*, new species, USNM 386175; (*D*) *G. erdmani*, new species, USNM 399348. Scale = 3 cm.

quadrates, mandible, sternum (Fig. 25A, C), furcula, right and left scapulae, left humerus (Figs. 21A, 24A, 26B), right and left femora (Fig. 22A), fibulae, tarsometatarsi (Figs. 22C, 28A), and first metatarsals, all pedal phalanges except one p1 dI and the left p2 dII (Fig. 23A), eight vertebrae, and various ribs and ossified tendons. The bones were collected both at the surface and at depths up to 40 cm or more in loose sand over an area at least 2 m in diameter, but certainly represent a single individual (see Olson and James 1982b:19). The preservation is excellent, the bones being unweathered, so burial must have been rapid.

Type locality: Vicinity of sites 5 and 10, Moomomi dunes, Molokai, Hawaiian Islands.

FIG. 28. Tarsometatarsi of *Grallistrix geleches*, new genus and species (*A–D*) and *G. orion*, new genus and species (*E–H*) in anterior view showing possible sexual size variation in the former: (*A*) holotype USNM 386140; (*B*) BBM-X 146685; (*C*) BBM-X 146815; (*D*) BBM-X 146856; (*E*) holotype USNM 386170); (*F*) BBM-X 155106; (*G*) USNM 386225; (*H*) BBM-X 155105. Scale = 3 cm.

Distribution: Molokai: Moomomi and Ilio Point dunes.

Etymology: Greek, *geleches,* sleeping on the ground; from the accumulations of fossil pellets and bones, both on Molokai and Kauai, indicating that owls of this genus roosted at times on open sand dunes or in low dune vegetation.

Measurements (mm) of holotype: Rostrum: length from nasofrontal hinge, 33.8; width at juncture of quadratojugals, 19.0; width at nasofrontal hinge, 14.0; length of premaxillary symphysis from anterior margin of nasal fossa, 14.1; length of nasal fossa, 13.5. Cranium: length from nasofrontal hinge, 44.3; width across postorbital processes, 44.8; depth through occipital condyle, 28.4. Quadrate: dorsoventral depth, 15.3. Mandible: length, 49.4; length and posterior width of symphysis, 8.4 × 8.5; width of articulation through internal process, 13.1. Furcula: length, 42.2. Sternum: length along midline, 42.6; width across second costal facet, 28.1; depth through apex of carina, 18.2. Scapula: length, 49.0. Pelvis: length of sacrum along midline, 42.8; width through antitrochanters, 33.8; greatest diameter of acetabulum, 5.8; greatest diameter of ilioischiatic fenestra, 10.0. Humerus: length, 80.2; proximal width, 16.3; shaft width at midpoint, 5.2; distal width, 14.8. Femur: length, 64.1; proximal width, 12.4; shaft width at midpoint, 5.3; distal width, 13.2. Tarsometatarsus: length, 85.0; proximal width, 12.3; shaft width at midpoint, 5.1; distal width, 12.8. Pedal phalanges (greatest length): Digit I—p1, 14.4; p2, 12.8. Digit II—p1, 10.4; p2, 19.2; p3, 18.2. Digit III—p1, 8.6; p2, 12.5; p3, 15.9; p4, 17.3. Digit IV—p1, 4.9; p2, 3.9; p3, 4.8; p4, 12.4; p5, 13.5.

Paratypes: Length measurements (mm) follow in parentheses when available. Associated rostrum and anterior portion of mandible, BBM-X 147272-3; anterior
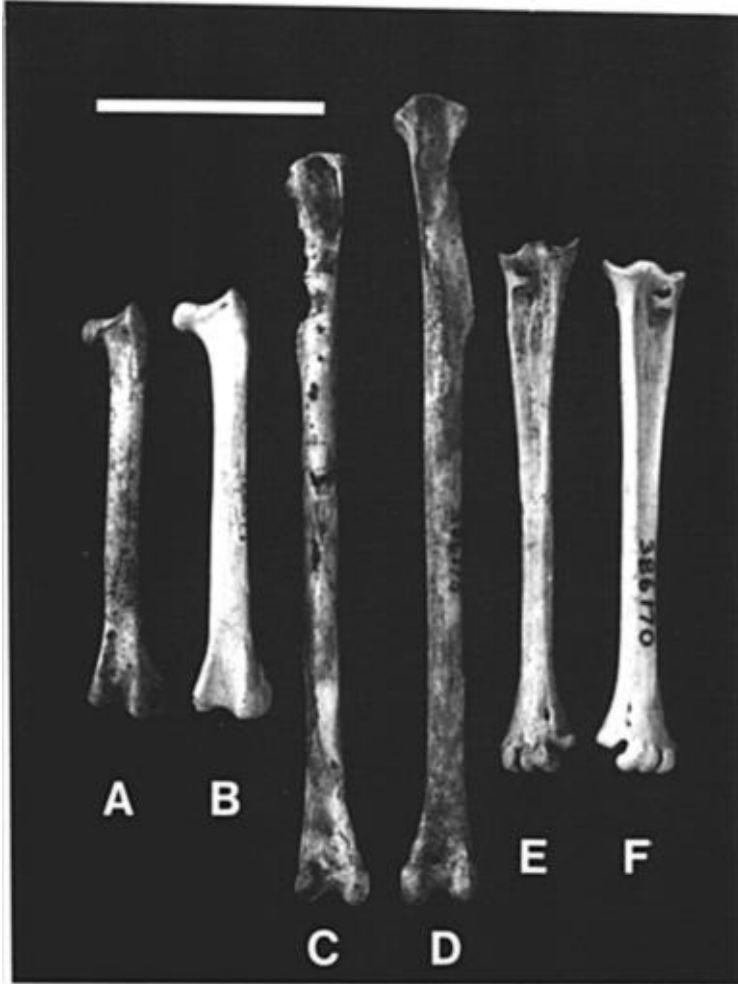
FIG. 29. Hindlimb elements of *Grallistrix erdmani*, new genus and species, holotype USNM 426129 (*A, C, E*), compared with *Grallistrix orion*, new genus and species (*B, D, F*); *A, B*, femora (*B*, BBM-X 155517); *C, D*, tibiotarsi (*D*, USNM 386175); *E, F*, tarsometatarsi (*F*, holotype USNM 386170). Scale = 3 cm.

portions of sterna, USNM 386166, BBM-X 147555; right coracoid, BBM-X 147983 (39.8) (Fig. 21D); proximal end of left humerus, USNM 386162; distal ends of right humeri, BBM-X 146737, BBM-X 146854; distal two-thirds of left humerus BBM-X 146628; right radius, BBM-X 152584 (84.0); right ulna, USNM 386150 (84.4); left ulnae, BBM-X 147320 (85.2), BBM-X 152434 (87.0) (Fig. 21B); left carpometacarpi, BBM-X 147322 (40.8), USNM 386164 (41.3) (Fig. 21C); left femora, BBM-X 146630 (62.5), BBM-X 147327 (64.9); right femur, BBM-X 146614 (65.0); right tibiotarsus BBM-X 147928 (116) (Figs. 22B, 27B); right tarsometatarsus, BBM-X 146685 (82.6) (Fig. 28B); left tarsometatarsi, BBM-X 146815 (78.0) (Fig. 28C), BBM-X 146855/6 (76.4) (Fig. 28D).

Measurements of paratypes: See above.

Diagnosis: Larger than *Grallistrix orion* or *G. erdmani* (Table 4). Differs from

G. auceps as follows: humerus with ventral tubercle in ventral view partly obscuring the pneumatic foramen (Fig. 24A); brachial depression of humerus not extending as far proximally; carina of sternum higher with anterior margin set back markedly from the manubrium (Fig. 25A, C), dorsal intercoracoidal notch wide and deep; rostrum not as deep.

Remarks: In the series of tarsometatarsi of this species there is variation that suggests sexual dimorphism in size (Fig. 28A–D). This is not evident in any of the available elements of *G. orion*; the material of *G. auceps* and *G. erdmani* is insufficient to assess intraspecific size variation.

Grallistrix erdmani, new species
(Figs. 26D, 27D, 29A, C, E)

"long-legged owl" Olson and James, 1984:77; James et al., 1987:2353.

Holotype: Nearly complete associated skeleton, USNM 426129. Collected 2 April 1986 by Storrs L. Olson, Helen F. James, R. Michael Severns, Avis C. James, Travis A. Olson, and Sydney B. Olson. The specimen consists of: right half of rostrum and fragments of cranium; various sclerotic plates, left quadrate, mandible lacking a portion of the postdentary ramus on each side, incomplete sternum, incomplete furcula, right scapula, right and left coracoids, incomplete pelvis, left humerus, proximal and distal portions of right humerus, right and left radii, ulnae, carpometacarpi, femora (Fig. 29A), tibiotarsi (Fig. 29C), fibulae, and tarsometatarsi (Fig. 29E), alar phalanx 1 digit II and a smaller alar phalanx, one radiale and one ulnare, one first metatarsal, 21 pedal phalanges, 19 presacral and 2 caudal vertebrae, various ribs, and ossified laryngeal cartilages. The preservation is variable, the bones having been exposed on bare lava and rendered rather friable, so that some are considerably eroded.

Type locality: Owl Cave near Puu Makua (1,402 m), Maui, Hawaiian Islands.

Distribution: Maui: lava tubes on the southern slope of Mt. Haleakala.

Etymology: To Pardee Erdman, owner of Ulupalakua Ranch, without whose active interest and cooperation we would know practically nothing about the former avifauna of Maui.

Measurements (mm) of holotype: (Measurements of paratype USNM 435165 are given in parentheses except for the pedal phalanges, which were omitted.)—Premaxillary symphysis: approximate length from anterior margin of nasal fossa, 10+ mm (11.8). Quadrate: dorsoventral depth, 12.0 (13.5). Mandible: length and posterior width of symphysis, 7.0 × 8.3 (ca. 6 × 7.9); width of articulation through internal process, 11.5 (—). Sternum: length along midline, ca. 33 (—); depth through apex of carina, 13.5+ (—). Coracoid: greatest length, 33.0 (31.6). Scapula: length, ca. 40 (—). Sacrum: length along midline, 34.2 (37.5). Humerus: length, 70.7 (70.2); shaft width at midpoint, 4.8 (4.6); distal width, 11.7 (12.4). Ulna: length, 76.1 (76.6); proximal depth, 8.1 (8.1); shaft width at midpoint, 3.2 (3.2); distal width, 6.1 (5.7). Radius: length, 72.0 (72.6). Carpometacarpus: length, 35.6 (37.3); proximal depth, 8.8 (8.8). Alar phalanx 1 digit II: length, 16,4 (17.4). Femur: length, 54.5 (55.0); proximal width, 9.2 (9.7); shaft width at midpoint, 4.2 (4.4); distal width, 10.3 (11.1). Tibiotarsus: length, 96.7 (98.2); proximal width, 8.6 (9.3); shaft width at midpoint, 4.5 (4.7); distal width, 9.4 (9.6). Tarsometatarsus: length, 68.6 (70.1); proximal width, 10.3 (10.4); shaft width at midpoint,

4.0 (4.2); distal width, 10.1 (10.5). Pedal phalanges (greatest length): Digit I—p1, 11.6; p2, ca. 10. Digit II—p1, 9.7; p2, 17.2; p3, ca.14. Digit III—p1, 7.2; p2, 11.3; p3, 14.2; p4, 15.0. Digit IV—p1, 4.4; p2, —; p3, 4.6; p4, 10.9; p5, 11.1.

Paratypes; Length measurements (mm) follow in parentheses. Right coracoid, USNM 399421 (34.1); left coracoid, USNM 399041 (34.6); right humerus, USNM 384403 (73.0) (Fig. 26D); left carpometacarpus, USNM 397870 (37.4); right tibiotarsus, USNM 399348 (99.1) (Fig. 27D); associated skeleton, USNM 435165 (for measurements, see above).

Measurements of paratypes: See above.

Diagnosis: Much smaller than *Grallistrix auceps* or *G. geleches* (Table 4). Most similar to *G. orion* but limb elements more gracile; proportions of hindlimb differ in that the femur in *G. erdmani* is shorter, whereas the tarsometatarsus is longer and more slender than in *G. orion* (Fig. 29). The shaft of the humerus is more slender and curved (Fig. 26).

Remarks: The comparisons between this small species and *G. orion* suffer from the lack of associated material from Oahu. Nevertheless, the two associated skeletons of *G. erdmani* from Maui show that the hindlimb proportions of that species are quite distinct from those of the Oahu bird. The femora are shorter than any of those from Oahu, whereas the tarsometatarsi are longer. Furthermore, the small species from Maui is separated geographically from the small Oahu bird by the much larger species *G. geleches* of Molokai.

It is curious that the four known species of *Grallistrix* alternate in size from island to island, the progression from Kaui, to Oahu, to Molokai, to Maui, being large, small, large, small. That Molokai and Maui should each have a different species is particularly strange considering that these islands were at times connected during the Pleistocene. It is conceivable that these two owls were sympatric, with the larger *G. geleches* in the lowlands of both islands and the smaller *G. erdmani* at higher elevations, but the material from as low as 305 m on Maui at Puu Naio is referable to *G. erdmani.* Furthermore, *G. orion,* which occupied the lowlands on Oahu, is a small species. It would be most interesting to know the nature of the species that may have occurred on Hawaii, but so far we have no trace of *Grallistrix* from that island.

DISCUSSION

The known geographical distribution of endemic species of non-passerine birds in the Hawaiian Archipelago is summarized in Table 5. The many gaps evident here are in most cases indicative of the inadequacies of the fossil record. There is no reason, for example, why all four genera of raptors should not have occurred on all the main islands. The gaps are even more striking when it is recalled that no resident endemic land birds of any sort were ever recorded from Kahoolawe or Niihau, each of which must have harbored representatives of most of the groups that colonized the rest of the archipelago. Unfortunately, we have as yet no fossil record from either island to substantiate this supposition.

Although dividing an avifauna into passerines and non-passerines is an arbitrary convenience (and an artificial one in the sense that "non-passerines" do not constitute a taxon), the evolutionary and post-human histories of these two categories in the Hawaiian Islands differ considerably, so that there is a certain logic in making this division. The fossil record shows that although endemic species

TABLE 5

DISTRIBUTION OF ENDEMIC SPECIES OF NON-PASSERINE BIRDS IN THE HAWAIIAN ARCHIPELAGO. F, FOSSIL RECORD (INCLUDES ARCHAEOLOGICAL CONTEXTS). H, HISTORIC RECORD. LY = LAYSAN, N = NIIHAU, K = KAUAI, O = OAHU, MO = MOLOKAI, LN = LANAI, MA = MAUI, H = HAWAII. * PLEISTOCENE ONLY

	Ly	N	K	O	Mo	Ln	Ma	H
Family Procellariidae								
Pterodroma jugabilis				F				F
Family Plataleidae								
Apteribis glenos					F			
Apteribis brevis							F	
Apteribis sp.							F	
Family Anatidae								
Moa-nalos								
Chelychelynechen quassus			F					
Thambetochen xanion			F					
Thambetochen chauliodous					F		F	
Ptaiochen pau							F	
True Geese (Nene and Relatives)								
Branta spp., aff. *B. hylobadistes*			F	F				
Branta sandvicensis			F		F	F	F	FH
Branta hylobadistes							F	
Geese of Uncertain Affinity								
Supernumerary Oahu Goose				F				
Geochen rhuax								F
Very large Hawaii Goose								F
Ducks								
Anas laysanensis	H							
Anas wyvilliana		H	FH	FH	FH		FH	FH
Family Rallidae								
Group 1								
Porzana palmeri	H							
Porzana ziegleri			F					
Porzana menehune					F			
Porzana keplerorum							F	
Porzana sp., small Hawaii rail								F
Group 2								
Porzana sp., medium Kauai rail			F					
Porzana sp., medium Maui rail							F	
Porzana sandwichensis								FH
Group 3								
Porzana sp., large Kauai rail			F					
Porzana ralphorum				F				
Porzana severnsi							F	
Porzana sp., large Hawaii rail								F
Volant species								
Fulica alai		H	H	FH	H		H	H
Fulica sp.				F*				
Family Recurvirostridae								
Himantopus knudseni		H	H	FH	H		H	H
Family Accipitridae								
Haliaeetus sp.				F	F		F	
Buteo sp.				F*				
Buteo solitarius					F			H
Circus dossenus				F	F			
Family Strigidae								
Grallistrix auceps			F					
Grallistrix orion			F					
Grallistrix geleches					F			
Grallistrix erdmani							F	

of non-passerine land birds once occurred throughout the main Hawaiian Islands, none of these survived into the historic period except on the island of Hawaii (we exclude from this discussion such purely aquatic species as stilts and coots). Virtually all of the extinct non-passerine land birds were either raptorial or flightless—conditions that are not found among any of the passerines.

Although we know so far of three genera and at least four species of the ponderous flightless ducks we have called moa-nalos, all were gone before the arrival of Europeans. These birds may also have existed on Niihau, Lanai, and Kahoolawe, and perhaps additional species occurred on islands such as Kauai, Oahu, and Molokai, where only one species has been found to date. Two other enigmatic goose-like anatids are reported here from Oahu and Hawaii. The genus *Branta* persisted historically only on Hawaii, although the extant species occurs as a fossil as far west as Kauai. Larger, extinct forms of *Branta,* at least some individuals of which were flightless, are known from Kauai, Oahu, and Maui.

Among rails, we assume that endemic flightless species were present on all the main islands prior to the arrival of man. The fossil record shows that there were certainly or probably three species each on Maui and Hawaii, at least two each on Kauai and Oahu, and one on Molokai. Assuming that originally there were at least two species on each of the main islands, then perhaps as many as 18 species, or at least populations, of flightless rails may have existed contemporaneously. Only one of these has been documented as persisting into the historic period, the species *Porzana sandwichensis,* known from seven specimens from Hawaii and presumed to have become extinct in the mid-19th century.

Flightless ibises were an unexpected element in the Hawaiian avifauna. The genus *Apteribis* appears to have evolved on, and to be restricted to, the islands of Maui Nui, where at least two species are known. Three or more species may have existed in the archipelago if ibises were present on Lanai or Kahoolawe. The only other flightless ibis yet known is from Jamaica, although it seems likely that others, not yet discovered, evolved on islands elsewhere. No flightless ibis survived to be known historically.

The repeated and rapid evolution of flightlessness within and among various groups of insular non-passerines, as now proven by the fossil record, provides compelling evidence that under certain circumstances there is a strong selective advantage in being flightless (Olson 1973a). On the other hand, the pervasiveness of extinction of flightless birds following human colonization underscores the extreme vulnerability of flightless birds once man and introduced predators are added to insular environments.

The raptorial birds present another case. Discounting the Short-eared Owl, *Asio flammeus,* which colonized the islands in post-Polynesian times, only one species of raptor survived into the historic period in the archipelago—the Hawaiian Hawk, *Buteo solitarius,* on the island of Hawaii. The genus is also known from fossils on Molokai and from the Pleistocene of Oahu. Yet prior to the arrival of man there were three additional lineages of raptors in the archipelago: a harrier of the genus *Circus,* an eagle of the genus *Haliaeetus,* and a radiation of at least four species of owls of a new genus, *Grallistrix,* derived from the genus *Strix.*

None of these raptors was flightless, yet all have disappeared with as much finality as the moa-nalos, ibises, and flightless rails. Several possible causes for such pervasive extinction among raptors suggest themselves. The elimination of

all resident, non-passerine prey species from all islands but Hawaii must have had an effect on population sizes of at least some raptors. All of the raptors would have exploited rails, young ibises, and perhaps young moa-nalos, although the eagle was the only one capable of taking adult ibises or moa-nalos. Some individuals of the eagle should have been able to sustain themselves for a time on seabirds after the flightless species were gone, however.

Another factor that may have played a role in the extinction of raptors is nest-site selection. It is probable that most Hawaiian raptors nested mainly on the ground. With the exception of the somewhat aberrant Australian species *Circus assimilis,* all of the species of harriers are ground nesters (Brown and Amadon 1968). Many kinds of owls normally nest on the ground and even among those that usually nest in trees, some individuals will occasionally build nests on the ground. Because of the large accumulations of pellet remains in sand dunes, owls of the genus *Grallistrix* appear to have roosted on the ground, and so probably nested there as well. At least four of the species of *Haliaeetus* have been reported as nesting on the ground at times (Brown and Amadon 1968).

In an environment such as the Hawaiian Archipelago, where no terrestrial nest predators of any sort existed, there may have been little advantage in a raptor troubling to find a suitable site and building a secure arboreal nest, or even bothering to conceal a nest on the ground. On the other hand, terrestrial nesting and lack of appropriate nest concealment or defense behavior, may have made Hawaiian raptors especially vulnerable to extinction when faced with a sudden influx of humans and rats.

Whereas prior to our fossil discoveries it would have appeared that the Hawaiian avifauna evolved in an environment with very little predation pressure, we now find that this is an erroneous impression caused by the differential extinction of raptorial birds subsequent to the arrival of man. Small forest birds had to contend with two predators, a harrier and an owl, both of which had evolved limb proportions similar to *Accipiter* and were presumably proficient bird catchers, as are species of that genus.

The fossil record of birds shows that no realistic assessment of evolutionary or ecological phenomena in the Hawaiian Islands is possible without giving due consideration to the effects of man-caused environmental degradation over the past 16 centuries.

ACKNOWLEDGMENTS

SUMMARY

Paleontological studies in the past two decades in the main islands of the Hawaiian Archipelago have uncovered thousands of bones of previously unknown, extinct species of birds. These remains are mostly of late Holocene age. Prehistoric avian extinctions in the Hawaiian Islands are attributed mainly to

predation and environmental degradation by Polynesians and introduced pred-
ators. Fossil sites are briefly reviewed and occur in variety of geological settings:
sand dunes, limestone sinkholes, lava tubes, a crater lake, and in Polynesian
midden deposits. Remains of prehistorically extinct species of birds have been
found on the islands of Kauai, Oahu, Molokai, Maui, and Hawaii.

Three fossil genera and species of Hawaiian birds, all non-passerines, had been
described previously. The present paper provides formal scientific descriptions
for 3 new genera and 16 new species of Hawaiian non-passerine birds and calls
attention to perhaps as many as 11 additional species for which diagnoses are not
yet advisable. Descriptions of the fossil passerines will be found in an accom-
panying contribution (James and Olson 1991).

Although the fossil record documents the extirpation of several species of sea-
birds from the main Hawaiian Islands, the only apparent complete extinction was
of a very small gadfly petrel, *Pterodroma jugabilis,* new species, of uncertain
affinity, that is known from bones from Oahu and Hawaii.

The previously described flightless ibis *Apteribis glenos* Olson and Wetmore,
is here restricted to Molokai, with *Apteribis brevis,* new species, being described
from Maui. The latter appears to have been a small upland form, whereas the
lower elevations of Maui were occupied by a larger form possibly distinct from
either *A. glenos* or *A. brevis.* Description of this lowland form from Maui is deferred
pending more detailed statistical analyses.

The most unusual members of the extinct avifauna were flightless anseriform
birds with tiny wings, massive hindlimbs, and strange beaks. Although they were
terrestrial and herbivorous, like geese, we now know from the presence of a duck-
like syringeal bulla that these strange birds were derived either from shelducks
(Tadornini), or more likely from dabbling ducks (Anatini), quite possibly from
the genus *Anas.* They may have had an ecological role similar to that of the large
tortoises of the Galapagos and islands of the western Indian Ocean. Because we
now recognize three genera and four species of these birds, and because they are
neither phyletically geese nor functionally ducks, we have coined a new word,
moa-nalo, as a more convenient general term for all such flightless, goose-like
ducks of the Hawaiian Islands.

Chelychelynechen quassus, new genus and species, from Kauai, is the most
divergent of the moa-nalos, with a massive rostrum and mandible that are very
suggestive of those of a tortoise. *Thambetochen chauliodous* Olson and Wetmore,
described previously from Molokai, had a less massive beak with tooth-like pro-
jections on the tomia. Abundant material from Maui is tentatively referred to
this species. *Thambetochen xanion,* new species, is described as a more gracile
species from Oahu, though it is still remarkably similar to *T. chauliodous.* A
second moa-nalo, *Ptaiochen pau,* new genus and species, also inhabited Maui,
apparently mostly at higher elevations than *Thambetochen.* It, too, had tooth-like
projections on the tomia but differs so markedly in skull structure and certain
aspects of postcranial osteology that generic separation is warranted for it. Remains
of two additional species of goose-like birds are known from Oahu and Hawaii,
but these are insufficient for determining relationships even though it is certain
that they represent new species.

The systematics of the Hawaiian fossils referable to the genus *Branta* are com-
plex. The extant species *B. sandvicensis* is known from fossils on Kauai, Molokai,

Lanai, and Maui, whereas it is known historically only from Hawaii. Considerably larger forms of *Branta*, but with reduced wings, occur as fossils on Kauai, Oahu, and Maui. These are all more similar to *B. sandvicensis* than to mainland species of *Branta*. Only the best represented of these populations, that from Maui, is formally described as *Branta hylobadistes*, new species. At least some individuals of *Branta* from Maui were certainly flightless.

Flightless rails, all of which are referred to the genus *Porzana*, are abundant in the fossil record. Five of these are described as new here, whereas the others are left unnamed pending the collection of better material. These rails fall into three size groups. The first is composed of very small birds, the species from Molokai being the smallest member of the family Rallidae. These are: *Porzana ziegleri*, new species, from Oahu; *P. menehune*, new species, from Molokai; *P. keplerorum*, new species, from Maui; and an unnamed form from Hawaii. The second group of medium-sized rails is scantily represented by fossils of unnamed forms from Kauai and Maui, and by the historically known species *P. sandwichensis* of Hawaii. The last group, containing the largest species, comprises an unnamed form from Kauai; *P. ralphorum*, new species, from Oahu; *P. severnsi*, new species, from Maui; and an unnamed form from Hawaii.

Bones of an extirpated species of eagle of the genus *Haliaeetus* have been found on Oahu, Molokai, and Maui. We have as yet been unable to distinguish these bones from those of the Palearctic "superspecies" *H. leucocephalus*/*H. albicilla*. A second extinct accipitrid, originally identified as an *Accipiter*, is instead a harrier, *Circus dossenus*, new species, that is strikingly convergent with *Accipiter* in its limb proportions. It is known from Oahu and Molokai but is very rare.

A most important fossil discovery was a previously unknown radiation of owls, also convergent with *Accipiter* in having very long legs and short wings. Skull structure suggests that these owls were derived from the genus *Strix*, but they are so divergent that we have separated them as *Grallistrix*, new genus. We recognize four species: *G. auceps*, new species, from Kauai; *G. orion*, new species, from Oahu; *G. geleches*, new species, from Molokai; and *G. erdmani*, new species, from Maui. Curiously, the species from Kauai and Molokai are large, whereas each is flanked by smaller species on Oahu and Maui. The species of *Grallistrix* were important predators of small birds as shown by fossilized pellet deposits.

The endemic, non-passerine forest birds of the Hawaiian Islands suffered much greater levels of extinction than passerines. None persisted into the historic period except on the island of Hawaii. Virtually all were either flightless or were raptors. The disadvantages of flightlessness in the face of man and introduced predators are obvious enough. Raptors may have been rendered similarly vulnerable by the adoption of terrestrial nesting habits as well as by reduction in availability of prey.

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