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Article

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Extraordinary cranial specialization in a new genus of extinct duck (Aves: Anseriformes) from Kauai, Hawaiian Islands

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Abstract

Talpanas lippa is described as a new genus and species of waterfowl from Kauai, Hawaiian Islands, that is unlike any other known member of the order. It is characterized by a short, stout tarsometatarsus and a braincase that is shallow and wide relative to its length with very small orbits. In comparison with extant species, the optic foramen of *Talpanas* is remarkably small whereas the maxillo-mandibular foramen, which is the exit point of the trigeminal nerve, is grossly enlarged. Relative to skull length and foramen magnum area, the maxillo-mandibular foramen is one order of magnitude larger in cross-sectional area than that of extant Anseriformes. We conclude that *Talpanas* had reduced visual abilities, as reflected externally by its small orbits and optic foramen, and a grossly hypertrophied trigeminal foramen. Taken together, this suggests that *Talpanas* may have been more heavily reliant upon somatosensory (tactile) cues for foraging than any living species of bird. Pectoral elements are unknown, but the evident lack of keen eyesight suggests that the species was flightless, as were many other insular waterfowl.

Key words: Anatidae, somatosensory, trigeminal nerve, optic nerve, vision, Hawaiian Islands

Introduction

The Hawaiian Islands have provided a wealth of information concerning the evolution and diversification of insular biotas. The fossil record has greatly enriched the known diversity of birds in the islands, with at least 39 new species having been documented from deposits throughout the archipelago (Olson & James 1982, 1991; James & Olson 1991, 2003, 2005, 2006). Most, indeed probably all, of those species apparently became extinct in the past 1500 years or so since the islands were first colonized by humans (opp. cit.). Included are songbirds, raptors, and a diverse array of flightless taxa derived from at least 6 independent colonizations that included rails (Rallidae), an ibis (Plataleidae), and waterfowl (Anatidae). Among the last and perhaps the most unusual are the moa-nalos—3 genera and 4 species of large herbivores with tiny wings, that are evolutionarily derived from dabbling ducks (Sorensen *et al.* 1999). Here, we describe another new and extraordinary species of waterfowl from the island of Kauai that is strikingly unlike any anatid previously known in Hawaii or elsewhere in the world. An exquisitely preserved neurocranium excavated in Holocene lake sediments establishes that this bird had very small eyes and hence probably poor vision. These features, combined with enhanced somatosensory abilities, indicate a dramatic adaptation for tactile foraging that appears to have been better developed than in any other known bird.

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Materials and methods

Measurements. Measurements were made with dial calipers to the nearest (0. 1) mm on the holotype and 508 additional specimens representing 144 species in the collections of the Division of Birds and Department of Paleobiology, National Museum of Natural History, Smithsonian Institution (Table 1). These measurements included: 1) skull length from the nasofrontal hinge to caudal-most point of the braincase, 2) interorbital width, 3) braincase depth from vertex to basisphenoid, 4) width of the nasofrontal hinge, 5) maximum braincase width, 6) width at the postorbital processes, 7) width at the supraorbital processes, and 8) width at the lacrimal processes. We also measured the cross sectional area of the maxillo-mandibular foramen, optic foramen, and foramen magnum in skulls of the aforementioned specimens and the foramina of four extinct species from the Hawaiian Islands: *Branta* sp. (n = 2), *Branta hylobadistes* (n = 1), *Thambetochen chauliodous* (n = 1) and *Ptaiochen pau* (n = 5) (Table 2).

We also made measurements of the paratypes including the lengths of all elements and angular divergence of the palatines (Table 2), which were determined using digital photographs taken from the ventral aspect. The angle subtended by the two palatines was then measured on the digital images using the freeware image analysis program ImageJ (Rasband 1997–2008, available from http://rsb.info.nih.gov/ij/).

Body mass estimation. To estimate the body mass of the species, we calculated allometric relationships between recorded body mass and cross sectional area of the acetabulum, circumference of the proximal end of the shaft of the tibiotarsus, and mid-shaft circumference of the tarsometatarsus of 189 museum specimens representing 76 species (Table 3). All measurements were $\log_{10}$-transformed and least-squares linear regressions were performed using body mass of the specimens themselves as the independent variable. The equation for the allometric line describing the linear relationship between body mass and the dependent variable was then used to estimate the body mass of the species, as in previous studies (Campbell & Marcus 1992; Iwaniuk *et al.* 2004).

Statistical analyses. A principal component analysis (PCA) was performed on correlations of all eight skull measurements to determine how divergent the skull morphology of *Talpanas lippa* was from other anseriforms. Three principal components, which explained 94.41% of the variation (Table 4), were saved. To examine variation in the relative size of the maxillo-mandibular and optic foramina, we calculated residuals from least-squares linear regressions of $\log_{10}$-transformed foramen area plotted against $\log_{10}$-transformed skull length (mm) and foramen magnum area (mm^2). Significant outliers in all analyses and boxplots were detected using both Mahalanobis and jackknife distances as performed in JMPIN (v. 5.1.2, SAS Institute).

Order Anseriformes

Family Anatidae

The new taxon is assigned to the Anatidae based on the following combination of traits: neurocranium with strongly developed postorbital processes, but lacking zygomatic processes or any ossification of the aponeuroses zygomatica; large basipterygoid processes present on the parasphenoid rostrum anterior to the basitemporal plate; ossified cartilage present in the caudal nasal concha; lacrimals fused and elongated anteroposteriorly; mandible with strongly upturned retroarticular processes.

Genus *Talpanas* new genus (Olson & James)

Type species. *Talpanas lippa* Olson and James, new species, by original designation.

Included species. Type species only.

Distribution. Kauai, Hawaiian Islands.

Etymology. L. *talpa* (f.) a mole, plus *anas* (f.), a duck, in allusion to the greatly reduced size of the eyes. The gender is feminine. Among mammals, the closest analog of the new genus of duck in the appearance of the cranium, as well as in the similarity in trigeminal enlargement (Home 1802), is the platypus (*Ornithorhynchus anatinus*), an alternate vernacular of which among Australian colonists was "duck-mole." The reduced eyes and poor vision of moles (Talpidae) are well known.

Diagnosis. Anatidae with braincase very broad and dorsoventrally compressed, with greatly reduced orbits. Maxillo-mandibular foramen and foramen n. olfactorii greatly enlarged relative to all other waterfowl. The orbit is greatly reduced in size and laterally displaced, allowing the nasal cavity to extend caudally and directly abut the brain cavity. There is consequently no mesethmoidal sulcus for the olfactory nerves, whereas in other anatids the orbit separates the olfactory and brain cavities, requiring long olfactory nerves to traverse the orbit. The nasal gland depressions are seated against extensive flat surfaces of the frontal that face laterad, whereas in most other Anatidae these depressions face dorsad.

TABLE 1. Sample sizes (n) and mean linear dimensions (in mm) of the skulls of the 145 species included in our analyses. Details regarding the landmarks used for all eight measurements are provided in the text. Data for *Talpanas lippa* are shown in bold.

Species	n	Skull length	Interorbital width	Skull depth	Naso-frontal hinge width	Supra-orbital process width	Lacrimal width	Post-orbital process width	Braincase width
Aix galericulata	6	43.8	8.8	23.9	9.8	17.0	19.6	24.0	22.6
Aix sponsa	4	45.6	8.1	25.3	12.0	18.0	20.9	25.5	23.3
Alopochen aegyptiacus	4	58.9	12.8	28.9	15.6	23.9	27.7	33.5	29.7
Amazonetta brasiliensis	4	43.8	8.2	23.0	10.4	15.0	19.0	24.1	20.9
Anas acuta	6	52.6	9.3	25.2	11.5	16.5	20.0	26.6	24.4
Anas americana	6	47.5	6.4	23.8	10.1	13.8	18.5	24.0	22.1
Anas aucklandica	1	46.8	6.0	22.1	9.6	15.2	17.4	23.3	22.8
Anas bahamensis	4	47.4	7.7	23.2	11.6	16.0	18.8	24.1	22.6
Anas capensis	1	44.1	5.6	21.3	9.8	16.1	18.8	22.9	21.1
Anas castanea	4	47.5	8.4	24.1	10.6	16.7	18.0	24.2	22.1
Anas clypeata	8	51.6	6.9	22.6	10.5	13.8	18.8	23.3	20.9
Anas crecca	8	42.6	12.0	21.7	8.9	13.1	16.2	21.5	19.4
Anas cyanoptera	5	44.6	6.9	21.8	9.7	11.9	16.4	21.2	19.1
Anas discors	6	43.9	6.5	21.5	9.4	12.3	16.4	21.6	19.2
Anas erythrorhyncha	4	46.8	8.5	23.1	11.3	15.2	18.9	24.7	22.6
Anas falcata	4	50.6	7.0	24.8	11.8	16.8	21.0	26.1	23.4
Anas flavirostris	4	43.7	6.6	22.4	9.2	14.9	18.1	22.7	20.4
Anas formosa	3	45.6	7.5	22.7	11.0	13.9	19.6	24.2	21.6
Anas georgica	3	48.3	9.4	24.5	11.2	15.6	19.7	26.1	22.8
Anas gracilis	3	47.3	7.0	22.0	9.5	14.2	16.9	23.0	21.3
Anas hottentota	4	40.6	6.1	20.6	8.5	12.7	16.4	20.3	19.1
Anas laysanensis	4	39.0	8.2	21.9	8.9	11.9	13.5	22.0	19.7
Anas luzonica	3	51.6	9.0	25.3	12.6	16.1	21.6	27.3	24.4
Anas melleri	1	55.6	8.2	25.4	13.1	13.5	22.9	27.8	24.5
Anas penelope	4	46.0	5.8	22.7	10.4	14.9	18.3	24.3	22.2
Anas platalea	3	49.3	6.9	22.3	12.1	15.9	21.4	24.2	20.7
Anas platyrhynchos	7	56.5	9.7	26.8	13.3	16.2	22.7	28.6	25.6
Anas poecilorhyncha	4	55.8	9.8	26.5	13.4	16.8	23.6	29.1	23.1

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TABLE 1. (continued)

Species	n	Skull length	Interorbital width	Skull depth	Naso-frontal hinge width	Supra-orbital process width	Lacrimal width	Post-orbital process width	Braincase width
Anas querquedula	3	42.0	5.7	20.9	9.4	11.8	16.5	21.6	19.1
Anas rhynchotis	2	50.9	5.8	22.4	10.6	15.0	20.0	23.2	20.2
Anas rubripes	4	56.5	7.8	27.2	13.1	16.7	23.2	28.7	26.4
Anas sibilatrix	4	48.1	7.2	22.9	10.3	14.9	17.3	25.2	21.6
Anas smithii	4	50.1	6.8	22.6	11.2	16.2	18.9	23.8	20.6
Anas sparsa	2	52.0	9.4	24.9	11.5	15.2	20.2	27.7	24.5
Anas specularis	1	56.3	9.0	26.8	14.5	18.2	23.3	28.7	24.2
Anas strepera	5	49.6	6.8	22.9	10.3	15.4	18.0	24.9	22.5
Anas superciliosa	4	49.3	8.5	24.1	11.8	14.2	20.8	25.3	22.8
Anas undulata	2	52.6	9.1	27.0	14.2	16.9	22.8	27.6	24.5
Anas versicolor	4	42.7	6.8	22.4	9.1	14.3	16.0	22.5	20.2
Anas wyvilliana	4	45.7	8.6	23.8	11.1	13.9	19.0	24.4	23.1
Anser albifrons	6	53.5	13.2	31.9	18.5	21.4	25.4	35.0	30.8
Anser anser	4	62.9	17.7	38.2	26.7	31.7	35.9	43.8	35.6
Anser caerulescens	4	53.9	14.7	33.6	19.8	22.9	27.5	36.3	32.2
Anser canagicus	4	50.5	9.5	31.3	17.9	21.9	25.7	34.6	31.6
Anser cygnoides	2	72.6	20.5	35.5	25.9	29.2	31.6	42.3	34.7
Anser fabalis	6	53.8	14.0	33.5	18.5	23.5	25.5	34.3	31.8
Anser indicus	2	51.9	11.3	30.3	16.5	22.2	26.1	32.0	30.2
Anser rossii	5	45.9	11.7	28.7	15.4	17.9	22.1	29.0	28.0
Anseranas semipalmata	3	56.6	14.2	33.2	17.2	23.9	24.8	37.9	32.4
Aythya affinis	5	46.4	6.9	23.7	10.8	15.7	17.7	26.3	23.8
Aythya americana	4	51.2	6.2	25.0	13.1	15.8	19.0	28.8	25.2
Aythya australis	3	51.3	9.9	24.5	13.8	15.9	20.4	28.0	24.2
Aythya baeri	1	48.9	9.5	23.8	13.5	16.0	20.4	27.2	24.6
Aythya collaris	4	47.9	9.2	24.3	13.5	16.1	19.8	28.4	25.1
Aythya ferina	4	50.8	8.1	24.5	12.2	14.7	18.5	28.2	25.3
Aythya fuligula	4	45.0	8.1	22.8	11.2	14.3	16.3	25.8	23.2
Aythya innotata	1	49.4	9.3	24.3	12.3	15.3	19.1	28.1	25.2
Aythya marila	4	50.5	7.4	24.3	13.0	16.7	21.0	29.6	25.2
Aythya novaeseelandiae	1	47.1	7.1	22.0	10.3	13.0	16.0	24.5	22.5
Aythya nyroca	3	43.4	8.7	23.3	11.9	13.4	17.1	25.0	22.8
Aythya valisineria	4	57.9	8.5	26.2	12.5	15.2	18.9	29.4	27.0
Biziura lobata	2	49.7	7.3	25.5	13.2	15.1	24.0	29.0	26.6
Branta bernicla	4	48.8	8.5	26.0	14.6	22.2	23.6	30.4	27.5
Branta canadensis minima	4	44.0	8.0	26.3	12.2	16.4	17.5	26.9	25.4
Branta canadensis moffitti	3	60.7	13.9	34.3	19.7	24.9	28.7	34.6	33.5
Branta canadensis taverneri	3	49.7	11.0	29.9	14.6	20.6	21.9	30.2	30.1
Branta leucopsis	1	46.8	9.6	28.4	12.7	21.2	19.8	29.9	27.8
Branta ruficollis	3	43.3	10.0	26.5	12.7	17.8	22.8	26.6	24.2
Branta sandvicensis	3	50.2	12.7	29.1	16.8	20.5	23.8	31.6	29.4

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TABLE 1. (continued)

Species	n	Skull length	Interorbital width	Skull depth	Naso-frontal hinge width	Supra-orbital process width	Lacrimal width	Post-orbital process width	Braincase width
Bucephala albeola	4	41.2	4.6	22.1	8.0	11.3	17.8	23.1	22.0
Bucephala clangula	4	52.9	12.2	29.1	14.1	17.2	23.3	29.9	26.7
Bucephala islandica	3	54.7	11.1	28.9	14.0	18.2	24.6	30.7	27.8
Cairina moschata	2	64.5	14.3	32.9	18.0	25.7	31.6	38.0	30.8
Cairina scutulata	4	62.1	14.7	31.6	16.6	23.7	27.8	35.7	30.5
Calonetta leucophrys	2	40.1	7.3	21.2	9.5	14.5	18.0	21.2	20.0
Cereopsis novaehollandiae	4	57.0	10.3	31.7	18.8	26.9	28.7	35.3	31.2
Chenonetta jubata	3	43.9	9.3	24.4	10.9	16.9	18.3	24.9	22.3
Chloephaga hybrida	4	57.6	10.2	29.6	14.1	25.3	28.5	32.0	28.6
Chloephaga melanoptera	3	59.9	15.4	30.0	15.9	26.1	28.7	34.9	29.5
Chloephaga picta	4	60.1	14.7	30.9	15.5	26.5	29.3	33.8	29.1
Chloephaga poliocephala	3	52.3	11.7	26.6	12.7	23.0	23.2	29.0	26.3
Chloephaga rubidiceps	1	50.9	7.3	26.4	12.2			28.1	27.4
Clangula hyemalis	7	47.8	5.6	22.3	9.3	13.7	18.6	27.1	24.9
Coscoroba coscoroba	4	68.3	11.9	28.4	17.1	25.4	28.5	35.6	32.9
Cyanochen cyanopterus	4	53.7	11.9	28.4	13.6	20.8	20.8	30.2	27.5
Cygnus atratus	4	70.0	13.8	33.9	22.7	27.9	30.9	40.6	36.7
Cygnus buccinator	5	90.3	20.1	42.1	24.6	32.5	39.9	48.8	44.6
Cygnus columbianus	4	81.5	16.5	37.5	22.2	29.5	35.6	44.2	40.1
Cygnus cygnus	1	88.0	18.3	39.3	23.9	30.6	36.9	46.0	41.6
Cygnus melancoryphus	4	66.1	12.2	30.9	19.4	24.8	30.4	37.6	33.6
Cygnus olor	4	85.2	17.1	34.6	23.4	34.1	41.0	48.7	42.0
Dendrocygna arborea	4	48.9	10.4	25.9	16.2	18.7	25.4	29.0	25.5
Dendrocygna arcuata	4	44.2	9.4	23.0	14.0	15.7	22.4	26.2	23.5
Dendrocygna autumnalis	4	47.7	11.4	24.4	15.6	17.0	23.3	27.4	24.2
Dendrocygna bicolor	3	47.4	10.3	24.0	14.3	15.3	22.7	26.3	23.4
Dendrocygna eytoni	4	43.9	12.5	25.4	14.4	20.1	24.0	26.8	24.5
Dendrocygna guttata	3	44.4	9.5	24.4	13.1	16.3	20.5	26.2	23.4
Dendrocygna viduata	4	46.2	11.3	24.5	15.1	17.2	23.0	26.1	24.0
Heteronetta atricapilla	2	44.7	7.1	20.6	11.2	13.1	17.7	24.1	19.7
Histrionicus histrionicus	5	45.7	5.9	23.9	8.7	13.0	17.4	26.1	24.6
Hymenolaimus malacorhynchus	1	48.8	8.7	23.0	9.7	12.9	17.6	26.1	25.8
Lophodytes cucullatus	4	41.4	7.2	21.4	9.9	12.0	17.7	24.8	24.1
Lophonetta specularoides	4	51.9	6.1	24.4	10.8	16.5	20.4	26.9	23.4
Malacorhynchus membranaceus	1	41.0	5.6	20.5	8.3	13.6	17.4	19.9	18.9
Marmaronetta angustirostris	4	45.7	7.8	21.8	11.6	16.2	19.2	24.3	21.6
Melanitta fusca	4	57.8	9.7	27.7	16.7	20.2	28.8	33.7	30.2

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TABLE 1. (continued)

Species	n	Skull length	Interorbital width	Skull depth	Naso-frontal hinge width	Supra-orbital process width	Lacrimal width	Post-orbital process width	Braincase width
Melanitta nigra	4	50.4	7.4	25.7	11.2	18.0	21.2	29.1	26.3
Melanitta perspicillata	7	53.2	7.4	24.9	12.1	16.8	21.0	29.5	26.6
Mergellus albellus	2	40.4	6.2	21.0	9.8	8.1		25.2	24.4
Mergus merganser	5	47.6	9.6	20.9	13.4	16.2	20.5	32.4	29.1
Mergus octosetaceus	1	42.3	7.5	18.4	7.5	14.2	17.7	29.6	26.8
Mergus serrator	6	42.8	5.8	20.0	10.5	13.0	18.0	28.2	26.5
Mergus squamatus	1	45.8	8.7	19.7	12.3	15.4	18.9	29.8	27.8
Neochen jubatus	4	51.1	14.0	26.8	13.7	23.0	25.4	30.2	27.3
Netta erythrophthalma	3	46.1	8.2	24.9	11.9	14.0	18.3	27.3	24.9
Netta peposaca	4	50.7	10.1	25.6	14.3	18.1	20.3	29.5	25.2
Netta rufina	4	50.0	7.5	23.6	13.5	16.6	19.6	28.6	24.7
Nettapus auritus	4	33.5	6.1	20.3	9.1	13.0	15.6	20.4	18.7
Nettapus coromandelianus	4	33.3	6.1	19.3	12.3	12.8	14.3	19.0	17.9
Nettapus pulchellus	1	33.9	6.4	19.4	9.8	14.4	15.2	20.2	17.9
Oxyura australis	1	44.8	8.2	22.8	13.7	15.6	22.3	27.6	23.9
Oxyura dominica	4	39.1	6.4	20.7	12.6	14.2	18.9	23.9	21.1
Oxyura jamaicensis	5	43.7	6.5	22.0	11.7	12.9	17.2	24.8	22.0
Oxyura maccoa	2	47.1	9.3	23.4	15.5	17.8	22.3	26.7	24.0
Oxyura vittata	2	43.4	7.6	22.9	12.7	14.1	19.3	26.2	23.1
Plectropterus gambensis	4	74.4	20.9	39.0	23.3	32.6	35.8	43.6	35.2
Polysticta stelleri	5	50.0	6.8	23.2	9.6	15.6	14.8	26.2	25.4
Pteronetta hartlaubi	2	52.3	10.9	27.9	13.7	19.4	22.2	29.8	25.9
Sarkidiornis melanotos	4	58.1	13.7	29.1	17.2	24.1	26.4	31.7	27.9
Somateria fischeri	3	58.3	7.1	28.3	12.2	18.4	22.3	31.3	29.7
Somateria mollissima	5	68.1	7.6	28.1	12.9	20.7	24.3	35.0	32.0
Somateria spectabilis	4	58.6	8.1	26.5	12.6	19.4	20.2	30.2	27.9
Stictonetta naevosa	4	53.7	11.0	23.7	16.3	20.4	26.3	29.3	23.8
Tachyeres brachypterus	3	72.2	10.9	33.2	19.1	28.7	29.2	42.2	36.0
Tachyeres leucocephalus	1	68.4	8.5	31.7	17.0	22.3	25.8	38.5	32.6
Tachyeres patachonicus	2	67.0	9.8	31.7	17.7	24.5	28.2	38.9	31.3
Tachyeres pteneres	3	75.4	11.2	34.1	20.1	30.5	31.5	42.4	36.0
Tadorna cana	4	54.0	10.8	25.7	11.8	18.6	23.8	28.3	26.4
Tadorna ferruginea	4	53.4	10.1	24.7	12.6	18.7	24.1	29.3	26.1
Tadorna radjah	4	48.9	9.1	25.2	12.2	18.6	23.0	27.6	25.0
Tadorna tadorna	4	52.6	7.0	23.8	12.2	17.5	21.8	28.7	25.4
Tadorna tadornoides	1	56.0	10.2	24.8	12.6	19.0	23.5	29.2	26.4
Tadorna variegata	2	56.2	10.2	25.3	12.0	18.8	23.3	30.2	27.0
Thalassornis leuconotus	2	43.3	8.0	23.9	16.1	15.2	19.2	28.3	24.3
Talpanas lippa	**1**	**36.5**	**10.5**	**19.9**	**12.5**	**12.7**	**15.4**	**29.7**	**26.7**

TABLE 2. Samples sizes (n), mean cross-sectional areas of the trigeminal foramen (nV), optic foramen (nII) and foramen magnum and angle of the palatines for all 150 species measured. Extinct species are underlined and *Talpanas lippa* is shown in bold.

Species	n	nV foramen (mm²)	nII foramen (mm²)	Foramen magnum (mm²)	Palatine angle (°)
Aix galericulata	4	2.4	13.1	27.7	19.1
Aix sponsa	4	1.5	14.1	28.8	23.9
Alopochen aegyptiacus	4	3.8	16.6	48.0	23.9
Amazonetta brasiliensis	4	2.5	9.4	28.8	24.2
Anas acuta	6	4.7	8.8	35.7	23.5
Anas americana	5	3.7	9.4	30.9	20.4
Anas aucklandica	1	5.0	5.7	39.4	21.3
Anas bahamensis	4	3.8	7.6	33.0	24.8
Anas capensis	1	3.8	6.8	34.6	25.3
Anas castanea	4	3.8	7.6	30.0	22.4
Anas clypeata	8	4.9	6.9	32.6	19.7
Anas crecca	8	4.2	6.9	24.6	23.1
Anas cyanoptera	5	3.9	6.1	25.5	23.1
Anas discors	6	3.2	5.8	23.0	25.3
Anas erythrorhyncha	4	3.3	7.9	33.3	21.2
Anas falcata	4	3.7	9.7	31.7	19.2
Anas flavirostris	4	4.4	7.2	26.1	21.0
Anas formosa	3	3.5	7.5	27.5	23.6
Anas georgica	4	4.4	6.5	33.3	18.8
Anas gracilis	3	4.8	7.6	30.2	23.1
Anas hottentota	4	3.6	5.4	23.9	27.7
Anas laysanensis	3	3.5	6.3	30.3	21.6
Anas luzonica	3	4.2	11.2	35.3	27.4
Anas melleri	1	5.2	11.6	43.1	27.9
Anas penelope	4	2.8	8.3	30.1	22.9
Anas platalea	2	2.6	5.7	29.7	19.5
Anas platyrhynchos	7	5.7	10.4	44.0	23.2
Anas poecilorhyncha	3	5.0	11.4	45.3	22.8
Anas querquedula	3	5.0	6.0	23.7	22.0
Anas rhynchotis	2	3.6	6.9	26.1	-
Anas rubripes	5	5.5	10.2	42.9	27.1
Anas sibilatrix	3	3.1	8.0	32.6	22.2
Anas smithii	4	3.2	7.4	31.4	18.0
Anas sparsa	2	4.1	9.7	34.4	18.4
Anas specularis	1	5.1	11.6	53.4	23.5
Anas strepera	7	3.5	8.4	30.7	22.2
Anas superciliosa	4	4.1	11.2	38.1	21.5
Anas undulata	2	4.0	8.8	40.5	26.1

continued next page

TABLE 2. (continued)

Species	n	nV foramen (mm^2)	nII foramen (mm^2)	Foramen magnum (mm^2)	Palatine angle (°)
Anas versicolor	4	4.5	6.8	25.6	23.3
Anas wyvilliana	4	4.5	7.9	31.6	23.2
Anser albifrons	4	3.6	9.2	59.1	22.4
Anser anser	4	4.7	12.4	65.5	29.0
Anser caerulescens	4	4.7	10.2	53.7	26.0
Anser canagicus	4	4.9	10.2	53.3	22.0
Anser cygnoides	2	8.1	10.6	74.0	26.5
Anser fabalis	6	3.9	11.8	53.4	26.4
Anser indicus	2	3.7	12.1	59.1	24.7
Anser rossii	4	3.0	8.9	39.9	22.1
Anseranas semipalmata	3	6.2	9.7	45.6	26.0
Aythya affinis	5	4.0	7.4	32.2	27.2
Aythya americana	4	4.1	8.5	43.9	27.4
Aythya australis	2	2.8	8.8	45.0	25.2
Aythya baeri	1	3.0	10.2	38.7	26.9
Aythya collaris	4	3.3	8.9	36.5	26.1
Aythya ferina	4	5.4	8.5	47.5	28.4
Aythya fuligula	4	3.2	8.3	35.4	25.5
Aythya innotata	1	2.6	9.8	35.0	27.7
Aythya marila	4	4.3	7.3	41.4	26.3
Aythya novaeseelandiae	1	4.1	9.5	26.9	23.6
Aythya nyroca	3	4.0	9.2	31.4	26.9
Aythya valisineria	4	5.1	10.3	49.5	26.9
Biziura lobata	2	6.0	12.9	49.5	34.5
Branta bernicla	4	2.5	8.8	45.5	23.1
Branta canadensis minima	4	1.9	9.1	44.8	28.9
Branta canadensis moffitti	3	4.9	16.2	64.5	23.4
Branta canadensis taverneri	3	4.9	13.6	49.0	26.9
<u>*Branta hylobadistes*</u>	1	4.9	10.8	52.0	30.1
Branta leucopsis	1	2.6	13.0	52.5	22.8
Branta ruficollis	3	2.6	9.3	37.6	26.9
Branta sandvicensis	3	3.0	10.9	57.9	26.4
<u>*Branta sp.**</u>	2	5.4	13.7	87.6	24.0
Bucephala albeola	4	2.8	7.5	25.6	27.5
Bucephala clangula	4	2.5	10.7	39.5	24.2
Bucephala islandica	3	3.0	10.2	41.4	26.6
Cairina moschata	3	4.0	18.8	58.1	26.4
Cairina scutulata	4	5.8	14.6	56.0	25.3
Calonetta leucophrys	2	2.7	6.5	24.1	27.3
Cereopsis novaehollandiae	4	3.8	13.8	51.0	26.6

continued next page

TABLE 2. (continued)

Species	n	nV foramen (mm²)	nII foramen (mm²)	Foramen magnum (mm²)	Palatine angle (°)
Chenonetta jubata	3	1.6	8.2	30.1	26.5
Chloephaga hybrida	4	3.1	10.4	48.3	22.5
Chloephaga melanoptera	3	3.3	12.3	45.7	21.1
Chloephaga picta	3	2.7	12.7	46.8	19.2
Chloephaga poliocephala	3	2.3	13.0	40.4	15.8
Chloephaga rubidiceps	1	1.5	10.0	39.9	14.6
Clangula hyemalis	5	2.2	9.1	32.1	20.4
Coscoroba coscoroba	4	8.1	11.4	59.7	16.7
Cyanochen cyanopterus	4	3.0	12.5	48.3	19.4
Cygnus atratus	4	7.8	12.9	83.2	20.9
Cygnus buccinator	5	9.4	12.4	106.8	24.4
Cygnus columbianus	4	8.2	12.1	83.2	22.3
Cygnus cygnus	1	8.8	17.7	130.1	22.2
Cygnus melancoryphus	4	8.8	9.3	80.3	21.1
Cygnus olor	4	10.9	15.4	107.2	26.1
Dendrocygna arborea	4	5.4	11.3	42.6	23.6
Dendrocygna arcuata	4	4.7	7.3	35.2	19.8
Dendrocygna autumnalis	4	4.6	9.6	32.5	22.6
Dendrocygna bicolor	4	4.4	8.3	36.8	26.4
Dendrocygna eytoni	2	3.9	9.1	32.8	22.2
Dendrocygna guttata	4	5.5	9.0	29.8	25.9
Dendrocygna javanica	2	4.8	8.3	34.1	-
Dendrocygna viduata	4	3.5	8.5	30.8	22.1
Heteronetta atricapilla	2	3.7	5.1	25.4	24.0
Histrionicus histrionicus	4	1.4	9.5	33.0	26.1
Hymenolaimus malacorhynchus	1	6.3	10.5	45.5	22.9
Lophodytes cucullatus	5	1.7	11.2	31.2	26.5
Lophonetta specularoides	4	5.5	7.8	39.1	24.5
Malacorhynchus membranaceus	1	5.9	5.2	27.4	20.4
Marmaronetta angustirostris	4	2.2	6.2	28.6	-
Melanitta fusca	4	4.7	10.7	51.0	23.3
Melanitta nigra	4	3.1	9.5	40.8	17.3
Melanitta perspicillata	6	4.2	11.3	39.7	19.7
Merganetta armata	1	3.3	8.6	31.6	-
Mergellus albellus	2	2.1	9.7	32.2	-
Mergus merganser	5	1.5	14.2	43.2	24.1
Mergus octosetaceus	1	2.0	12.1	40.8	15.8
Mergus serrator	5	1.9	13.3	37.8	29.9
Neochen jubatus	4	2.5	12.8	42.7	21.6
Netta erythrophthalmica	4	2.4	9.6	41.6	31.4

continued next page

TABLE 2. (continued)

Species	n	nV foramen (mm²)	nII foramen (mm²)	Foramen magnum (mm²)	Palatine angle (°)
Netta peposaca	3	2.3	9.3	44.9	14.0
Netta rufina	4	3.5	10.5	38.5	13.3
Nettapus auritus	4	1.5	6.6	21.0	22.8
Nettapus coromandelianus	4	1.9	6.4	22.0	30.1
Nettapus pulchellus	1	1.7	5.7	20.3	23.7
Oxyura australis	1	7.0	5.8	35.1	24.6
Oxyura dominica	4	3.3	6.1	27.0	30.7
Oxyura jamaicensis	4	8.0	4.9	37.9	24.6
Oxyura maccoa	2	7.1	5.8	37.1	17.4
Oxyura vittata	2	6.5	4.1	38.8	24.1
Plectropterus gambensis	4	6.3	15.8	69.6	31.9
Polysticta stelleri	4	5.7	6.2	39.0	30.0
<u>*Ptaiochen pau*</u>	5	4.9	8.7	70.2	25.8
Pteronetta hartlaubi	2	3.2	14.1	41.7	37.5
Sarkidiornis melanotos	4	3.3	14.7	47.5	32.3
Somateria fischeri	3	4.9	10.0	48.6	24.1
Somateria mollissima	4	4.0	12.5	57.7	29.4
Somateria spectabilis	4	4.1	9.9	47.9	27.3
Stictonetta naevosa	4	6.0	7.2	34.6	26.5
Tachyeres brachypterus	3	7.3	13.2	70.1	25.7
Tachyeres leucocephalus	1	5.9	10.2	70.4	26.0
Tachyeres patachonicus	2	7.8	10.9	54.5	22.6
Tachyeres pteneres	3	7.6	16.2	76.5	20.5
Tadorna cana	4	3.7	11.1	40.1	16.9
Tadorna ferruginea	4	4.0	9.9	39.2	20.8
Tadorna radjah	4	5.6	10.5	32.8	24.9
Tadorna tadorna	4	4.3	8.9	36.5	25.9
Tadorna tadornoides	2	4.3	10.6	46.4	26.3
Tadorna variegata	3	4.3	8.6	47.8	20.6
Thalassornis leuconotus	2	6.4	7.6	48.6	20.7
<u>*Thambetochen chauliodous*</u>	1	6.8	10.7	79.4	31.5
Talpanas lippa	**1**	**15.4**	**2.3**	**35.0**	**42.3**

*undescribed species of *Branta* from the Hawaiian archipelago.

TABLE 3. Samples sizes (n), body masses and mean measurements of 81 species that were used to estimate the body mass of *Talpanas lippa*. Data for *Talpanas lippa* are shown in bold.

Species	n	Body mass (g)	Tibiotarsal circumference (mm)	Tarsal length (mm)	Acetabular area (mm²)	Tarsal circumference(mm)
Aix galericulata	2	499.6	17.0	38.3	13.2	11.4
Amazonetta brasiliensis	2	595.0	14.8	35.9	15.0	10.5

continued next page

TABLE 3. (continued)

Species	n	Body mass (g)	Tibiotarsal circumference (mm)	Tarsal length (mm)	Acetabular area (mm^2)	Tarsal circumference (mm)
Anas acuta	2	722.8	16.9	41.9	18.5	12.7
Anas americana	1	820.9	15.5	39.2	14.9	9.7
Anas bahamensis	4	572.5	16.2	40.7	14.4	11.5
Anas clypeata	4	457.0	15.2	36.1	12.1	10.1
Anas crecca	5	304.4	13.0	30.9	8.3	8.2
Anas cyanoptera	1	421.0	13.3	32.4	8.8	10.0
Anas discors	2	359.1	12.3	31.9	11.0	8.8
Anas erythrorhyncha	2	577.5	13.5	36.5	13.1	10.6
Anas flavirostris	4	429.5	14.4	34.0	9.7	9.4
Anas formosa	1	420.0	13.1	35.8	12.6	9.9
Anas fulvigula	1	1075.0	18.5	46.3	21.8	14.2
Anas georgica	4	617.5	16.7	41.4	17.1	11.4
Anas gracilis	2	397.5	14.2	36.6	11.4	10.1
Anas laysanensis	4	443.4	16.2	34.9	15.7	11.7
Anas melleri	1	1050.0	17.6	41.3	21.9	12.9
Anas penelope	4	618.3	16.4	38.4	16.9	10.4
Anas platalea	3	563.3	16.2	36.6	13.8	10.8
Anas platyrhynchos	4	1047.8	18.2	44.3	22.1	13.0
Anas poecilorhyncha	4	1196.5	21.1	47.8	24.3	14.2
Anas sibilatrix	3	760.0	16.1	41.3	18.0	11.2
Anas smithii	4	777.8	15.9	38.4	18.4	11.7
Anas specularis	1	1217.0	22.3	47.2	25.7	14.1
Anas specularoides	4	921.0	20.5	46.9	23.7	12.9
Anas strepera	3	939.0	16.0	39.6	15.0	10.6
Anas superciliosa	4	813.0	17.7	41.0	19.8	12.5
Anas versicolor	4	425.0	13.1	33.0	11.3	9.9
Anas wyvilliana	4	507.7	16.5	39.7	15.2	11.6
Anser albifrons	2	2725.5	28.7	72.2	46.3	19.5
Anser canagicus	1	1786.0	25.0	62.5	38.3	17.0
Anser fabalis	4	2680.0	29.8	72.6	53.3	20.0
Anser rossii	2	1165.0	26.0	73.9	40.6	16.5
Anseranas semipalmata	1	1880.0	30.5	103.1	45.2	19.7
Aythya affinis	1	980.0	15.2	34.7	15.1	10.7
Aythya australis	1	321.8	12.4	30.8	15.3	10.9
Aythya ferina	1	525.0	15.8	38.7	21.6	13.3
Aythya fuligula	3	525.0	14.1	33.4	20.0	11.3
Aythya innotata	1	685.0	13.2	34.9	20.0	--
Branta bernicla	4	1542.5	23.4	60.7	33.0	14.9
Branta canadensis taverneri	3	1960.3	25.2	68.7	41.8	18.0
Branta ruficollis	2	1065.0	23.6	60.5	29.7	14.6

continued next page

TABLE 3. (continued)

Species	n	Body mass (g)	Tibiotarsal circumference (mm)	Tarsal length (mm)	Acetabular area (mm^2)	Tarsal circumference (mm)
Cairina moschata	1	2650.0	31.3	63.2	64.9	19.3
Cairina scutulata	2	2120.0	23.8	58.1	48.8	18.4
Calonetta leucophrys	1	238.2	13.3	32.3	6.7	9.0
Chenonetta jubata	1	745.0	18.0	48.9	24.4	11.8
Chloephaga hybrida	4	2666.8	29.7	68.5	60.5	19.1
Chloephaga picta	1	2400.0	28.2	84.1	72.0	22.7
Chloephaga poliocephala	1	958.0	26.9	75.3	37.6	17.4
Clamgula hyemalis	5	751.2	13.5	34.8	21.8	9.1
Cygnus buccinator	4	7218.9	46.4	121.1	132.8	33.7
Cygnus columbianus	2	7058.9	39.6	112.2	107.3	31.4
Cygnus cygnus	1	6803.9	48.9	--	--	--
Cygnus melancoryphus	1	3000.0	35.3	86.3	34.3	22.5
Dendrocygna eytoni	2	707.3	17.6	63.5	20.4	14.2
Dendrocygna viduata	4	706.3	18.1	58.8	21.3	14.4
Histrionicus histrionicus	4	670.5	15.8	36.5	16.1	10.5
Lophodytes cucullatus	1	610.0	15.0	32.2	13.9	11.8
Melanitta nigra	4	723.3	18.5	45.1	32.4	13.6
Melanitta perspicillata	3	885.3	16.6	43.0	23.6	11.6
Mergus albellus	2	348.8	15.5	31.5	16.3	10.1
Mergus merganser	3	1509.0	21.6	49.0	32.2	13.9
Mergus serrator	2	992.5	18.6	45.2	27.1	12.9
Netta erythrophthalma	1	900.0	15.5	37.0	18.8	12.1
Netta peposaca	1	1100.0	15.8	45.4	21.5	12.9
Netta rufina	2	1200.0	16.6	44.9	24.1	13.7
Oxyura australis	1	1020.0	15.3	37.4	25.6	13.9
Oxyura dominica	1	360.0	12.3	26.6	13.1	10.1
Oxyura jamaicensis	2	639.0	14.8	34.3	22.0	11.8
Oxyura maccoa	2	862.5	16.3	36.4	29.5	13.6
Oxyura vittata	1	570.0	14.9	31.8	19.8	12.3
Polysticta stelleri	3	870.7	15.6	39.8	24.3	11.0
Somateria mollissima	1	1786.0	19.0	48.2	48.6	14.3
Somateria spectabilis	4	1256.3	18.8	46.1	34.6	13.3
Stictonetta naevosa	4	990.0	18.9	43.8	26.1	14.4
Tachyeres leucocephalus	1	2800.0	26.1	62.5	57.0	20.0
Tachyeres patachonicus	3	2686.7	27.5	58.9	49.3	18.8
Tachyeres pteneres	2	5050.0	33.3	73.2	66.5	24.7
Tadorna tadorna	4	963.1	20.9	55.6	22.3	14.3
Tadorna variegata	1	1520.0	25.4	69.5	33.0	17.9
Talpanas lippa	**1**	**SEE TEXT**	**15.6**	**32.8**	**24.2**	**16.0**

TABLE 4. Table of principal components derived from a principal component analysis of the skull measurements and their associated eigenvalues, eigenvectors and the percentage of variation explained.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Eigenvalue	6.97	0.38	0.20	0.15	0.11	0.11	0.06	0.02
% variation	87.17	4.72	2.52	1.87	1.40	1.33	0.76	0.23
Cumulative %	87.17	91.89	94.41	96.28	97.68	99.01	99.77	100
Eigenvectors								
Skull length	0.34	-0.56	0.37	0.36	0.27	0.32	0.34	0.13
Interobital width	0.33	0.68	-0.05	0.61	0.22	0.01	0.00	0.01
Braincase depth	0.36	0.00	0.20	0.11	-0.80	0.28	-0.29	-0.09
Nasofrontal hinge width	0.35	-0.32	-0.14	-0.58	0.05	0.49	0.39	0.15
Supraorbital process width	0.36	0.08	0.33	-0.17	-0.18	-0.73	0.39	0.05
Lacrimal width	0.36	0.00	0.35	-0.32	0.43	-0.06	-0.67	-0.03
Postorbital process width	0.37	-0.22	-0.44	-0.01	0.09	-0.08	0.07	-0.78
Braincase width	0.36	-0.27	-0.61	0.06	-0.05	-0.20	-0.19	0.59

***Talpanas lippa*, sp. nov. (Olson & James)**

Holotype. USNM 535683; complete neurocranium lacking quadratojugals and any elements of the palate (Fig. 1) and with the surface of the basitemporal plate eroded away.

Locality. Hawaiian Islands, Kauai, south coast. Maha'ulepu/Pa'a district, Makauwahi Cave (Burney *et al.* 2001), 5 km ESE of the town of Koloa, 21˚53'17.5" N 159˚25' 08.5"W.

Chronology and stratigraphy. Mid to late Holocene (Burney *et al.* 2001). All specimens are from Excavation EP (5) at depths of 2.6 to 3.5 m below datum (= 1.4 to 1.7 m below sea level). A fruit of *Cordia* from the same square and level as the holotype had a calibrated radiocarbon age range of 5490-5305 YBP. The paratypes were all from somewhat deeper in the deposits.

Etymology. L. *lippus*, nearly blind.

Distribution. Known only from the type-locality on the island of Kauai, Hawaiian Islands.

Diagnosis. As for the genus. Body mass estimates compared with the mass of living species (Dunning 2008) as well as standard markers, such as diameter of the acetabulum (see Materials and Methods), indicate a medium-large duck (692–1072 g) about the size of a Northern Pintail (*Anas acuta*) or female Mallard (*Anas platyrhynchos*), but with a much shorter, stouter leg.

Measurements (mm) of holotype. Overall length 36.5; width of brain case 26.7; depth of brain case 19.9; minimum distance between the two orbits (taken dorsally) 10.5; width of nasofrontal hinge 12.5; width across lacrimals 15.4; width across supraorbital processes 12.7; width across postorbital processes 29.7.

Paratypes. Figure 2 shows the six paratypes in comparison with elements of the Laysan Duck (*Anas laysanensis*). The paratypes are as follows: fused vomer and right and left palatine bones (broken and repaired) USNM 535684 (Figs. 2B,C); right postdentary portion of mandible USNM 535685 (Figs. 2E, G); fragment of left innominate with antitrochanter and portion of acetabulum USNM 535688; proximal end of right tibiotarsus USNM 535689 (Fig. 2L); right tarsometatarsus USNM 535690 (Fig. 2I); left tarsometatarsus USNM 535691 (Fig 2J); and right innominate lacking most of pubis and anterior margin of ilium USNM 535686 (Fig. 2N).

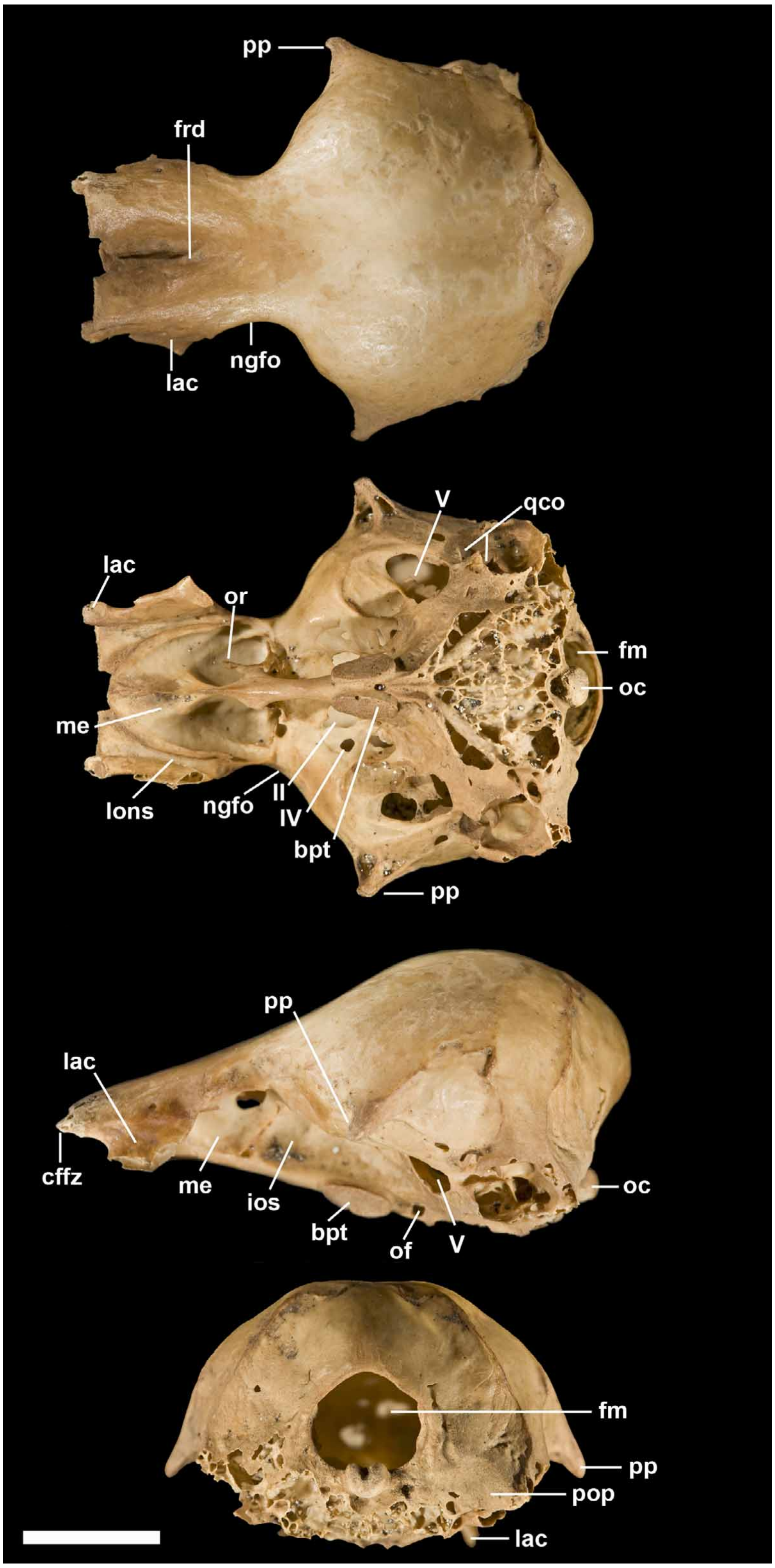

FIGURE 1. Holotype of *Talpanas lippa*, new species (USNM 535683), shown in the following views in order from top to bottom: dorsal, ventral, lateral and posterior. Abbreviations refer to the following structures: **bpt**, basipterygoid facet on parasphenoid rostrum; **cffz**, craniofacial flexion zone; **fm**, foramen magnum; **frd**, frontal depression; **ios**, ossified interorbital septum; **lac**, lacrimal bone; **lons**, lateral orbitonasal sulcus; **me**, mesethmoid; ulcus; **ngfo**, fossa for nasal gland; **oc**, occipital condyle; **of**, orbital foramen (for sphenoid artery); **or**, olfactory region of nasal cavity; **pop**, paroccipital process; **pp**, postorbital process; **qco**, cotylae for squamosal and otic capitula of quadrate; **II**, optic nerve foramen; **IV**, trochlear nerve foramen; **V**, trigeminal foramen. Scale bar = 1 cm.

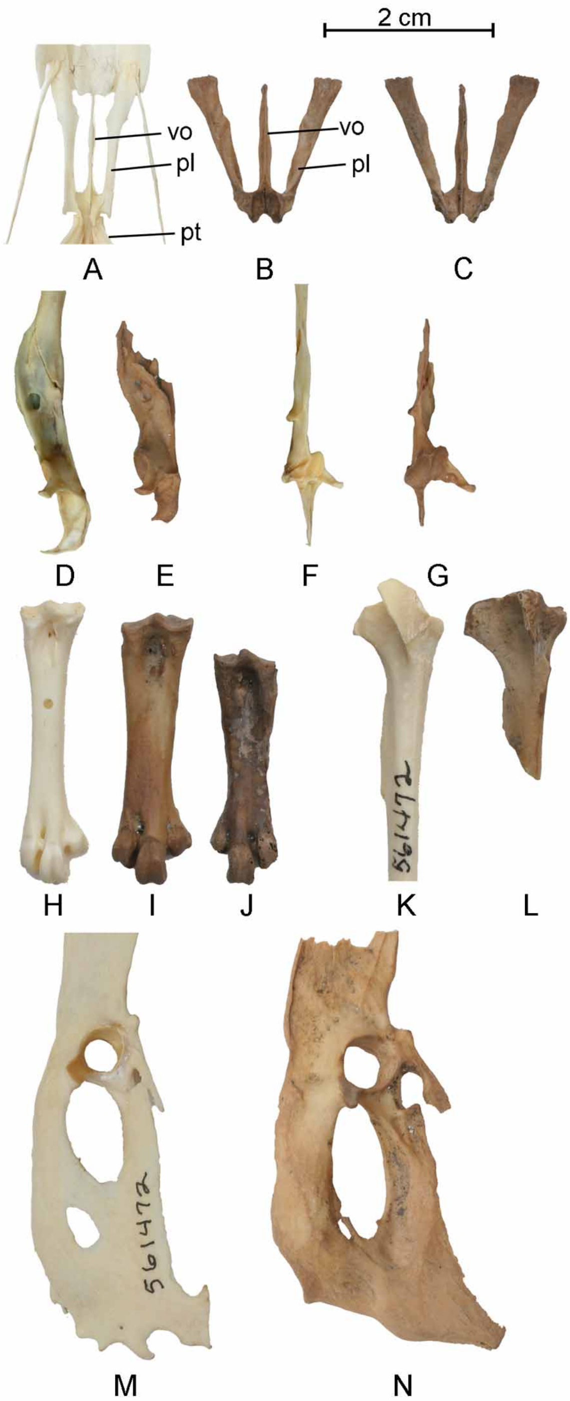

FIGURE 2. Paratypes of *Talpanas lippa*, new species (B, C, E, G, I, J, L, N), compared with Laysan Duck *Anas laysanensis* (A, D, F, H, K, M) as follows: palatal bones in ventral (A, B) and dorsal (C) views, left postdentary portion of mandible in medial (D, E) and dorsal (F, G) views, tarsometatarsi in anterior view (H–J), proximal ends of right tibiotarsi in anterior view (K, L), and right innominate bones in lateral view (M, N). Specimen numbers are as follows: USNM 561472 – *Anas laysanensis*; USNM 535684, USNM 535685, USNM 535690, USNM 535691, USNM 535689, USNM 535686 – *Talpanas lippa*. Scale bar = 2 cm.

Measurements (mm) of paratypes. Palatines: length 18.6; anterior width 2.9, posterior width (lateral edge of palatines) 19.3, posterior width (medial edge of palatines) 12.0. Mandible: least depth of ramus 4.2; width of articulation including medial process 8.4; length of retroarticular process 5.3; depth of retroarticular process at base 3.2. Pelvis: length from posterior margin of acetabulum to posteriormost edge of ischium 30.4;

depth of ilium just anterior to acetabulum 12.4; width of ilium just posterior to antitrochanter 7.5; depth of antitrochanter 3.9; greatest diameter of acetabulum 6.0; length and depth of ilioischiadic foramen 16.1 x 7.4. Tibiotarsus: greatest width and depth of articular surface not including cnemial crests 8.7 x 10.0; width and depth of shaft proximal to fibular crest 5.7 x 3.8. Tarsometatarsi (535691 in parentheses): length 32.9 (28.7); proximal width 8.9 (8.0); proximal depth through hypotarsus 8.9 (---); least width and depth of shaft 5.7 x 3.4 (5.0 x 2.9); distal width 9.8 (8.5); width of middle trochlea 3.5 (3.3).

Description. The length of the tarsometatarsus, relative to its midpoint circumference, was significantly smaller in *Talpanas* than in other anseriforms (Fig. 3A), thus indicating a relatively short and stout leg. The disparity in size of the two known tarsometatarsi of *T. lippa* (Fig. 2I, J) suggests that the species may have been sexually dimorphic, as in many waterfowl in which the males are larger (Dunning 2008). The morphology of the pelvic appendage argues against underwater foraging behavior in *Talpanas*. The lack of medio-lateral compression or medial flattening of the tarsometatarsus, the lack of elevation and retraction of the inner trochlea, the shallow cnemial crests, and the broad posterior half of the pelvis are opposite to the modifications observed in typical foot-propelled diving ducks. The trochleae of the tarsometatarsus are rather widely splayed and, although that for digit II is somewhat elevated it is not retracted with a bladelike posterior edge, as in diving ducks. The overall similarity of the pelvic appendage lies with graviportal terrestrial species.

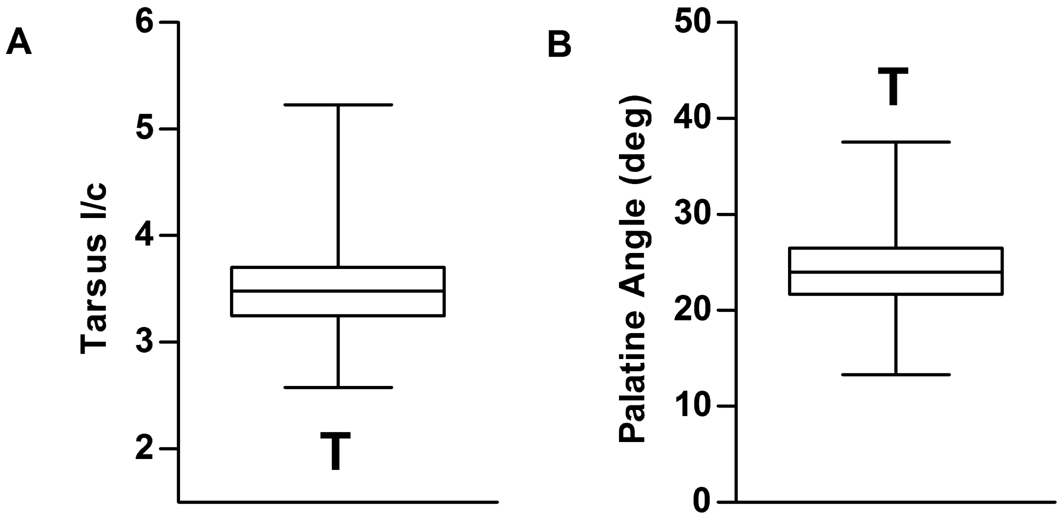

FIGURE 3. Morphometrics of the tarsometatarsus (A) and palatines (B) of *Talpanas lippa* illustrated with box and whisker plots. In both plots, the 'T' indicates *Talpanas*, the box indicates the interquartile range of all waterfowl with the central line running through it representing the mean and the vertical lines indicate the maximum and minimum values for all waterfowl apart from *Talpanas*. (A) is a vertical box and whisker plot of the ratio of tarsometatarsal length ('l') to tarsometatarsal circumference ('c'). Note that *Talpanas* has a significantly lower ratio than all other waterfowl, indicating a short and thick tarsometatarsus. (B) a vertical box and whisker plot of palatine divergence ('Palatine angle') measured in degrees (degs) (for measurement details see Materials and Methods). Again, note that *Talpanas* ('T') has a significantly higher value than all other waterfowl, indicating highly divergent palatines.

The retroarticular process of the mandible is much shorter and less curved than in typical waterfowl (Fig. 2), probably reflecting a decrease in use of M. depressor mandibulae for the rapid bill movements that occur during feeding in waterfowl (Goodman & Fisher 1962). The vomeropalatines are also highly distinctive; the palatines are narrowly tapered posteriorly and are fused, unlike those of typical waterfowl, and the palatines diverge at a very wide angle anteriorly (Figs. 2B, C), which is significantly greater than in other anseriforms (Fig. 3B, Table 2). This may indicate a broadening of the base of the bill, but may also be a reflection of the great foreshortening of the anterior portion of the cranium so that a greater angle would be required to reach the same point of attachment to the base of the bill.

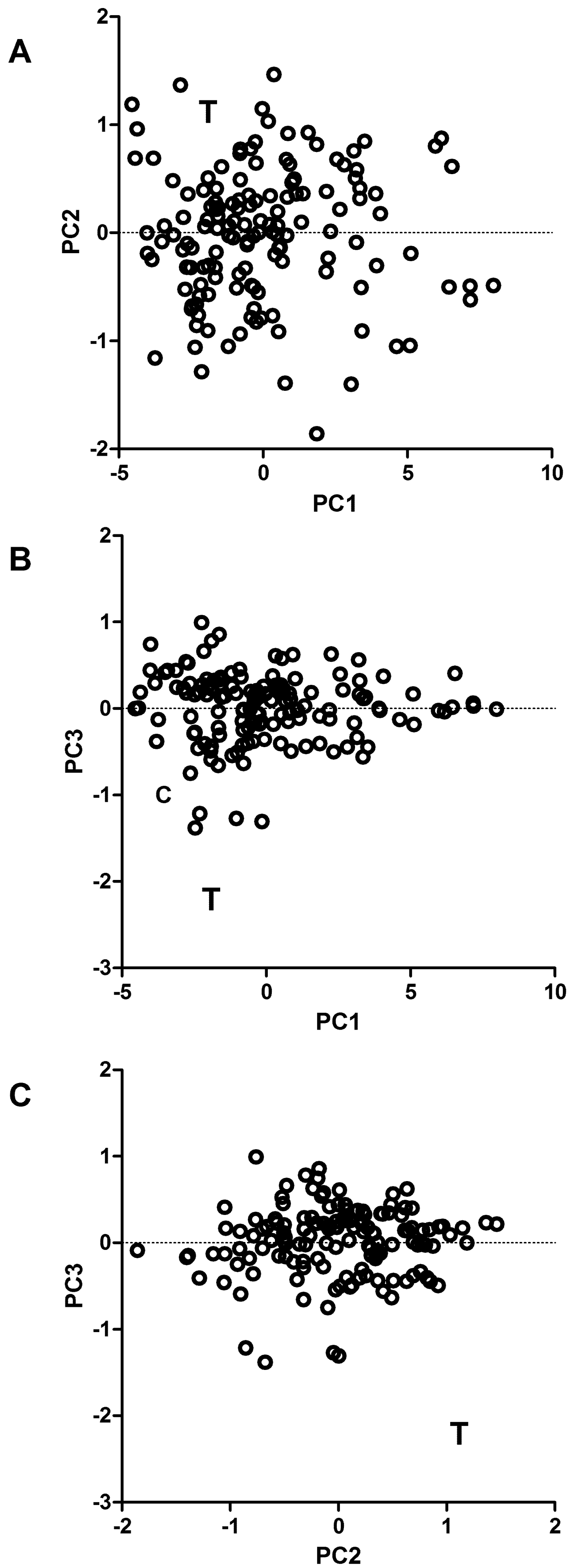

FIGURE 4. Scatterplots of the first three principal components (PC1-3) resulting from a principal components analysis of eight skull measures (see Table 4) places *Talpanas* ('T') in a unique position in multivariate space in both B and C.

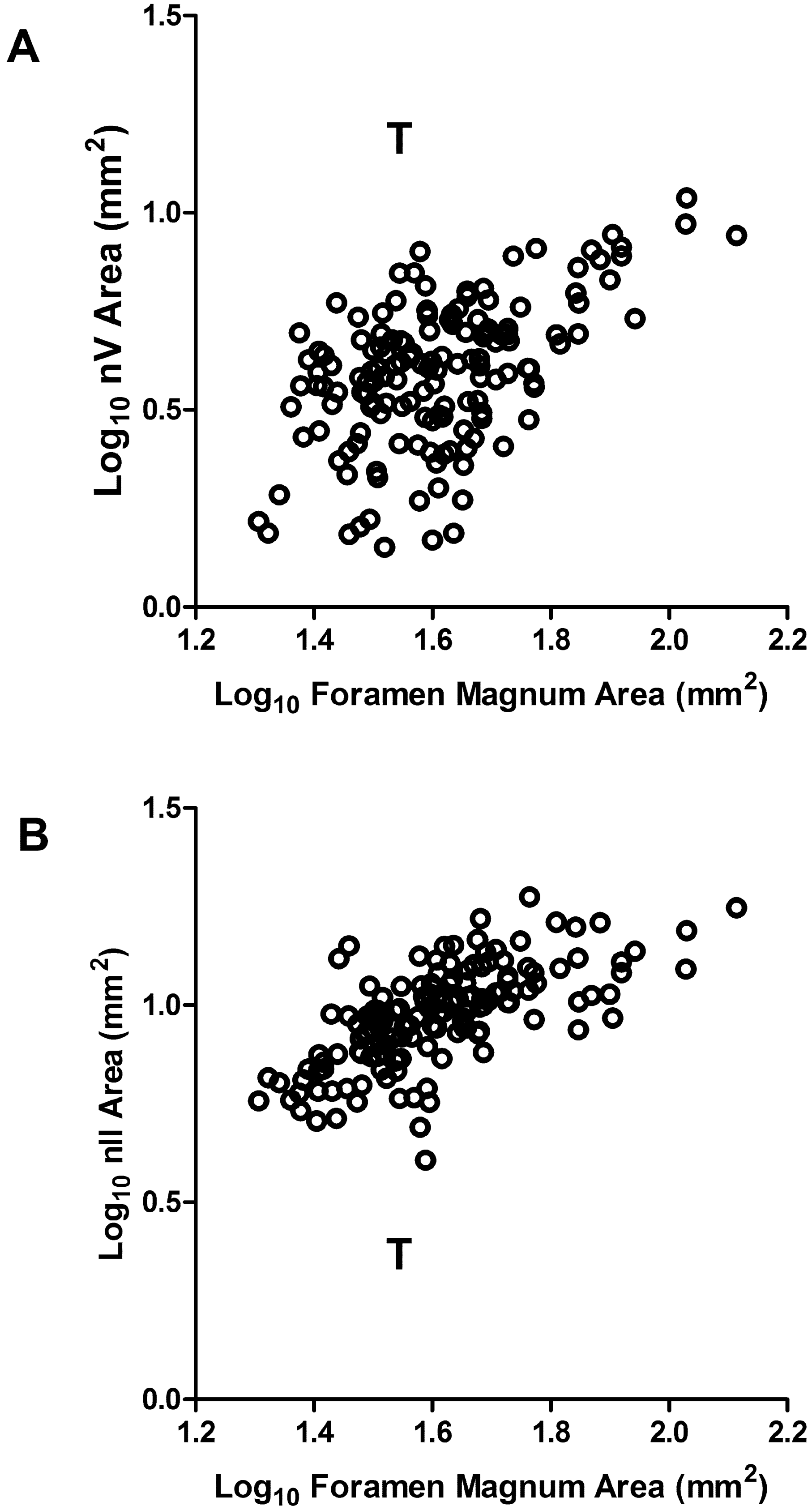

FIGURE 5. Scatterplots of the (A) maxillo-mandibular (nV) foramen and (B) optic foramen (nII) cross-sectional areas (mm^2) against foramen magnum cross-sectional area (mm^2). The maxillo-mandibular foramen is significantly larger (A) and the optic foramen is significantly smaller (B) in *Talpanas* ('T') relative to foramen magnum area.

The braincase of *Talpanas* is unique in several respects. Plots of the first three principal components from an analysis of eight measurements show that *Talpanas* is significantly different from other anseriforms in multivariate space (Fig. 4). Specifically, *Talpanas* has a wide nasofrontal hinge, interorbital region, braincase and postorbital processes combined with a short skull, narrow supraorbital process and lacrimal width, and a shallow braincase. Based on the position and size of the fossa for the nasal gland, which demarcates the lateral border of the orbit (Witmer 1995), the eyes were small and laterally displaced (Fig. 1) compared with other anatids. *Talpanas* lacks the fenestra on either side of the foramen magnum (fonticulus occipitalis) characteristic of many anatids, but these are absent in a number of species and may even be individually variable.

The most unusual aspects of *Talpanas* concern the relative size of the foramina associated with the optic (nII) and trigeminal (nV) nerves as shown by the cross-sectional area of the maxillo-mandibular (M-M) foramen and the optic foramen. The cross-sectional area of the M-M foramen, the primary exit point of the trigeminal nerve, is significantly larger in *Talpanas* relative to skull length and foramen magnum area than in any other anseriform (Fig. 5A). In contrast, the relative cross-sectional area of the optic foramen is significantly smaller in *Talpanas* than in other anseriforms (Fig. 5B). Thus, *Talpanas* has both the smallest optic foramen and largest trigeminal foramen of any anseriform examined.

Conclusions

The braincase of *Talpanas* is much wider and shallower for its length, the tarsometatarsus is extremely stout for its length and, most remarkably, the trigeminal system is grossly enlarged and the visual system greatly reduced compared with other anseriforms. Because of these unique specializations and the limited knowledge of the rest of the skeleton, the relationships of *Talpanas* to other anseriforms are as yet uncertain. The braincase lacks the inflated nasofrontal region typical of geese (*Branta*, *Anser*), which suggests that *Talpanas* was not derived from the Anserini.

Fossil birds have been found on Kauai only in two areas, the lake deposits where the remains of *Talpanas* were found (Burney *et al.* 2001) and the adjacent Makawehi dunes (Olson & James 1982), where no remains of *Talpanas* have been recovered. The dunes were hot, dry, open areas with strand vegetation, although with forest nearby. The lake deposits, on the other hand, although very close to the coast, were surrounded by mixed forest (Burney *et al.* 2001). Even here, *Talpanas* was very rare, the minimum number of individuals recovered being only two. The preferred habitat of the bird was probably moist, closed canopy forest with abundant litter, so that the species may have been more abundant in wetter areas at higher elevation.

The relatively stout and short tarsometatarsus combined with a lack of large muscle scars suggests that *Talpanas* was not a swimmer, but a graviportal terrestrial bird that most likely was flightless. Vision is critical for flight in birds because it is the only sense that can provide spatial information at sufficient resolution and speed to guide movement through the air. Furthermore, flightless birds in general have relatively small eyes compared with their volant relatives (Ritland 1982; Brooke *et al.* 1999; Martin *et al.* 2007). Therefore, the reduced visual abilities implied by the small orbits and optic foramen of *Talpanas* suggest that the bird was unlikely to have been capable of flight. Flightlessness has evolved independently numerous times in waterfowl (Feduccia 1999), particularly those isolated on islands, including the Hawaiian archipelago (Olson & James 1982, 1991), so it would not be unusual if another species had evolved flightlessness.

Flightlessness and reduced visual abilities suggest that *Talpanas* may have been nocturnal or at least capable of activity at night as well as day. In general, nocturnality in birds is associated with an increase in eye diameter (Hall & Ross 2007), as in owls and nightjars, but relatively smaller eyes do occur in at least two nocturnal and flightless taxa: kiwis (*Apteryx* spp.) and the parrot *Strigops habroptilus* (Ritland 1982; Martin *et al.* 2007). Likewise, other nocturnally active or fossorial vertebrates that do not rely on vision, such as echolocating bats, moles, and mole-rats, have relatively small eyes (Ritland 1982) and poorly developed visual systems (Catania 2000; Crish *et al.* 2006; Nemec *et al.* 2008). Thus, the reduction in size of the optic foramen and the orbits together suggest both flightless and nocturnal habits in *Talpanas*.

Although the holotypical cranium did not have an associated beak, the divergence of the palatines suggests that the base of the beak was relatively broad. Although its overall shape is unknown, the beak was likely the primary means of searching for and detecting prey, based on the enlargement of the trigeminal foramen. The trigeminal nerve, which passes through the foramen, receives somatosensory input from receptors on the face and in the oral cavity and, in some species, also receives input from infrared-receptors, electroreceptors and magnetoreceptors (Butler & Hodos 2005). In fact, the platypus, which is well known for its electroreceptive abilities (Pettigrew 1999), shares with *Talpanas* a grossly enlarged trigeminal nerve (Home 1802). This raises the intriguing possibility that *Talpanas* may have relied on more than simple tactile input in prey detection.

The only anatids approaching *Talpanas* in the enlargement of the trigeminal foramen are the stiff-tail ducks of the tribe Oxyurini, which feed mainly on small aquatic invertebrates taken when dabbling on the surface or while diving underwater (Brua 2001). Unlike other ducks with similar diets, stiff-tail ducks do not appear to use vision to locate prey when diving. Instead, they insert the bill into the substrate and move the head back and forth in lateral arcs (Tome & Wrubleski 1988) and appear to rely on tactile cues. Despite this apparent reliance on somatosensory input in stiff-tail ducks, they have not undergone a reduction in the visual system, so whatever *Talpanas* was doing was unique.

Based on the morphology of the holotype and paratypes, we conclude that *Talpanas* was likely a nocturnal, flightless duck that relied primarily upon somatosensory cues for foraging and prey capture. Olfaction may also have played a role, but the inferred massive size of the trigeminal nerve suggests that somatosensation was preeminent in foraging. As a result of its probable flightless condition and reduced orbits and optic foramen size, *Talpanas* may be viewed as a duck that evolved into a kiwi-like niche on Kauai. That is to say, a nocturnal, flightless species that foraged using non-visual cues (olfactory, somatosensory or a combination thereof).

Acknowledgments

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