

An extinct species of tooth-billed pigeon (*Didunculus*) from the Kingdom of Tonga, and the concept of endemism in insular landbirds

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Abstract

The tooth-billed pigeon *Didunculus strigirostris* lives on three islands in Western (Independent) Samoa. A larger, extinct species, *Didunculus placopedetes*, is described from bones recovered in late Quaternary cave deposits on `Eua, Kingdom of Tonga. Also referred to *D. placopedetes* are bones from archaeological sites on the larger Tongan island of Tongatapu and the smaller, lower islands of Lifuka, Ha`ano, `Uiha and Ha`afeva. As with so many other landbirds in Polynesia, the extinction of *D. placopedetes* occurred since the arrival of people and presumably was due to human impact. The peopling of Tonga is why the genus *Didunculus* is considered to be endemic to Samoa. The biogeographic implications of the new data on *Didunculus* are not unique; human activities have reduced or eliminated the natural range of nearly every genus and species group of Polynesian landbird. The reduced ranges of surviving taxa have created a situation (herein called 'pseudo-endemism') where a taxon that seems today to be endemic to a restricted area (often one or two islands) was much more widespread at first human arrival. As the prehistoric record of insular birds improves in the Pacific and elsewhere, the list of pseudo-endemic taxa will continue to grow.

Introduction

The tooth-billed pigeon *Didunculus strigirostris* occurs on the islands of Savai`i, Upolu and Nu`utele in Western Samoa. Ever since its scientific discovery (Strickland, 1844; Jardine, 1845; Peale, 1848), *D. strigirostris* (Samoan name *manume`a*) has been regarded as one of the South Pacific's most spectacular and unusual birds (Bennett, 1863, 1864; Ramsay, 1864; Wallace, 1865; Whitmee, 1874, 1875; Mayr, 1941, 1976). In particular, this large, colourful pigeon has a very stout bill with a hooked and pointed culmen and a 'toothed' gonyx. The supposedly parrot-like features of the jaw and tongue of *Didunculus* are convergent, however, and do not indicate a closer relationship to parrots than in any other columbid (Burton, 1974). An inhabitant of primary and secondary forests at elevations of up to 1350 m (duPont, 1976, p. 72), the total population of *D. strigirostris* was estimated at about 1600–2400 birds on Upolu and 3200–4800 on Savai`i (Beichle, 1987, 1991). I heard two individuals of *D. strigirostris* on the tiny Nu`utele Island on 10 April 1999, part of a population or subpopulation that probably is <20 individuals (Freifeld, Steadman & Sailer, 2001). In spite of some protection from hunting and the establishment of national parks (Merlin & Juvik, 1985), deforestation threatens the future of *D. strigirostris* (Beichle, 1987; Evans, 1992).

The first purpose of this paper is to describe a new species of *Didunculus* from the Kingdom of Tonga. The second is to

examine the concept of endemism in landbirds of West Polynesia (Fiji, Tonga, Samoa and outliers; Fig. 1). This is necessary because the distribution and diversity of endemic Polynesian landbirds have been altered by massive human-caused extinctions over the past 3000 years (Steadman, 1995, in press).

Materials and methods

For 10 weeks in 1987–1989, my colleagues and I excavated 15 bone deposits in limestone caves and rock shelters on the large, high (87 km², elevation 325 m) southern Tongan island of `Eua (Pregill, 1993; Steadman, 1993, 1995; Koopman & Steadman, 1995; Fig. 2 herein). Most bones in these deposits represent the prey of barn owls *Tyto alba lulu* and post-date the arrival of humans on `Eua at c. 2850 calendrically calibrated years before present (cal BP). An exception is `Anatú ('Ground-Dove Cave'), a relatively dry cave near the southern tip of `Eua. The sediment sequence at `Anatú represents three distinct time intervals. Stratum I is the upper 40–60 cm of stratified, organic, dark brown sediment containing bones deposited by both humans and barn owls. Unlike the underlying strata, it contains cultural features, artefacts, ash, charcoal and bones of non-native species (the chicken *Gallus gallus*, Pacific rat *Rattus exulans*, pig *Sus scrofa* and dog *Canis familiaris*). Four vertically concordant radiocarbon dates within stratum I range from 500–670 to

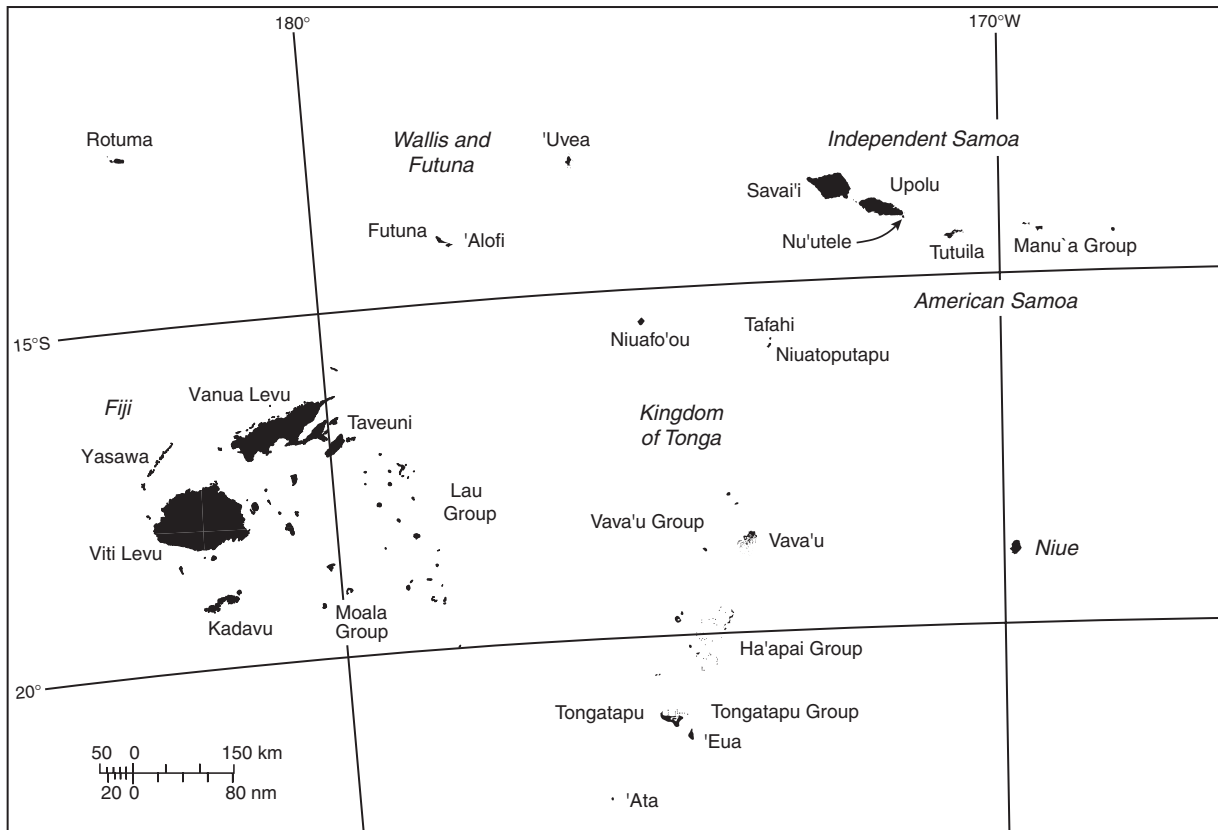


Figure 1 West Polynesian faunal region, showing major islands and island groups.

2710–2970 cal BP (95.4% confidence; Steadman, 1993, in press). Strata II and III consist of a combined 100–140 cm of poorly stratified, calcareous, yellowish orange sediment. Strata II and III are similar lithologically but are separated by a 2–5-cm-thick bed of calcite flowstone with three uranium-series dates that range from $60\,000 \pm 3000$ to $78\,800 \pm 2700$ years old. Strata II and III lack evidence of human presence and contain bones of native lizards, birds and bats, most species of which are now extinct on 'Eua.

A second site on 'Eua to yield bones of *Didunculus* is That Cave, a shallow but dry site on a limestone cliff above the north-eastern coast (Steadman, 1989, 1993; Pregill, 1993). Although lacking artefacts or other evidence of human activity, the bones in That Cave are < 2850 cal BP from their association with bones of *R. exulans*, which was introduced to 'Eua (and elsewhere in Oceania) by prehistoric people (Flannery *et al.*, 1988; Steadman & Kirch, 1990). The predominance of *R. exulans* bones suggests that *Tyto alba* was the primary or sole bone-accumulating agent at That Cave.

Bones of *Didunculus* have also been found in archaeological sites on the larger but lower (259 km², elevation 65 m) Tongan island of Tongatapu and on the four much smaller islands of Lifuka, Ha'ano, 'Uiha and Ha'afeva (1.8–11.4 km², elevation 11–16 m) in the Ha'apai group (Fig. 2). These sites consist of calcareous sands with rich, culturally derived deposits of pottery, shellfish and bones (Burley, 1994, 1999; Dickinson, Burley & Shutler, 1994, 1999; Burley, Nelson &

Shutler, 1995; Steadman, Plourde & Burley, 2002; Steadman, Pregill & Burley, 2002). The bones of *Didunculus* were found only in the lower strata of these sites, which date to c. 2850 cal BP.

The bones from all Tongan sites were obtained from vertically controlled excavations by sieving sediment through screens of 3.2 or 1.6 mm mesh. The specimens are catalogued at the Florida Museum of Natural History (UF). Modern comparative skeletons are from UF as well as the American Museum of Natural History (AMNH), the British Museum (Natural History) (BMNH), the National Museum of Natural History, Smithsonian Institution (USNM) and the University of Washington Burke Museum (UWBM). Osteological nomenclature generally follows Baumel *et al.* (1993).

Systematics

I refer the prehistoric bones to *Didunculus* rather than other genera of South Pacific columbids (*Ducula*, *Ptilinopus*, *Drepanoptila*, *Macropygia*, *Chalcophaps*, *Gallucolumba*, *Caloenas*) because of the following characteristics that are shared uniquely with *D. strigirostris*. *Mandible*: ramus deep and wide, with extensive fusion of individual skeletal elements; retroarticular process well developed; articulating surface and processus mandibularis medialis nearly parallel with, rather than perpendicular to, the ramus; unique location of

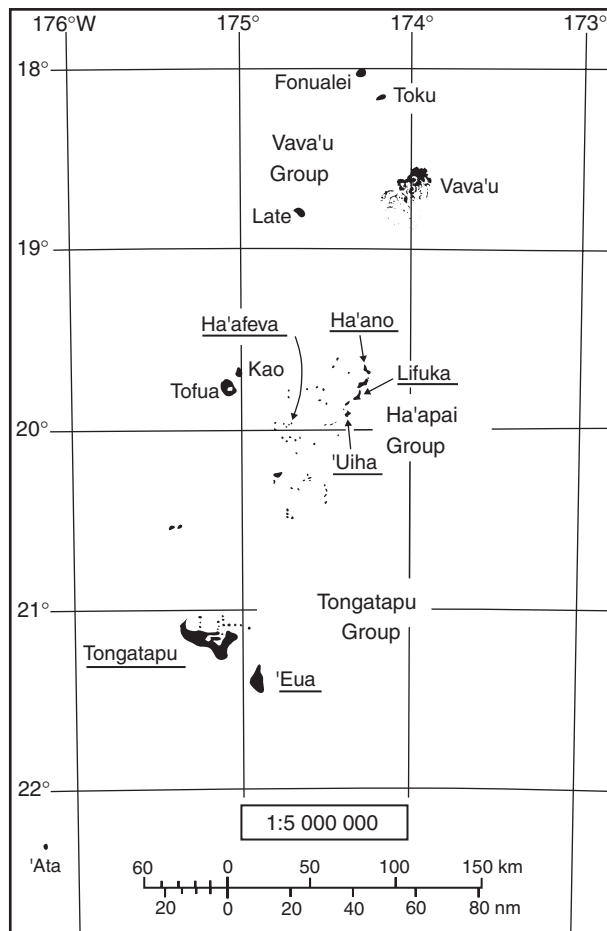


Figure 2 Kingdom of Tonga, excluding the northern volcanic outliers. Islands where bones of *Didunculus placopedetes* have been found are underlined.

small nutrient foramen on the medial surface of the ramus. *Coracoid*: humero-ventral portion of corpus coracoideus convex. *Scapula*: depression on the costal surface between tuberculum coracoideum and acromion relatively deep. Other post-cranial characteristics that distinguish South Pacific genera of columbids, some first reported by Steadman (1992), are given below under Comments.

***Didunculus placopedetes* sp. nov.**

Holotype

UF 50641, incomplete mandible. That Cave, 'Eua, Tonga. Collected by D. W. Steadman, V. C. Carter and J. G. Stull on 26 November 1988.

Paratypes

That Cave, 'Eua: UF 50237, 50272, 51166, 51175 (coracoid, ulna, hallux, pedal phalanx). 'Anatu, 'Eua: UF 50480, 51762, 51765, 51881, 51969, 51978, 52014, 52015, 52061,

52309, 52325, 52484, 52505, 52541, 52618, 52696, 52744, 52777, 52867, 52869, 52877, 53093, 53102, 53657, 53659 (three coracoids, three scapulae, furcula, humerus, ulna, radius, ulnare, carpometacarpus, two manus phalanges, tibiotarsus, five tarsometatarsi, five pedal phalanges). Tongoleleka site, Lifuka: UF 57364–57366, 58001, 58643 (quadrate, two coracoids, ulna, tibiotarsus). Pukotala site, Ha'ano: UF 57381 (ulna). Vaipuna site, 'Uiha: UF 57363, 58942 (coracoid, humerus). Mele Havea Site, Ha'afeva: UF 56141, 57975 (scapula, ulna). Ha'ateiho site, Tongatapu: UF 59494, 59624, 59638 (scapula, ulna, radius). Nearly all of these specimens are incomplete.

Diagnosis

Didunculus placopedetes differs from *D. strigirostris* in being 20–25% larger in linear skeletal measurements (Table 1) and as follows. *Mandible* (Fig. 3): in dorsal aspect, medial tip of processus mandibulae medialis oriented more parallel (less perpendicular) to os dentale. *Coracoid* (Fig. 4): facies articularis sternalis proportionately deeper, especially in the medial half. *Scapula* (Fig. 5): less medio-lateral expansion (relative to shaft) of facies articularis clavicularis. *Humerus* (Fig. 5): attachment of latissimus dorsi posterioris raised higher above the plane of corpus humeri; crista pectoralis forms a more obtuse angle with corpus humeri. *Radius*: sulcus ligamentum more convex. *Tibiotarsus*: medial margin of corpus tibiotarsi less rounded; sulcus musculo fibularis is oriented more laterally (less anteriorly).

Age

Holocene and late Pleistocene: The specimens from That Cave date to <2850 cal BP by being associated with bones of introduced *R. exulans*. Specimens from 'Anatu are from three strata of different ages: layer I (three specimens) is <2850 cal BP (associated with radiocarbon-dated cultural deposits); layer II (11 specimens) is >2850 cal BP but <60 000–80 000 years old; and Layer III (six specimens) is >60 000–80 000 years old. Five other specimens are from mixed strata II/III. All specimens from Ha'apai are <2850 cal BP and culturally associated. *Didunculus placopedetes* became extinct after people colonized Tonga about 2850 years ago. It is not known from historic (18th or 19th century) specimens or observations, and probably died out in prehistoric times (Steadman, 1993).

Etymology

The name *placopedetes* is from the Greek words *plakos* (f., anything flat and wide, plate, tablet) and *pedetes* (m., leaper) (Brown, 1956, pp. 467, 616). The phrase 'plate jumper' refers to the complex geology of the region once occupied by *Didunculus*, with Tonga being on the Australian plate, whereas Samoa lies on the Pacific plate. The name *placopedetes* is a masculine noun in apposition to *Didunculus*.

Table 1 Measurements (in mm) of skeletal elements of *Didunculus*, with mean, range and sample size

	<i>D. placopedetes</i>	<i>D. strigirostris</i>
<i>Mandible</i>		
Width at articulation	6.1 1	5.0 4.6–5.5 2
Length of articular surface	5.9 1	5.0 1
Minimum depth in front of articulation	5.3 1	4.1 3.8–4.4 3
Depth at bend of ramus	6.7 1	5.6 5.1–6.2 2
Width at bend of ramus	2.3 1	1.4 1.3–1.5 2
<i>Coracoid</i>		
Total length	41.8 1	36.8 35.6–38.0 2
Length from sternal end to cotyla scapularis	29.8 29.3–30.2 2	26.8 25.6–28.1 2
Length through facies articularis humeralis and cotyla scapularis	9.4 8.8–9.8 4	7.4 1
Least width of shaft	4.4 4.2–4.9 4	3.8 3.6–4.0 2
Least depth of shaft	3.9 3.8–4.2 4	3.2 3.0–3.5 2
<i>Scapula</i>		
Width of facies articularis humeralis	4.8 4.6–5.1 4	4.4 4.3–4.5 2
Width through facies articularis humeralis and collum scapulae	8.6 8.1–9.1 5	7.2 7.1–7.4 2
Minimum width of shaft	3.6 3.3–3.9 5	2.8 2.8 2
<i>Humerus</i>		
Depth at distal end of latissimus dorsi posterioris attachment	5.4 5.3–5.5 2	4.6 4.4–4.8 2
<i>Radius</i>		
Distal width	5.2+ 1	4.6 4.2–5.0 2
Least depth of shaft	2.6 2.5–2.6 2	1.9 1.8–2.0 2
<i>Tibiotarsus</i>		
Depth at distal end of crista fibularis	4.0 1	3.6 3.4–3.7 4

Table 1 Continued

	<i>D. placopedetes</i>	<i>D. strigirostris</i>
Width at medio-distal papilla	6.6 1	4.5 4.4–4.6 2
<i>Tarsometatarsus</i>		
Minimum width of shaft	5.2 1	3.3 3.1–3.4 5
Depth of shaft at middle of fossa metatarsi	3.4 1	2.5 2.4–2.7 5

Specimens of *D. placopedetes* are from the Tongan islands underlined in Fig. 2. Modern specimens of *D. strigirostris* are AMNH 205859 (Savai'i ♂), AMNH 205861 (Savai'i ♀), BMNH 1875.10.16.6 and 1952.3.50 (both 'Samoa' unsexed) and USNM 17793 ('Samoan Islands' ♀).

AMNH, American Museum of Natural History; BMNH, British Museum (Natural History); USNM, National Museum of Natural History, Smithsonian Institution.

Comments

In spite of its unusual bill, *Didunculus* resembles *Gallicolumba*, *Caloenas* and *Chalcophaps* in post-cranial osteology enough to preclude its recognition as a separate subfamily of the Columbidae. The following post-cranial characteristics, shared by *Didunculus*, *Gallicolumba*, *Caloenas* and

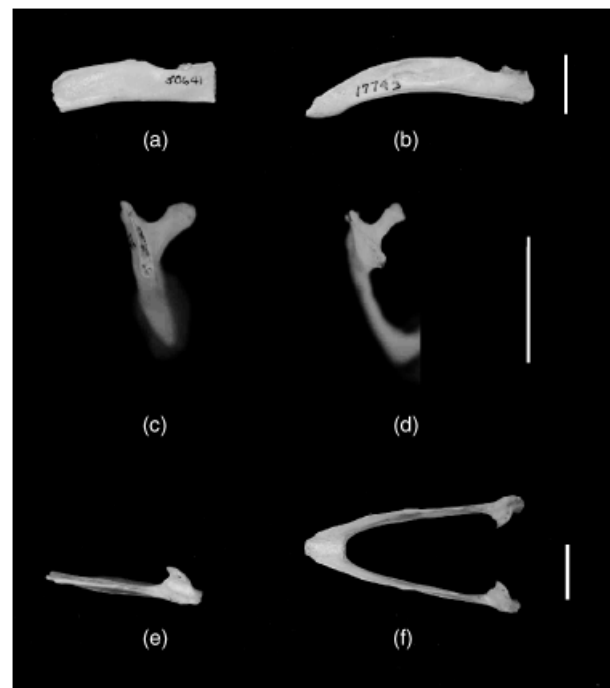


Figure 3 Mandible of *Didunculus* in lateral (a, b), posterior (c, d) and dorsal (e, f) aspects. (a, c, e) *Didunculus placopedetes*, new species, holotype, UF 50641, 'Eua, Tonga. (b, d, f) *Didunculus strigirostris*, USNM 17793, Samoa. Scale bars = 10 mm.

Chalcophaps, do not occur in other Polynesian columbid genera (*Ducula*, *Ptilinopus*, *Drepanoptila*, *Macropygia* or *Columba*). *Coracoid*: facies articularis humeralis large, with a deep depression between it and corpus coracoideus. *Scapula*: facies articularis humeralis more protrudent from corpus scapulae. *Humerus*: caudal surface of the distal portion of caput humeri with a distinct knob, impressio musculo coracobrachialis cranialis large. *All leg elements*: long relative to wing elements. *Tibiotarsus*: in posterior aspect, condylus medialis deep, in posterior or lateral aspect, condylus lateralis shallow. *Tarsometatarsus*: narrow overall,

foramina vascularia proximalia small, trochlea metatarsi medialis long relative to trochlea metatarsi lateralis.

The relationships of *Didunculus* were not studied by Sibley & Ahlquist (1990, pp. 421–426) or Johnson & Clayton (2000) in their molecular assessments of columbid phylogeny. Shapiro *et al.* (2002) proposed that *Didunculus* is the sister of a clade comprising *Goura*, *Caloenas*, *Pezophaps* and *Raphus*, and quite distinct from the clades containing *Gallinocolumba* or *Chalcophaps*. Pending further morphological and molecular study, the phylogeny of *Didunculus* is poorly resolved.

The cranial elements of *Didunculus* are the most robust and specialized among living Columbidae but are approached in robustness by such stout-billed species as *Trugon terrestris* (as first noted by Wallace, 1865) and *Henicophaps albifrons* of New Guinea, and *Reinwardtoena crassirostris* of the Solomon Islands. The most unusual osteological feature of *Didunculus* is the parrot-like, antero-posterior orientation of articulating surfaces on the quadrate and articular, which allows the 'sawing' movement of the mandible when slicing fleshy fruits (Beichle, 1987).

Discussion

Palaeoecology and extinction

In Samoa today, *D. strigirostris* eats primarily seeds from the fleshy, globular fruits of *Dysoxylum maota*, *D. samoense* and *D. huntii* [Meliaceae; Beichle, 1987; see Pennington & Styles (1975, pp. 504–507) for a morphological description of *Dysoxylum*]. The first two species are locally dominant trees in lowland forests, whereas *D. huntii* is often dominant in montane forests (Whistler, 1984, 1992). Of lesser importance as food to the tooth-billed pigeon are fruits of *Rhus taitensis* (Anacardiaceae), nutmegs *Myristica* spp. (Myristicaceae), *Faradaya powelli* (Verbenaceae) and mountain plantain cf. *Heliconia laurfao* (Musaceae), and tubers of wild yams *Dioscorea* sp. (Dioscoreaceae) (Stair, 1897; Watling, 1982; Beichle, 1987; Steadman & Freifeld, 1999). Except for the mountain plantain, congeners or conspecifics of all reported Samoan food plants also live on 'Eua, including

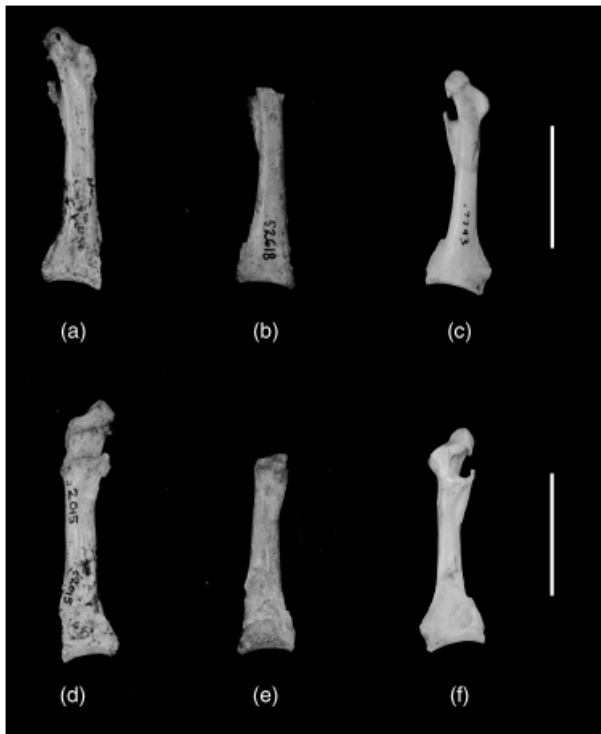


Figure 4 Coracoid of *Didunculus* in ventral (a–c) and dorsal (d–f) aspects. (a, b, d, e) *Didunculus placopedetes*, new species, paratypes, UF 52015 (a, d), UF 52618 (b, e), 'Eua, Tonga. (c, f) *Didunculus strigirostris*, USNM 17793, Samoa. Scale bars = 20 mm.

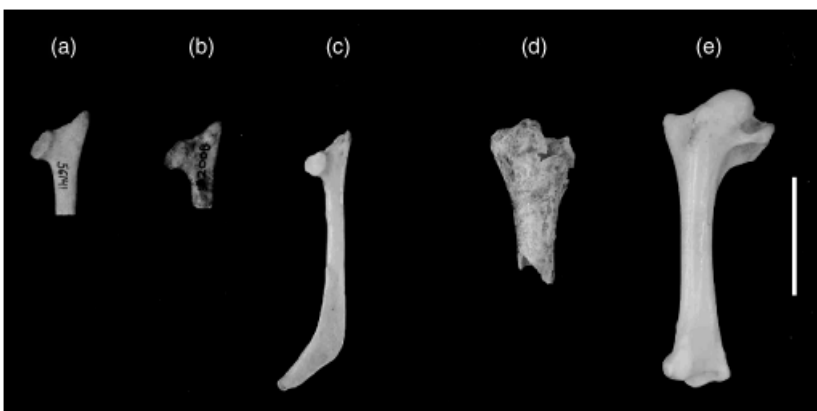


Figure 5 Scapula of *Didunculus* in lateral aspect (a–c) and humerus of *Didunculus* in anconal aspect (d, e). (a, b, d) *Didunculus placopedetes*, new species, paratypes, UF 56141 (a; Ha'afeva, Tonga), UF 52008 (b; 'Eua, Tonga), UF 52325 (d; 'Eua, Tonga). (c, e) *Didunculus strigirostris*, USNM 17793, Samoa. Scale bars = 20 mm.

two species of *Dysoxylum* (Yuncker, 1959; Drake *et al.*, 1996; McConkey, Meehan & Drake, 2004). No species of *Dysoxylum* occur today on Lifuka, Ha'ano, 'Uiha or Ha'afeva, four islands that lack mature forest because of widespread agriculture (Steadman, 1998). I am not sure of the status of *Dysoxylum* on Tongatapu; if it occurs there, it must be rare on this largely deforested island.

Didunculus placopedetes may have become extinct from some combination of habitat loss and predation from humans and other non-native species, these being the most frequently and logically invoked causes of extinction in islandbirds, whether in historic or prehistoric times (Diamond, 1985; Steadman, 1997a). In Samoa, the rarity of *D. strigirostris* dates at least to the 19th century (Bennett, 1863; Stair, 1897; Nicoll, 1904). Its scarcity in recent centuries probably is due mainly to deforestation, with selective cutting of *D. huntii* (Whistler, 1995) and hurricanes (Elmqvist *et al.*, 1994) being particularly harmful, as well as predation from humans and possibly rats and cats. That *D. strigirostris* survived in Samoa but *D. placopedetes* did not in Tonga may be because Samoa's two largest islands are much larger, higher, steeper and wetter than any islands in Tonga. These factors help to curb human impact on island biotas (Steadman & Martin, 2002; Rolett & Daimond, 2004).

Given the high similarity in landbird faunas among Fiji, Tonga and Samoa (Steadman, 1993), a form of *Didunculus*

Table 2 Chronology of indigenous, resident landbirds from 'Eua, Tonga

FAMILY Species	Pre- human record	Archaeo- logical record	Extant in 1988	Recorded elsewhere in T-S-F
HERONS				
<i>Egretta sacra</i>	–	X	X	TSF
<i>Nycticorax</i>	X	–	–	T
undescribed sp. ^b				
DUCKS				
<i>Anas superciliosa</i>	–	–	X	TSF
HAWKS				
<i>Accipiter cf. rufitorques</i> ^a	X	–	–	F
MEGAPODES				
<i>Megapodius alimentum</i> ^b	X	X	–	T
<i>Megapodius pritchardii</i> ^a	X	–	–	T
<i>Megapodius</i> undescribed sp. ^b	X	X	–	–
RAILS				
<i>Gallirallus</i> undescribed sp. ^b	X	–	–	t
<i>Gallirallus philippensis</i>	–	X	X	TSF
<i>Porzana tabuensis</i> ^a	–	X	–	TSF
<i>Porphyrio porphyrio</i>	–	X	X	TSF
PIGEONS AND DOVES				
<i>Gallicolumba stairi</i> ^a	X	X	–	TSF

Table 2 Continued

FAMILY Species	Pre- human record	Archaeo- logical record	Extant in 1988	Recorded elsewhere in T-S-F
<i>Didunculus placopedetes</i> ^b	X	X	–	Ts
<i>Ptilinopus porphyraceus</i>	X	X	X	TSF
<i>Ptilinopus perousii</i>	X	X	X	TSF
<i>Ducula</i> undescribed sp. ^b	X	X	–	Tf
<i>Ducula pacifica</i>	–	X	X	TSF
Undescribed genus and species ^b	X	X	–	T
PARROTS				
<i>Vini solitarius</i> ^a	X	–	–	TF
<i>Vini australis</i> ^a	X	X	–	TSF
<i>Electus</i> undescribed sp. ^b	X	X	–	T
BARN OWLS				
<i>Tyto alba</i>	–	X	X	TSF
SWIFTS				
<i>Collocalia spodiopygia</i>	–	X	X	TSF
KINGFISHERS				
<i>Halcyon chloris</i>	X	X	X	TSF
TRILLERS				
<i>Lalage maculosa</i> cf. <i>Lalage</i> sp. ^{a/b}	X	X	X	TSF
	–	X	–	TS
MONARCHS				
<i>Clytorhynchus vitiensis</i> ^a	X	X	–	TSF
<i>Myiagra sp.</i> ^a	X	X	–	SF
WARBLERS				
cf. <i>Cettia</i> sp. ^{a/b}	X	–	–	F
THRUSHES				
<i>Turdus poliocephalus</i> ^a	X	X	–	TSF
STARLINGS				
<i>Aplonis tabuensis</i>	X	X	X	TSF
HONEYEATERS				
<i>Myzomela cardinalis</i> ^a	X	X	–	TSf
<i>Foulehaio carunculata</i>	X	X	X	TSF
WHITE-EYES				
Genus uncertain ^b	X	–	–	T
Total species ^a	10–12	7–8	0	–
Total species ^b	9–11	6–7	0	–
Total species ^{a/b}	21	14	0	–
Total species	27	26	13	–
# sites/# bird bones	1/401	14/918	–	–

Pre-human record ≥ 2850 cal BP (strata II, III of 'Anatú); archaeological record = 2800–200 yr BP (15 sites); T-S-F, Tonga–Samoa–Fiji; t-s-f, records of allospecies in Tonga–Samoa–Fiji. From Steadman (in press), which includes improvements in the data presented in Steadman (1993).

^aExtirpated species.

^bExtinct species.

may also have occurred once in Fiji, where the prehistoric record of birds is growing (Worthy, 2000, 2001; Steadman, in press) but is not nearly as extensive as in Tonga. Five species of *Dysoxylum* live on the large Fijian island of Viti Levu (Kirkpatrick & Hassall, 1985), although the genus does not occur east of the Fiji–Tonga–Samoa region.

Distributional deception: true endemism versus pseudo-endemism

The bones from `Anatu portray the avifauna of `Eua both before and after the arrival of people. Human colonization depleted the Tongan avifauna more than any climatic, tectonic or biological event of the past *c.* 100 000 years (Steadman, 1993). Of the 21 species of extinct or extirpated landbirds recorded from `Eua (Table 2), the nearest records (whether prehistoric or modern) of conspecifics or allospecies are from elsewhere in Tonga (17 species), Fiji or Samoa (three species), or unknown (one species). If the fossil record were complete, I believe that each of these taxa, except for the flightless rail *Gallirallus* undescribed sp., would be found to have been widespread in Tonga prehistorically. From Tongatapu and the Ha`apai group, in spite of having less extensive fossil coverage than `Eua, 14 of these 21 species have already been found in prehistoric sites.

Whether in Tonga or elsewhere in Oceania, many if not most volant species of insular birds have distributional gaps that lack an obvious geographical or ecological basis. I regard these gaps, including 'checkerboard' distributions (Diamond & Marshall, 1976, 1977; Sanderson, Moulton & Selfridge, 1998), to be more likely because of human activities than natural processes. The gaps become larger as more island populations are lost anthropogenically, until a species is confined to a few islands or even a single island. Species with such highly limited modern ranges, but that would have much broader ranges if not for people, may be said to be 'pseudo-endemic' to their modern range. The species that survive on an island or two are the lucky ones. For most species of Polynesian landbirds, all populations are gone; the extinction process is complete.

Pseudo-endemism can operate at any taxonomic or geographic level. The genus *Didunculus*, for example, is pseudo-endemic to Samoa because it survives only there but occurred prehistorically in Tonga. The species *D. strigirostris* may be pseudo-endemic to the three Samoan islands where it survives because it probably used to live also on the nearby Apolima and Manono Islands, as well as on Tutuila and other islands in American Samoa. Another pseudo-endemic species is the megapode *Megapodius pritchardii*, which is known in recent centuries only from the volcanic island of Niuafo`ou (34.9 km², 260 m elevation) in northern Tonga, although its bones have been found on five limestone islands in central and southern Tonga ranging 1.8–87 km² in area and from 10–325 m in elevation (Steadman, 1993, in press). Many other examples of pseudo-endemism have also been discovered among landbirds in the Hawaiian Islands (James & Olson, 1991; Olson & James, 1991), New Zealand (Worthy & Holdaway, 2002), Micronesia (Steadman, 1999),

the West Indies (Pregill, Steadman & Watters, 1994, Williams & Steadman, 2001) and elsewhere.

Conclusions

Before human arrival, a 'tooth-billed' pigeon *Didunculus* occurred in Tonga as well as in Western Samoa. Bones of *Didunculus* should be sought in Fiji as well. In Tonga, Fiji or Samoa, where inter-island distances seldom exceed 100 km, any volant species believed to be a single-island endemic is suspect. It is likely to be pseudo-endemic, with a range that has been reduced during the nearly 3000 years of human activity.

Island size is regarded as an important factor in inter-specific differences in the distribution of columbids (Diamond & Marshall, 1976; McNab, 1994). Before the period of human impact, however, island size had little influence on the distribution of Polynesian species of *Gallinolumba*, *Didunculus*, *Caloenas*, *Ducula* or *Ptilinopus* (Steadman, 1997b). The living species of *Didunculus* occurs on small (1.05 km², elevation 200 m) Nu`utele Island (Freifeld *et al.*, 2001) as well as two much larger, higher Samoan islands (each > 1000 km², > 1500 m elevation). The larger, extinct *D. placopedetes* used to occur on Tongan islands at least as small as Ha`afeva (1.8 km², elevation 11 m).

Distinguishing pseudo-endemism from true endemism gives us a much more realistic picture of avifaunas as they would exist without human influence. Documenting the natural ranges of insular species is not only of interest in palaeontology and historic biogeography. These data are also important for providing new possibilities for translocating populations of endangered species (Franklin & Steadman, 1991; Steadman, 1999; Williams & Steadman, 2001), whether in the Pacific, West Indies or any other island setting.

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