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A new species of extinct scops owl (Aves: Strigiformes: Strigidae: *Otus*) from São Miguel Island (Azores Archipelago, North Atlantic Ocean)

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Abstract

The extinct São Miguel Scops Owl *Otus frutuosoi* **n. sp.** is described from fossil bones found in Gruta de Água de Pau, a volcanic tube in São Miguel Island (Azores Archipelago, North Atlantic Ocean). It is the first extinct bird described from the Azores and, after the Madeiran Scops Owl (*O. mauli* Rando, Pieper, Alcover & Olson 2012a), the second extinct species of Strigiformes known in Macaronesia. The forelimb elements of the new taxon are shorter, the hindlimb elements are longer, and the pelvis is shorter and broader than in the Eurasian Scops Owl (*O. scops* Linnaeus). The new species differs from *O. mauli* in the smaller size of many of its bones, especially the ulna and tibiotarsus. Its measurements (estimated weight, wing area, and wing loading, and the ratio of humerus + ulna + carpometacarpus length/femur length) indicate weak powers of flight and ground–dwelling habits. The latest occurrence of the new species, as evidenced by a radiocarbon date of 1970±40 BP from bone collagen, indicates a Late Holocene extinction event subsequent to 49 cal BC, and was probably linked to human arrival and subsequent habitat alterations.

Key words: AMS 14C, extinction, evolution of island biotas, Macaronesia, *Otus frutuosoi* **n. sp.**, Quaternary, São Miguel Scops Owl

Introduction

Archipelagos have provided useful models for the study of colonization and adaptive radiation. The diversity and the high level of endemism in some historically known groups of island vertebrates are well known, examples being the honeycreepers of Hawaii and the anoles of the Antilles (Pratt 2005; Losos 2009). However, Quaternary faunas on oceanic islands indicate that current levels of autochthonous biodiversity are only poor remnants of the original faunas (e.g., Olson & James 1982; Worthy & Holdaway 2002; Steadman 2006; Turvey 2009; Hume & Walters 2012). In most cases the impoverishment took place after human arrival in the islands, so that extant taxa are only relicts of a greater past diversity with most of the original members now being extinct. Extinction episodes have been dramatic in remote islands, such as those of Polynesia, where most of the original avifauna became extinct during the last few millennia (Olson & James 1982; Steadman 2006). Discovering and describing the pristine biodiversity of oceanic archipelagos is essential for understanding and calibrating human impacts on island ecosystems.

The volcanic Azores Islands constitute the most isolated archipelago of Macaronesia, and are spread over a distance of c. 600 km in the North Atlantic Ocean. They are located c. 1350 km west of Portugal and 1700 km from America, and consist of nine main islands, ranging northwest to southeast roughly between 37º to 40º N and 25º to

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31º W. They can be divided into a western group (Corvo and Flores), a central group (Graciosa, Faial, São Jorge, Pico and Terceira) and an eastern group (São Miguel and Santa Maria) (Figure 1). The age of the islands ranges from 8.12 My (Santa Maria) to 0.25 My (Pico) (Nunes 1999).

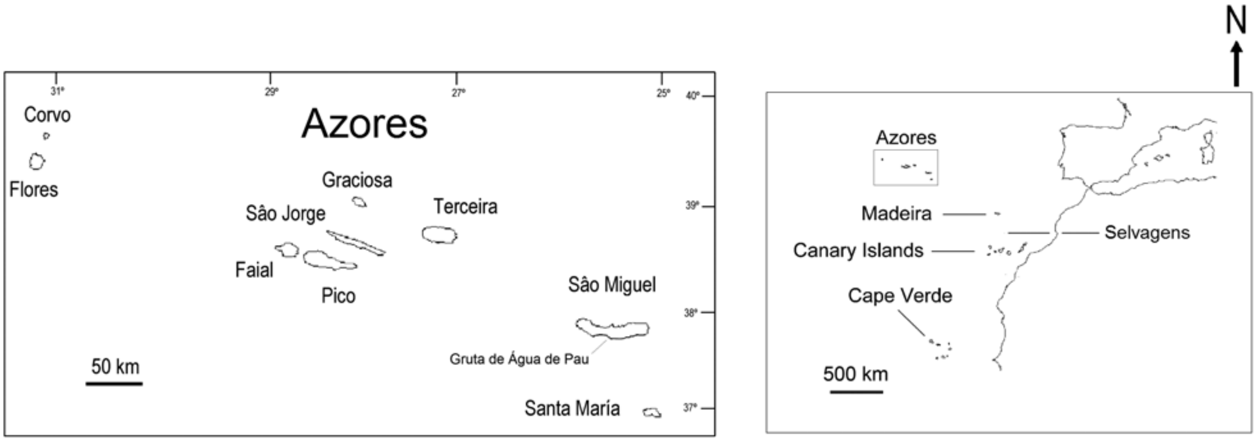

FIGURE 1. Geographic position of Macaronesia, showing the Azores Archipelago. The bones described in this paper were collected on São Miguel at Gruta de Água de Pau.

Because of their isolation, the Azorean native terrestrial vertebrate fauna consists only of bats and birds. The existing autochthonous resident bird fauna comprises around 34 species, two of them being endemic to the archipelago: a passeriform, the Azores Bullfinch or Priolo *Pyrrhula murina* Godman, and a procellariform, the Monteiro`s Storm Petrel *Oceanodroma monteiroi* Bolton (Borges *et al.* 2010). The sole bird of prey currently present on the archipelago is the Azorean race of Common Buzzard *Buteo buteo rothschildi* (Swann), whose biology and diet has been studied by Schäfer & Fraga (2002). No remains of extinct birds have been published from the Azores until now. Le Grand (1993) claims, without documentary evidence, the extinction of seven species in the archipelago (*Falco peregrinus* Tunstall, *Pterodroma* sp., *Columba* sp., *Gallinula chloropus* (Linnaeus), *Fulica atra* Linnaeus, *Anas platyrhynchos* Linnaeus and *Anas crecca* (Linnaeus). Bones of *Pterodroma* sp., *Columba* sp., and a single bone of *Falco* sp. (of the size of a male *Falco peregrinus*) were obtained in 2001 and 2003 in Santa Maria by Pieper (unpublished data), and bones of the first two genera were later obtained on the same island in 2011 by Rando and Alcover. At least three of the species considered as extinct by Le Grand (1993) currently breed on the islands (*Gallinula chloropus* regularly, and *Anas platyrhynchos* and *Fulica atra* sporadically). Monteiro *et al.* (1996) report that seabirds have largely disappeared from the main islands, where they once occurred in large numbers. Newton (2003) claims that the Azores almost certainly held more endemic land birds when people first arrived than they now do.

Given the large number of islands in the archipelago (nine main islands) and their degree of isolation from the mainland and each other, the low number of extant endemic birds (two species) contrasts with that of the other Macaronesian archipelagos, such as Madeira (with two main islands and four extant endemic birds), Canary Islands (with seven main islands and five extant endemic birds) and Cape Verde (10 main islands and six extant endemic birds). In addition, several extinct endemic species from the Canary Islands and Madeira archipelagos are known. Pieper (1985) reported the extinction of several endemic birds (at least three flightless rails, a quail, and several passerines) including the Madeira Scops Owl *Otus mauli* Rando, Pieper, Alcover & Olson, all from Quaternary sites in Madeira and Porto Santo. Six endemic extinct birds have been described so far from Quaternary sites of the Canary Islands: the Lava Shearwater *Puffinus olsoni* McMinn, Jaume & Alcover 1990; the Dune Shearwater *P. holeae* Walker, Wragg & Harrison 1990; the Canarian Quail *Coturnix gomerae* Jaume, McMinn & Alcover 1983; and three passerines, the Trias's Greenfinch *Carduelis triasi* Alcover & Florit 1987; the Slender–billed Greenfinch *C. aurelioi* Rando, Alcover & Illera 2010, and the Long–legged Bunting *Emberiza alcoveri* Rando, López & Seguí 1999. The Canary Islands Oystercatcher *Haematopus meadewaldoi* (Bannerman), which disappeared in the 20th century (Martín & Lorenzo 2001), should be added to the extinct fauna. These background data suggest that a higher avian diversity should have been present during the Holocene in the Azores Islands. The first human settlement in the Azores took place in the fifteenth century (Newitt 2005), so it is expected that the main ecological alterations of the Holocene occurred after that.

The aim of this paper is to describe an endemic species of scops owl (genus *Otus*), the first extinct bird described from the Azores Archipelago. The limb bone proportions of the new taxon are here compared with other extinct and extant Strigiformes and are used to attempt to infer lifestyle. Morphological and radiocarbon data are used to discuss the causes and chronology of the extinction of the new taxon.

Material and methods

Paleontological fieldwork in volcanic tubes of São Miguel Island (eastern Azores) in search of vertebrate remains resulted in the discovery of bird bones in Gruta de Água de Pau, a cave in the south side of the island (Figure 1). Most of the bones, some slightly mineralized, had been washed by flowing water within the cave onto a flat area, c. 6 m^2, where some small pieces (c. 1 cm in diameter) of pumice were also deposited. The remains of one owl specimen were found in association, although unfortunately they were fragmented (probably as a result of trampling by previous visitors). Several bones of small passeriforms were also obtained in the same place.

The fossil specimens are housed in the collections of: Museu Carlos Machado (MCM, 21 isolated bones and an associated skeleton), Ponta Delgada, São Miguel; Department of Zoology of the University of La Laguna at the Canary Islands (DZUL, two bones); and Institut Mediterrani d'Estudis Avançats at the Balearic Islands (IMEDEA, two bones). We compared the fossil material with recent skeletons of *Otus scops* and related species housed in the IMEDEA. Measurements from limb bones of additional species of scops owls, other extant taxa, and extinct owls from Hawaii are from specimens in the IMEDEA and in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), from a specimen of *Sceloglaux* held at the Canterbury Museum (Christchurch) and from *Sceloglaux* bones housed at the Te Papa Tongarewa – National Museum of New Zealand, Wellington (NMNZ). Comparative material used is listed in the Appendix. Anatomical terminology follows Baumel (1993) and Livezey and Zusi (2006). We took measurements with digital calipers to the nearest 0.01 mm, following the criteria of Campbell and Bocheński (2010), although all the measurements were rounded to 0.1 mm. In addition, the length from the cranial border of the *processus marginis caudalis* to the cranial border of the *ala praeacetabularis ilii* (LS) was measured.

Mensural differences between the new *Otus* and *O. scops* Linnaeus were evaluated using a multivariate analysis of variance (MANOVA) on the length of limb bones (humerus, ulna, carpometacarpus, and femur). Bones with only three lengths (tarsometatarsus and tibiotarsus) were compared with a non-parametric test (Mann–Whitney U tests).

In order to estimate the weight of the new taxon we used the expression $Y = 0.56\ X^{0.342}$, where the femur length is the independent variable (X), and the estimated weight of the bird (Y) is the dependent variable (Olmos *et al.* 1996). In order to calculate wing area (to estimate wing loading) we photographed six expanded wings of scops owl (*Otus scops*) at the same distance and orientation. The areas were calculated using the program ImageJ V 1.45s (Rasband 1997). We analyzed wing surface and loading of the new species following the methodology used by Olson (1975), that is, bones of *O. scops* were situated in their anatomical position on an expanded wing. By reducing this photographically to the size of the wing bones of the new species a maximum estimate of wing surface was calculated. In addition, we attempted to assess flight capability with a comparison of the ratios of combined humerus, ulna, and carpometacarpus lengths to femur length (Millener 1989; Millener & Worthy 1991; Rando *et al.* 1999, 2010).

The proportions of hind- and forelimb bones were used to infer the habitat use of the new taxon. We performed a Principal Component Analysis (PCA) to summarize the segregation of taxa and to explore morphological patterns in relation to wing and leg bone proportions among scops and other owls. All statistical analyses were performed with SPSS 18.0 (PASW Statistic 18 2011).

To obtain chronological information about the new taxon, we dated bones by accelerator mass spectrometer radiocarbon analysis (AMS ^{14}C). The collagen of some bones of the new taxon (a right femur without the proximal end, a right femur without the distal end, proximal half of a left femur; proximal half of a left tibiotarsus, and a distal end of a left humerus, with a total weight of 0.54 g) was extracted at the Radiocarbon Laboratory of the Royal Institute for Cultural Heritage (Brussels, Belgium) and directly dated. The ^{14}C age was derived from a sample of two or more individual birds from the same stratigraphic horizon. Because it was determined from a mixture of two or more real-aged specimens, the ^{14}C age represents an intermediate age for the actual span of ages represented in the original sample. We use it conservatively to estimate when the species was present on São Miguel Island. We expressed the ^{14}C age as 2σ intervals (i.e., p = 95.45%), and its interpretation is based exclusively on the extreme values of this interval (in order to have a p > 95.45% that the true age of the dated material is more recent than the lower extreme value of the 2σ interval, and more ancient than the upper extreme of this interval) (Zilhão 2001; Bover & Alcover 2003). The extinction of this taxon therefore must postdate the lower extreme value of the 2σ interval. We present dates from the calibration of radiometric results as 'cal BP', and calibrate the radiocarbon date following the program OxCal. V4.1.7 using IntCal09 calibration curve (ORAU 2012).

Results

Systematic Paleontology

Order Strigiformes Wagler

Family Strigidae Leach

Genus *Otus* Pennant

Twenty-five complete or nearly complete isolated bones, an incomplete associated skeleton, and fragments of five more bones of a small species of Strigiformes were collected. These bones are referred to the genus *Otus*. The **premaxilla** is laterally compressed, whereas it is broader in other Palearctic genera of Strigiformes with species of similar size (such as *Athene* and *Aegolius*), and the palatine is characteristically deep and narrow. The **pelvis** has inconspicuous *cristae iliosynsacralis* in *Otus*, whereas in *Athene* they are prominent. The shape of the *alae praeacetabularis ilii* is different in *Otus* and *Athene*, with a deeper notch in the latter. The generic anatomical differences among the remaining postcranial bones of *Otus* and the other Palearctic genera of Strigiformes have been described, bone by bone, in Rando *et al.* (2012a), and they apply here. Additionally, the discovery of associated material demonstrates that all the bones belong to a single new species of *Otus*.

Otus frutuosoi, new species

(Figures 2 & 3)

Holotype: MCMa 1779.012, complete right tarsometatarsus.

Type locality: Gruta de Água de Pau (São Miguel Island, Azores Archipelago). All the material was collected on 28.VIII.2011 by J.C.R and J.A.A.

Horizon: Holocene. 1970±40 BP (49 cal BC125 cal AD) is the ^{14}C age of the dated sample (lab code: KIA–47427).

Status: Extinct.

Etymology: The species name honours Gaspar Frutuoso (b. 1522 Ponta Delgada–d. 1591 Ribeira Grande), an early historian and chronicler of Macaronesia, who in the last years of his life wrote the huge work *As Sáudades da Terra*, in six volumes (not published until 1867). He is considered to be the first great historian of the Portuguese Atlantic islands. Frutuoso provided detailed ornithological information, including a list of the birds of São Miguel (Knecht & Scheer 1972).

Paratypes: MCMa 1780.02, complete left tarsometatarsus, proximal part slightly encrusted; IMEDEA 94638, nearly complete right tarsometatarsus, with the trochlea metatarsi II broken; MCMa 1781.012, complete right femur; MCMa 1782.012, complete right femur; MCMa 1783.012, complete left femur; DZUL 3057, left femur broken at the shaft, glued; MCMa 1784.012, left tibiotarsus, distal part slightly broken; MCMa 1785.012, right tibiotarsus, distal part slightly broken; MCMa 1786.012, nearly complete left tibiotarsus, with the *condylus lateralis* slightly eroded; MCMa 1787.012, complete right humerus, slightly encrusted; MCMa 1788.012, complete

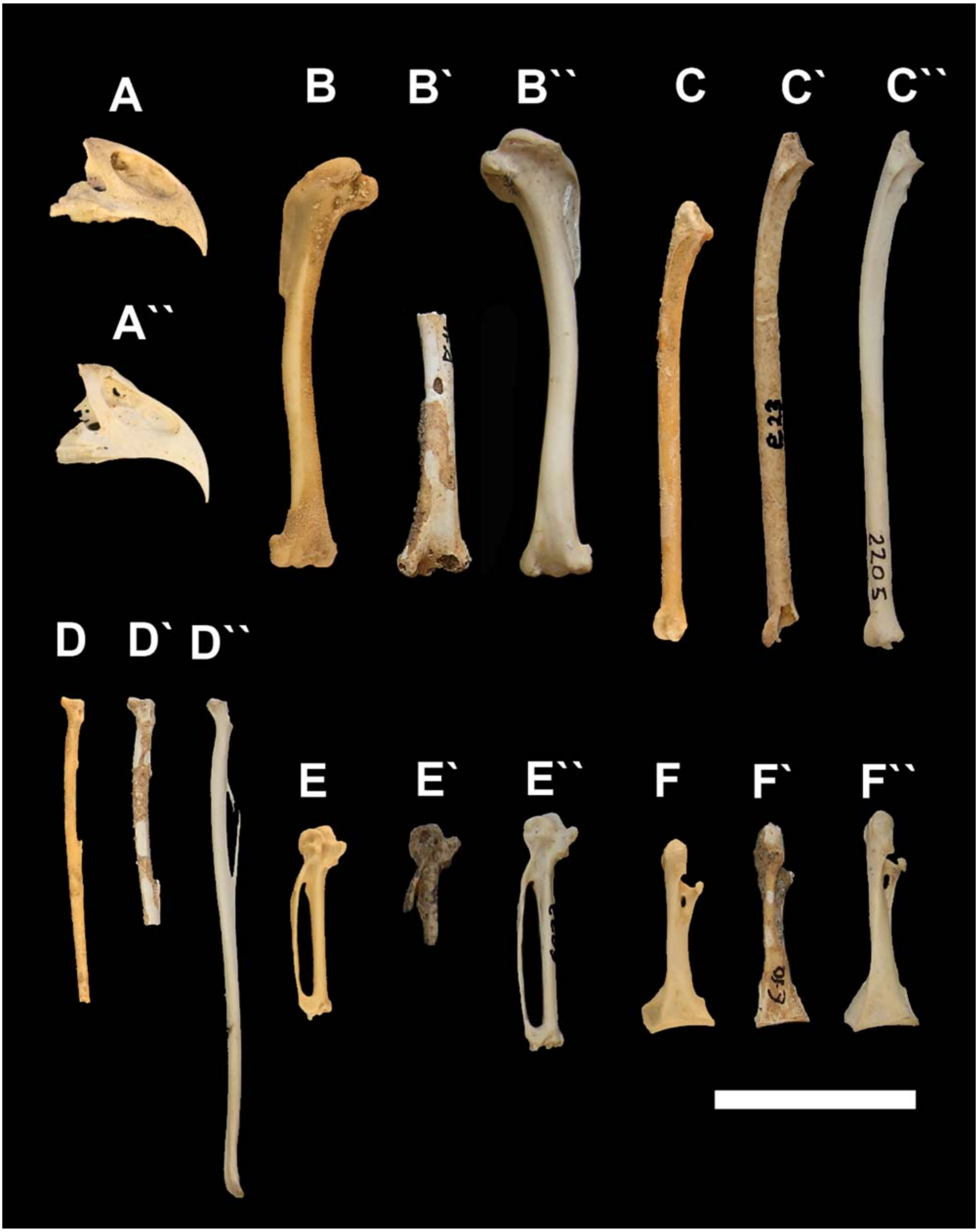

FIGURE 2. Comparison of premaxilla, lateral view, of *O. frutuosoi* **n. sp.** (A, MCMa 1800.012) and *O scops* (A``, IMEDEA 2205), and wing bones of *Otus frutuosoi* **n. sp.** (B–F), *O. mauli* (B`–F`) and *O. scops*, IMEDEA 2205 (B``–F``). (B, MCMa 1790.012; B`, MMF 41633; B``) left humeri, caudal view; (C, MCMa 1793.012; C`, MMF 41636; C``) left ulnae, ventral view; (D, MCMa 1794.012; D`, MMF 41636; D``) left radii, lateral view; (E, DZUL 3058; E`, MMF 41643; E``) left carpometacarpi, ventral view; (F, MCMa 1795.012; F`, MMF 41632; F``) right coracoids, ventral view. Scale = 2 cm.

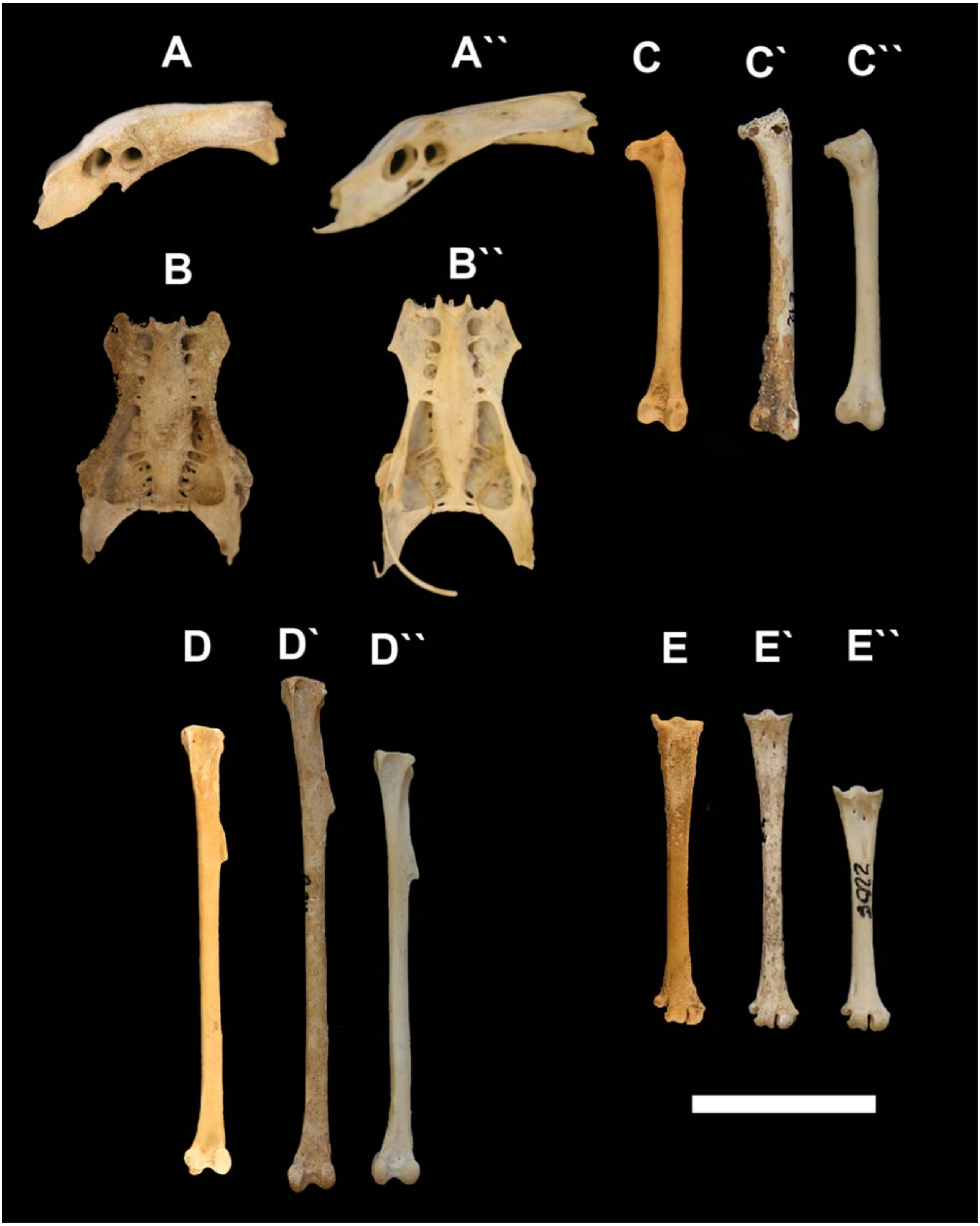

FIGURE 3. Comparison of pelvis of *Otus frutuosoi* **n. sp.** (A–B, MCMa 1799.012) and *O. scops* (A``–B``, IMEDEA 2205), lateral and ventral views, and leg bones of *O. frutuosoi* (C–E), *O. mauli* (C`–E`), and *O. scops* IMEDEA 2205 (C``–E``). (C, MCMa 1782.012; C`, MMF 41638; C``) right femora, caudal view; (D, MCMa 1786.012; D`, MMM 41641; D``) left tibiotarsi, cranial view; and (E, MCMa 1779.012; E`, MMF 41628, E``) right tarsometatarsi, dorsal view. Scale = 2 cm.

left humerus, slightly encrusted; MCMa 1789.012, nearly complete left humerus, slightly encrusted, with some damage to the deltoid crest; MCMa 1790.012, complete left humerus, slightly encrusted; MCMa 1791.012, complete right ulna; MCMa 1792.012, complete left ulna; IMEDEA 94639, complete left ulna, slightly encrusted; MCMa 1793.012, complete left ulna; MCMa 1794.012, proximal two thirds of left radius with the *arcus origo musculi extensor longus digiti majoris* broken; MCMa 1795.012, complete right coracoid; MCMa 1796.012, complete right carpometacarpus; MCMa 1797.012, complete right carpometacarpus; MCMa 1798.012, complete left carpometacarpus; DZUL 3058, complete left carpometacarpus; MCMa 1799.012; nearly complete ossa cinguli membri pelvis (synsacrum + pelvis), with both *scapus pubis* broken; MCMa 1800.012, damaged associated skeleton, partially encrusted, including premaxilla, skull fragments, jaw fragments, a nearly complete right humerus, slightly broken at its distal end, two distal ends of ulnae, two fragmented radii, two scapulae, a fragmented right coracoid, two complete femora, two proximal ends of tibiotarsi, a fragmented right tarsometatarsus, some fragments of pelvis, three vertebrae, and some ribs.

Other material belonging to *O. frutuosoi*: Five fragmentary bones (three femora, one tibiotarsus, one humerus), used to obtain a ^{14}C AMS date.

Suggested English name: São Miguel Scops Owl.

Diagnosis: A small species of *Otus* with forelimb elements (humerus, ulna and carpometacarpus) shorter than those of *O. scops*, but with the femur, tibiotarsus and especially tarsometatarsus longer. The pelvis is shorter and broader than in *Otus scops*. The premaxilla is less robust than in *Otus scops*, with its tip less directed downward than in that species, giving a less pointed appearance in lateral view (Figure 2). The new species differs from the extinct *O. mauli* in the significantly smaller size of all its bones (excepting the scapula and tarsometatarsus), especially the ulna and tibiotarsus (Table 1; Figures 3 & 4).

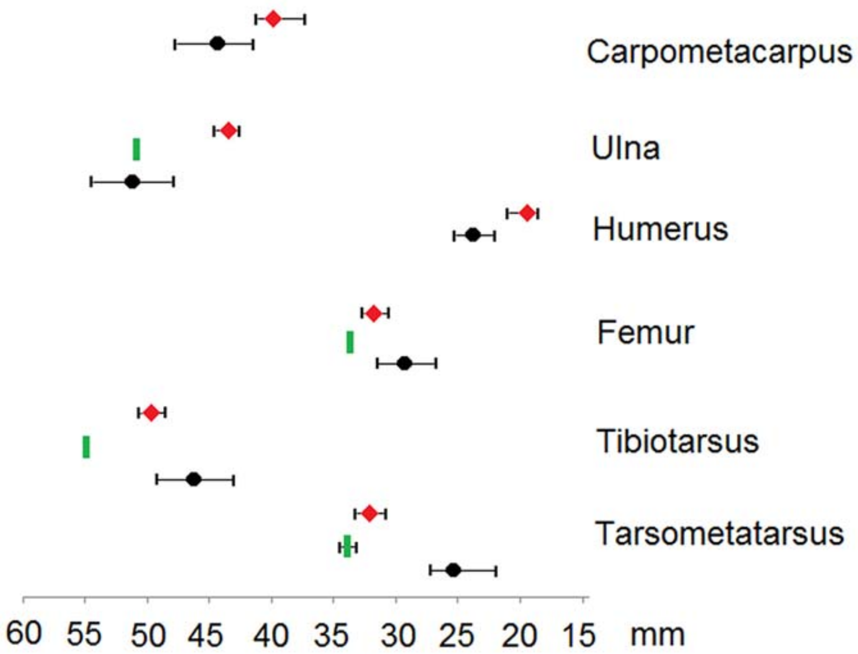

FIGURE 4. Wing (carpometacarpus, ulna and humerus) and leg bone (femur, tibiotarsus and tarsometatarsus) lengths (mean ± standard error in mm) of *O. frutuosoi* **n. sp.** (rhombi), *O. mauli* (bars), and *O. scops* (circles).

Remarks: The new species is most similar to *O. scops* and *O. mauli* in its overall morphology. The tarsometatarsus of the new species is similar in size to that of *O. mauli* ($U = -1.1$; $p = 0.4$) but is more robust (Figure 3). The femur is likewise similar (31.0 vs. 33.2 mm), but *O. frutuosoi* has a shorter ulna (43.6 mm) and tibiotarsus (49.5 mm) than *O. mauli* (c. 51.0 and 55.0 mm respectively), differences of 14.5% and 10% (Table 1 and Figures 3 & 4).

The MANOVA performed with the total lengths of humerus, ulna, carpometacarpus, and femur identified significant morphological differences between *O. frutuosoi* and *O. scops* (Wilks' lambda = 0.0017, d.f. = 4, 24; $p<0.001$). The new bird has a shorter humerus ($F_{1,29} = 36.55$; $p<0.001$), ulna ($F_{1,29} = 90.3$; $p<0.001$) and carpometacarpus ($F_{1,29}$ = 129.06; p<0.001) than *O. scops*, but a longer femur ($F_{1,29}$ = 11; p=0.003). In addition, the new species has a longer tarsometatarsus (U = -2.78; p<0.005) and tibiotarsus (U= -2.55; p=0.005) (Table 1; Figures 3 & 4).

The percent difference is not the same for each bone and the differences are larger for distal ends of wing and leg (Table 1). The total length of the wing bones (humerus + ulna + carpometacarpus) is 14% smaller in the new species than in *O. scops*, while the total leg length (femur + tibiotarsus + tarsometatarsus) is 11.6% greater in *O. frutuosoi* than in *O. scops*.

The estimated weight of *O. frutuosoi*, 144±35 g (128.6–151.6) (n = 5), is on average 34.6% higher than the weight of *O. scops* obtained by the same method, 107±10 g (82–130) (n = 25).

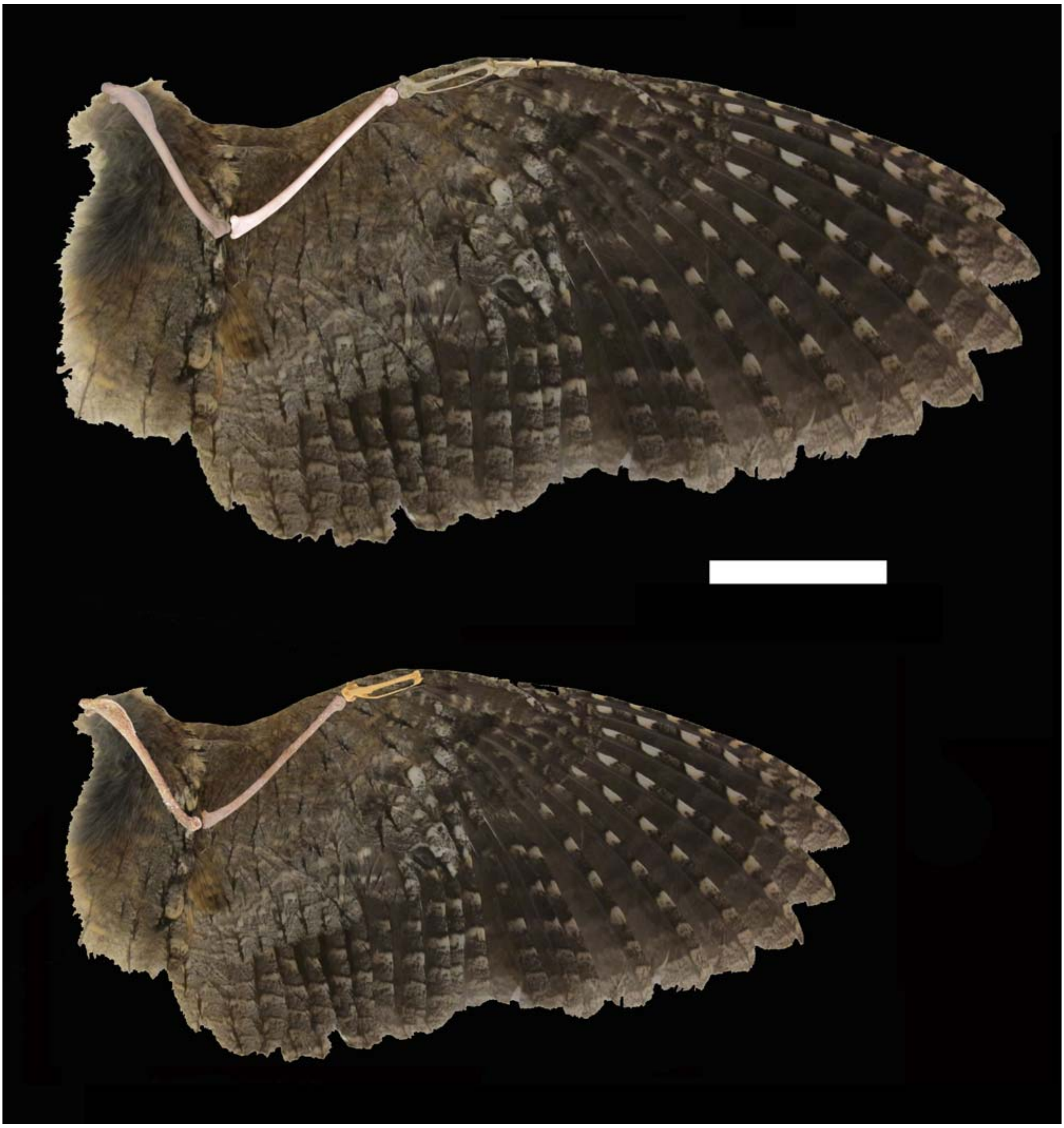

FIGURE 5. Right wing of *Otus scops* (above) and estimated wing size of *O. frutuosoi* **n. sp.** (obtained by reducing the upper photograph to the size of the wing bones of the new species), both with the major elements in anatomical position. Scale = 4 cm.

TABLE 1. Measurements of *Otus frutuosoi* n. sp., *O. mauli* and *O. scops*: sample size, mean length ± standard error (mm), and range. (%): percentage of variation for main measurements and (*p*): statistical significance from MANOVA (^{m}) and from Mann-Whitney U test (^{u}) between total lengths of limb bones of *O. frutuosoi* **n. sp.** and *O. scops*. Measurements as in Campbell and Bocheński (2010), plus length of *synsacrum* (LS) from the cranial border of the *processus marginis* to the *cranial border of the ala praeacetabularis ilii.*

	Otus scops	*Otus mauli*	*Otus n.p.*	%	*p*
Coracoid					
Length (A)	(25) 20.86±0.6 [19.64–22.02]	(1) 20.47	(1) 18.99	-9	
Depth of acrocoracoid (B)	(25) 2.29±0.18 [2.04–2.85]	(1) 2.48	(1) 2.32		
Width of acrocoracoid (C)	(25) 3.55±0.17 [3.34–4.09]	(1) 3.3	(1) 2.81		
Width of shaft at procoracoid (D)	(25) 4.04±0.18 [3.59–4.28]	(1) 3.7	(1) 3.6		
Scapula					
Length fac. artic. humeralis (B)	(25) 2.76±0.13 [2.55–3]	(1) 2.52	(1) 2.69	-2.5	
Width fac. artic. humeralis (C)	(25) 2.34±0.16 [2.12–2.69]	(1) 2.29	(1) 2.35		
Humerus					
Total length (A)	(25) 44.65±1.42 [41.54–47.66]	-	(5) 39.87±1.27 [37.52–41.13]	-10.7	$<0.001^{m}$
Proximal width (B)	(25) 8.41±0.24 [7.99–8.82]	-	(4) 7.82±0.3 [7.34–8.18]		
Distal width (C)	(25) 7.48±0.25 [7.02–7.93]	(1) 7.45	(2) 7.18±0.53 [6.65–7.72]		
Ulna					
Total length (A)	(25) 51.32±1.54 [48.1–54.34]	(1) c. 51.02	(4) 43.63±0.6 [42.87–44.47]	-15	$<0.001^{m}$
Proximal width (B)	(24) 4.82±0.18 [4.52–5.11]	(1) 4.82	(4) 4.4±0.07 [4.3–4.5]		
Proximal depth (C)	(25) 3.95±0.2 [3.54–4.45]	(1) 3.90	(4) 3.48±0.07 [3.38–3.58]		
Width of Condylus dorsalis (D)	(25) 3.64±0.19 [3.24–4.03]	(1) 3.5	(4) 3.34±0.1 [3.24–3.47]		
Carpometacarpus					
Total length (A)	(25) 23.81±0.65 [22.28–25.2]	-	(4) 19.49±0.84 [18.73–20.89]	-18.1	$<0.001^{m}$
Proximal width (B)	(24) 5.55±0.21 [5.18–5.93]	-	(4) 4.85±0.12 [4.72–5.04]		
Proximal depth (C)	(25) 2.83±0.19 [2.25–3.09]	-	(4) 2.67±0.12 [2.5–2.84]		
Depth of mid-shaft (D)	(25) 1.9±0.09 [1.76–2.09]	-	(4) 1.72±0.05 [1.64–1.76]		

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TABLE 1. (Continued)

	Otus scops	*Otus mauli*	*Otus n.p.*	%	*p*
Pelvis					
Neural arch height (A)	(16) 3.27±0.26 [2.82–3.85]	-	(1) 3.11		
Centre height through vertebra (B)	(15) 6.85±0.39 [6.22–7.42]	-	(1) 6.6		
Width through praezygapop (C)	(17) 3.94±0.17 [3.57–4.24]	-	(1) 4.16		
Width through antitrochanter (D)	(17) 16.89±0.71 [15.66–18.45]	-	(1) 18		
Length of synsacrum (LS)	(22) 28.86±1.18 [26.67–31.38]		(1) 26.24	-9.1	
Femur					
Length (A)	(25) 29.4±0.96 [26.94–31.49]	(1) 33.17	(5) 31.04±0.43 [30.26–31.53]	+5.6	$=0.003^{m}$
Proximal width (B)	(25) 5.36±0.21 [5.04–5.85]	(1) 6.26	(5) 5.78±0.13 [5.65–6.02]		
Width at mid-shaft (C)	(25) 2.4±0.11 [2.22–2.71]	(2) 2.82±0.06 [2.78–2.86]	(5) 2.47±0.08 [2.4–2.61]		
Depth at mid-shaft (D)	(25) 2.37±0.14 [2.04–2.68]	(2) 2.94±0.07 [2.89–2.99]	(5) 2.46±0.13 [2.28–2.67]		
Distal width (E)	(25) 5.5±0.2 [5.17–5.91]	(2) 6.15±0.04 [6.12–6.18]	(5) 5.99±0.23 [5.8–6.43]		
Distal depth (F)	(25) 4.5±0.2 [4.22–4.9]	(2) 5.31±0.04 [5.28–5.34]	(5) 4.93±0.09 [4.85–5.09]		
Tibiotarsus					
Total length (A)	(24) 46.24±1.65 [42.97–49.3]	(1) 55.02	(3) 49.49±0.66 [48.86–50.4]	+7	$=0.005^{u}$
Proximal width (B)	(25) 4.72±0.26 [4.27–5.09]	(1) 5.04	(3) 4.88±0.18 [4.63–5.01]		
Proximal depth (C)	(25) 5.27±0.26 [4.51–5.8]	(1) 6	(3) 5.37±0.27 [5.03–5.68]		
Width at mid-shaft (D)	(25) 2.24±0.17 [1.86–2.56]	(2) 2.37±0.15 [2.26–2.48]	(3) 2.07±0.05 [2.03–2.14]		
Distal width (E)	(25) 5.21±0.18 [4.93–5.58]	(1) 5.42	(1) 4.93		
Condylus lateralis depth (F)	(25) 4.2±0.23 [3.89–4.7]	(1) 4.37	(1) 3.88		
Condylus medialis depth (G)	(25) 4.13±0.19 [3.84–4.51]	(1) 4.36	(1) 3.67		
Tarsometatarsus					
Total length (A)	(24) 25.49±1.15 [21.91–27.36]	(3) 33.43±0.54 [32.81–33.78]	(3) 32.35±0.96 [31–33.1]	+26.9	$<0.005^{u}$
Proximal width (B)	(24) 5.12±0.14 [4.84–5.35]	(3) 5.41±0.2 [5.21–5.62]	(3) 5.22±0.17 [5.46–5.1]		
Hypotarsus length (C)	(24) 2.49±0.28 [1.93–3.1]	(1) 2.34	(2) 2.34±0.22 [2.12–2.57]		
Hypotarsus width (D)	(24) 1.41±1.32 [1.17–1.72]	(1) 1.34	(2) 1.18±0.16 [1.02–1.34]		
Minimum shaft width (E)	(24) 2.42±0.18 [2.05–2.68]	(4) 2.37±0.02 [2.28–2.45]	(2) 2.35±0.15 [2.14–2.47]		
Distal width (F)	(24) 5.5±0.25 [5.13–5.89]	(2) 5.6±0.15 [5.51–5.72]	(2) 5.64±0.05 [5.69–5.69]		

The average wing area of *O. scops* is 170±13 cm^2 (n=6), whereas the estimated maximum wing surface in *O. frutuosoi* (114 cm^2) is 33% smaller (Figure 5). Our approach assumes that the flight feathers of *O. frutuosoi* were reduced to the same proportion as the bones (Figure 5), although they may have been reduced even further.

The area of the spread wing directly contributed by the humerus is smaller than that contributed by the ulna and carpometacarpus (see Figure 5). The reduction of wing surface of *O. frutuosoi* in comparison with *O. scops* is mostly a factor of reduction in the distal wing elements, which are more shortened in *O. frutuosoi* than the proximal ones. Such a differential reduction has been observed in other flightless birds, in which the shortening of the manus precedes the reduction in other wing elements (Nudds & Davidson 2010). Because the surface reduces as the square of linear dimensions, the reduction of the whole wing surface in *O. frutuosoi* in relation to *O. scops* may have been greater than 33%.

The ratio of body weight to wing area (using the mean values) indicates a wing loading of 0.31 g/cm^{-2} for *O. scops* but this is estimated to have been nearly 100% greater in *O. frutuosoi* (0.63 g/cm^{-2}). This is likely an overestimate because of probable reduction in relative weight, compared to femur length, of flight musculature in *O. frutuosoi*. The ratio of combined humerus, ulna and carpometacarpus lengths to femur length is smaller in *O. frutuosoi* (3.30:1) than for *O. scops* (4.07:1) (data from Table 1), suggesting weaker powers of flight. Overall, these results strongly suggest that *O. frutuosoi* had ground–dwelling habits.

The PCA performed with the proportions of hind- and forelimb bones (Table 2; Figure 6) produced two principal components explaining 72.1% of the total variance. 43.9% is explained by PC1, which shows a high positive weighting for ulna and femur lengths, and a high negative weighting for tarsometatarsus and carpometacarpus. PC2 explained 28.2% of the variance and shows a high positive weighting for humerus length, and a high negative weighting for carpometacarpus and ulna.

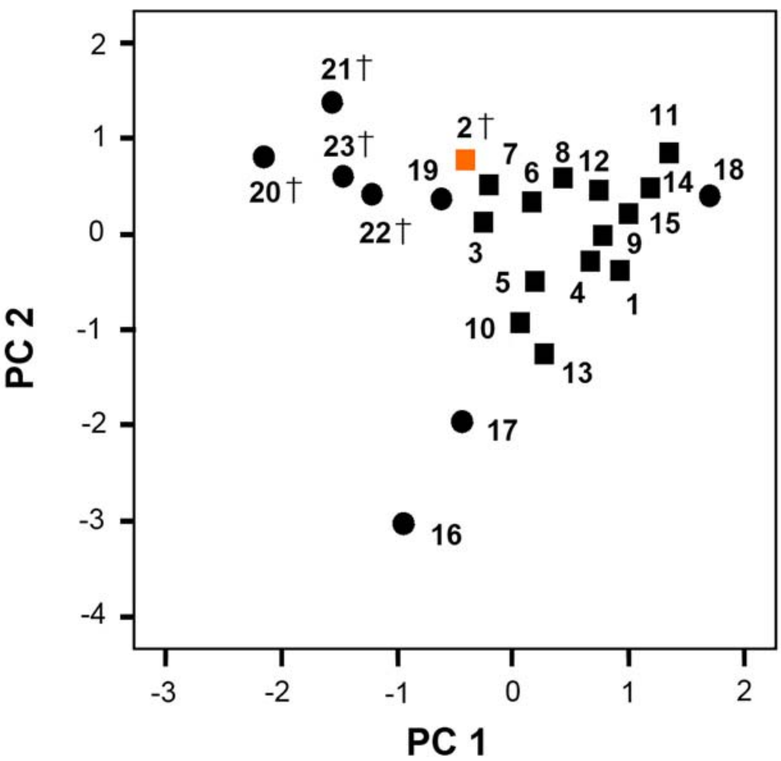

FIGURE 6. PCA plot for the two principal components obtained from wing (humerus, ulna and carpometacarpus) and leg bones (femur, tibiotarsus and tarsometatarsus) proportions of extant scops owls (*Otus* and *Megascops*, squares), related species and other extant and extinct (†) owls. Data from Table 2. 1: *Otus scops*; 2: *O. frutuosoi* **n. sp.**; 3: *M. nudipes* (Daudin); 4: *M. petersoni* (Fitzpatrick and O`Neill); 5: *M. asio* (Linnaeus); 6: *M. atricapillus*; 7: *M. clarkii*; 8: *M. choliba* (Vieillot); 9: *O. elegans* (Cassin); 10: *M. kennicottii* (Elliot); 11: *O. magicus* (Müller); 12: *O. megalotis* (Walden); 13: *M. trichopsis*; 14: *O. everetti* Tweeddale (Philippines); 15: *O. bakkamoena* (Thailand and Burma); 16: *Athene cunicularia* (Molina); 17: *A. noctua* (Scopoli); 18: *Ptilopsis leucotis* (Temminck); 19: *Gymnoglaux lawrencii*; 20: *Grallistrix erdmani* Olson and James; 21: *G. auceps* Olson and James; 22: *G. orion* Olson and James; 23: *Sceloglaux albifacies*.

TABLE 2. Measurements and proportions (%) of each limb bone of extant and extinct owls: minimum number of specimens for each variable (n), mean length (mm) of limb bones (H: humerus; Ul: ulna; Car: carpometacarpus; F: femur; Tbt: tibiotarsus; Tmt: tarsometatarsus).

	Otus scops		*O. frutuosoi* n.sp.		*O. elegans*		*O. magicus*		*O. megalotis*		*O. everetti*		*O. bakkamoena*		*Megascops nudipes*	
(n)	24	%	3	%	4	%	4	%	1	%	3	%	3	%	5	%
H	44.6	37.27	39.9	38.71	50.2	37.25	57.7	38.08	60.2	38.03	55.7	38.26	52.9	37.90	50.3	37.69
Ul	51.3	42.84	43.6	42.36	58.4	43.39	66.5	43.89	67.7	42.77	63.4	43.57	60.7	43.46	57.6	43.14
Car	23.8	19.88	19.5	18.92	26.1	19.36	27.3	18.03	30.4	19.20	26.4	18.17	26.0	18.63	25.6	19.17
F	29.4	29.05	31.0	27.50	32.6	27.21	36.1	28.10	43.5	29.37	38.9	29.91	36.9	29.04	34.3	25.36
Tbt	46.2	45.78	49.5	43.84	55.4	46.27	58.7	45.66	66.6	44.97	57.3	44.03	56.9	44.74	61.2	45.28
Tmt	25.5	25.17	32.3	28.66	31.8	26.52	33.7	26.23	38.0	25.66	33.9	26.06	33.3	26.21	39.7	29.36

	M. choliba		*M. kennicottii*		*M. petersoni*		*M. asio*		*M. trichopsis*		*M. atricapillus*		*M. clarkii*		*Athene noctua*	
(n)	5	%	6	%	1	%	6	%	1	%	1	%	1	%	7	%
H	51.5	37.96	54.9	37.08	50.9	37.79	54.1	37.66	43.2	36.64	54.8	38.06	55.2	38.49	47.7	36.24
Ul	58.0	42.77	63.3	42.76	57.5	42.69	61.1	42.54	51.4	43.60	61.4	42.67	60.6	42.26	56.3	42.77
Car	26.1	19.26	29.8	20.16	26.3	19.52	28.4	19.80	23.3	19.76	27.7	19.25	27.6	19.25	27.6	20.99
F	33.9	28.04	39.0	29.19	32.9	30.30	38.5	29.62	30.3	27.95	34.2	27.98	37.7	28.14	35.2	27.91
Tbt	55.0	45.58	58.8	44.02	47.9	44.07	57.0	43.91	48.0	44.31	54.7	44.72	59.0	43.98	55.6	44.05
Tmt	31.8	26.38	35.8	26.79	27.8	25.62	34.4	26.46	30.0	27.73	33.4	27.94	37.4	27.88	35.4	28.03

	A. cunicularia		*Ptilopsis leucotis*		*Gymnoglaux lawrencii*		*Grallistrix erdmani*		*G. auceps*		*G. orion*		*Sceloglaux albifacies*	
(n)	8	%	1	%	2	%	2	%	8	%	1	%	7	%
H	54.5	35.23	66.4	37.79	43.7	37.93	71.3	38.69	81.4	39.35	71.3	38.35	76.7	38.48
Ul	68.1	43.99	76.2	43.37	49.6	43.05	76.3	41.37	84.9	41.06	77.3	41.59	82.4	41.32
Car	32.1	20.77	33.1	18.84	21.9	19.01	36.8	19.94	40.5	19.59	37.3	20.06	40.3	20.19
F	38.0	25.50	44.1	29.94	29.0	24.37	51.6	23.58	63.2	25.72	58.2	26.06	57.7	25.57
Tbt	64.8	43.45	67.7	45.98	53.8	45.21	97.3	44.46	108.5	44.17	99.5	44.53	100.7	44.68
Tmt	46.3	31.05	35.5	24.08	36.2	30.42	70.0	31.97	74.0	30.11	65.7	29.41	67.1	29.74

Discussion

Otus frutuosoi is the second species of extinct scops owl described from Macaronesia, the first being *O. mauli*, an endemic species from Madeira (Rando *et al.* 2012a). As in the case of Madeira, the location of the Azores islands far from the mainland probably resulted in isolation of a population of *Otus*.

Although *O. mauli* is larger than *O. frutuosoi* (c. 152 g vs. 144 g), both species share long tarsi and short wings (Figures 2 & 3), and both were probably weak flyers. It is not yet known whether these similarities are due to a direct phylogenetic relationship between the two species, or evolutionary convergence from independent ancestral populations.

The leg bone proportions of *O. frutuosoi* (Table 2) are close to those of the extinct *Athene trinacriae* Pavia and Mourer-Chauviré from Sicily and *O. mauli* from Madeira, and to the living New World species *Megascops trichopsis* (Wagler), *M. atricapillus* (Temminck), *M. clarkii* (Kelso and Kelso) (see Rando *et al*. 2012a). The size of the wings and legs of *A. trinacriae* seem to indicate a terrestrial lifestyle (Pavia & Mourer-Chauviré 2002). In addition, the species of *Megascops* inhabit dense American forests and occasionally hunt on the ground (del Hoyo *et al*. 1999). As in the case of *O. mauli* (see Rando *et al*. 2012a), these data seem to indicate that *O. frutuosoi* may have inhabited the floor of laurel forest, an ecosystem that offered a variety of invertebrates (Oromí 1995) as food as well as protection from avian predators such as buzzards (*Buteo buteo*) that currently and in the past were present in the archipelago (Borges *et a*l. 2010). This idea is supported by PCA analysis performed with wing and leg bone proportions (Figure 6), which place *O. frutuosoi* very close to *M. clarkii* and *Gymnoglaux lawrencii* (Sclater & Salvin) and relatively close to the extinct *Grallistrix orion* Olson & James from Hawaii, and *Sceloglaux albifacies* (Gray), a recently extinct species of New Zealand that apparently hunted for its food by spending an appreciable amount of time on the ground, and roosted and nested under boulders or in fissures among rocks (Williams & Harrison 1972; Higgins 1999). The proximity of *Sceloglaux* and *Grallistrix* in the PCA analysis (Figure 6) could indicate a similar morphology due to living on remote islands with no terrestrial mammals in their original faunas.

As in other small species of scops owls, the diet of *O. frutuosoi* was probably dominated by invertebrates (del Hoyo *et al*. 1999). Due to the absence of rodents and reptiles in the island, small birds were the only vertebrates that could have formed part of its diet.

The latest known occurrence of *O. frutuosoi* (49 cal BC–125 cal AD) indicates a Late Holocene extinction event after 49 cal BC. Major ecological alterations in the Azores Islands during the two last millennia were the result of human arrival. The extinction of several species of vertebrates due to human perturbations has been well documented in the Canary Islands (Rando & Alcover 2008; Rando *et al*. 2008; Rando & Alcover 2010; Rando *et al*. 2012b), and has been suggested in Madeira to explain the extinction of *O. mauli* (Rando *et al*. 2012a). The first human settlements in the Azores, which were known to mariners in the fourteenth century, took place in the fifteenth century (Newitt 2005), so it is likely that the extinction took place subsequently.

Because of the absence of terrestrial predators, it is probable that *O. frutuosoi* bred on or close to the ground, as has also been indicated for the extinct Hawaiian owls (genus *Grallistrix*) (Olson & James 1991) and as has been suggested for *O. mauli* by Rando *et al*. (2012a). If so, the introduction of alien mammals could have had dramatic consequences. Exotic mammals could have preyed on eggs and fledglings of *O. frutuosoi* and competed with it for food, with deleterious results, as has been suggested for the historical extinction of *Sceloglaux* of New Zealand (Williams & Harrison 1972; Higgins 1999; Worthy & Holdaway 2002).

The presence in Gruta de Água de Pau of remains of at least four specimens of *O. frutuosoi* suggests that the species was a regular inhabitant of the area. Its distribution elsewhere in the Azores Archipelago remains to be documented.

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