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Original Article

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Petrel extinction in Macaronesia (North-East Atlantic Ocean): the case of the genus *Pterodroma* (Aves: Procellariiformes: Procellariidae)

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ABSTRACT

The Late Quaternary fossil record indicates that formerly in the North Atlantic volcanic Macaronesian archipelagos (Azores, Madeira, Selvagens, Canary Islands, and Cape Verde) there was a higher avian diversity, including numerous now extinct species. Currently, only three gadfly petrels (genus *Pterodroma*) remain in two archipelagos: the Fea's petrel, *Pt. feae*, in Cape Verde (islands of Santiago, Fogo, Santo Antão, and São Nicolau); the Zino's petrel of Madeira, *Pt. madeira*, on the island of Madeira; and the Desertas petrel, *Pt. deserta*, on the islet of Bugio (Desertas Islands, Madeira Archipelago). Herein we describe the former distribution of the genus in Macaronesia based on the palaeontological record. However, the original specific diversity cannot be accurately established through the biometry of their fossil bones but the fossil record of *Pterodroma* in Macaronesia indicates: (i) its former presence in all Macaronesian archipelagos; (ii) the extinction of at least 16 island populations (73% of its original distribution on these islands); and (iii) the extinction of, at least, one species from Azores, here named *Pterodroma zinorum* sp. nov.. Radiocarbon dates indicate than this species was still alive at sometime among 1104 and 1672 CE, documenting its extinction in the last millennium.

Keywords: extinction; gadfly petrels; Macaronesian Islands; new species; radiocarbon dates; sea birds

INTRODUCTION

Quaternary extinctions have had a dramatic effect on island biotas, with a high number of vanished insular land and sea birds during the Holocene. During the prehistoric period, in the Pacific islands, the number of terrestrial non-passerine extinct bird species was 983 (95% CI: 731–1332) (Duncan *et al.* 2013). Seabirds and passerines from these islands also suffered a high number of extinctions (Steadman 2006). Parallel extinction took place in other worldwide archipelagos like the Canary Islands or the Caribe (Hume and Walters 2012). A subsequent wave of historic extinctions followed this episode of prehistoric extinctions at these same archipelagos and on other islands that had remained uninhabited by humans until then, such as the Mascarene Islands, Madeira, and the Azores archipelago (Curnutt and Pimm 2001, Steadman 2006, Russell and Kuefrer 2019, Sayol *et al.* 2020). Thus, extinct insular birds represent 10%–20% of the original avian diversity (Fromm and Meiri 2021). Currently, the number of extinct terrestrial native birds widely overpasses that of the extant species in some archipelagos (e.g. Hawaii, 71% vs. 29%, respectively; Easter Island, 100% vs. 0%) (Steadman 1995, Boyer 2008). This loss of native insular vertebrates is a direct consequence of human activities and the

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introduction of alien species (Olson and James 1982, Worthy and Holdaway 2002, Blackburn *et al.* 2004, Steadman 2006, Turvey 2009, Hume and Walters 2012, Cooke *et al.* 2023).

Among seabirds, Procellariiformes are highly vulnerable to human settlement and to the introduction of alien mammals, because they mainly breed on islands free of terrestrial predators, they have a strong breeding-site fidelity, and they lack effective anti-predator behaviour (Warham 1996). This vulnerability could be why at least 56% of the species of Procellariiformes lost populations during the Holocene (Scofield 2009), and that more than 15 species have become extinct (Tyrberg 2009).

Within Procellariformes, the family Procellaridae contains 16 genera and 98 extant species (Winkler *et al.* 2020). Uncertainty arose from the difficulties in establishing the species' limits, mainly within the two most diversified genera, *Puffinus* (shearwaters) and *Pterodroma* (gadfly petrels). Limits among species of both genera are controversial (Ferrer Obiol *et al.* 2023) as different recognized species can present similar or only slightly different coloration patterns, body size, and proportions, or can be subtly or strongly differentiated by their voices, breeding behaviour, and/or migration patterns. Some species are highly variable along their distribution range, while others are more homogeneous. Different genetic criteria have been used to establish their relationships. There are populations prone to be differentiated more morphologically than genetically in both genera, while other populations are more similar morphologically than genetically. The great philopatry exhibited by these different populations, occasionally together with the breeding allochrony and geographic disparity, probably favours their evolutionary differentiation (Ferrer Obiol *et al.* 2023). All these factors create challenges to resolving phylogenetic relationships within both genera.

The gadfly petrels are small to medium-sized (26–46 cm and 150–800 g) found in all oceans but are more diverse in the subtropical South Atlantic. Their short, robust bills are adapted for soft prey captured dipping at the sea surface. They only come to land to breed in colonies on islands, with one white egg laid in a burrow or on open ground. They are nocturnal in the breeding colonies (Warham 1996, Harrison *et al.* 2021).

In this paper we focus on a group of the Northern Atlantic gadfly petrels (genus *Pterodroma*), the species found in the volcanic Macaronesian archipelagos (Azores, Madeira, Selvagens, Canary Islands, and Cape Verde), located in the north-east Atlantic Ocean (15°N–39°N and 10°W–30°W), and between ~100 km (Canary Islands) and ~1350 km (Azores) from Africa and Europe, respectively (Fig. 1). Three species of gadfly petrels (genus *Pterodroma*) are currently breeding in two archipelagos: *Pt. feae* (Salvadori, 1899) in Cape Verde (islands of Santiago, Fogo, Santo Antão, and São Nicolau), *Pt. madeira* Mathews, 1934 on Madeira Island, and *Pt. deserta* Mathews, 1934 on the islet of Bugio (Desertas Islands, Madeira Archipelago) (Hazevoet 1995, Jesus *et al.* 2009, Ramos *et al.* 2016). Initially, these three populations were considered to belong to *Pt. mollis* (Gould, 1844) due to their morphological similarities, later as one distinct species (*Pt. feae*) with three subspecies, or as two species (one in Madeira Island, *Pt. madeira*, and the other shared by Bugio and Cape Verde, *Pt. feae*), and recently as three species (see: Zino *et al.* 2008, Jesus *et al.* 2009, Gangloff *et al.* 2013).

The palaeontological record indicates a wider distribution of the genus in the past of Macaronesia. The island of El Hierro (Canary Island) had a population of this genus in former times, which probably went extinct after human colonization less than 2000 years ago (Rando 2002), and *Pterodroma* bones have been found in the archipelago of Selvagens (see: Gangloff *et al.* 2013) (Fig. 1).

Our palaeontological survey provided bones of gadfly petrels (genus *Pterodroma*) in both archipelagos of Madeira and the Azores. Specifically, in the islands of Madeira, Bugio, and Porto Santo in the former, and in São Miguel, Terceira, Pico, Faial, São Jorge, and Graciosa in the latter.

This paper provides information on the original diversity and distribution of the genus *Pterodroma* in these archipelagos before human settlement, including a description of a new extinct endemic species from the Azores, and discusses the chronology and possible causes for regression and extinction to explain its current narrow distribution in Macaronesia.

MATERIALS AND METHODS

Skeletons used for comparisons are from the Museu de História Natural do Funchal (MMF, Madeira, Portugal), the Institut Mediterrani d'Estudis Avançats (IMEDEA, Mallorca, Spain), and Departamento de Biología Animal, Geología y Edafología de la Universidad de La Laguna (DZUL, Canary Islands, Spain). The modern specimens used as comparative material are listed in the Appendix.

The material was collected from volcanic tubes in Madeira Island and São Miguel, Terceira, Pico, Faial, São Jorge, and Graciosa (Azores Islands, Portugal), at the sand dunes on Porto Santo, and at sedimentary sites on Madeira and Bugio (Madeira Archipelago). Information about the Azorean caves is available in Pereira *et al.* (2015).

The fossil specimens described herein are housed in the following collections: (i) Museu de História Natural do Funchal (MMF), Funchal, Madeira, Portugal; (ii) Museu de História Natural do Jardim Botânico da Madeira, Funchal, Portugal; (iii) Museu Carlos Machado (MCMa), São Miguel, Azores, Portugal; (iv) Museu dos Montanheiros, Angra do Heroísmo, Terceira, Azores, Portugal (without collection acronym); and (v) Institut Mediterrani d'Estudis Avançats (IMEDEA), Mallorca, Balearic Islands, Spain.

Measurements were taken with electronic digital callipers to 0.01 mm, and rounded to the nearest 0.1 mm. We followed the criteria of Rando (2002) for taking measurements of the bones. Osteological terminology follows that of Livezey and Zusi (2006). The lengths of the main bones, beaks, and jaws were measured to determine biometrical differences species of *Pterodroma* performing multivariate analysis of variances (MANOVA) and one-way analysis of variance (one-way ANOVA). The pairwise comparisons were made through *t*-test and elements known only from three specimens were pairwise compared with a nonparametric test (Mann–Whitney U-tests).

The collagen of selected bones was ^{14}C-dated using Accelerator Mass Spectometry (AMS) to obtain chronological information about the material. Two samples from Pico (Azores) were subjected to an improved collagen extraction (van Strydonck

Figure 1. Map of the Macaronesian Islands. The three species of endemics *Pterodroma* and the islands where they currently breed are shown by solid forms (*Pt. madeira* in Madeira; *Pt. deserta* in Bugio; and *Pt. feae* in Fogo, Santiago, São Nicolau and Santo Antão). The islands where bones of this genus have been found are shown by empty silhouettes (two empty silhouettes in the islands where two size classes of *Pterodroma* were found).

et al. 2005) by the modified Longin method (Brown *et al.* 1998) at the Koninklijk Instituut voor Het Kunstpatrimonium (Brussels). AMS measurements were performed on extracts of ultrafiltered bone gelatine from a sample from Porto Santo (Madeira Archipelago) at the Radiocarbon Dating Laboratory of The University of Waikato (Hamilton, New Zealand).

The ^{14}C ages are given by the laboratories in years before present (BP) and are expressed as 2σ intervals (i.e., $p = 95.45\%$). Their interpretation is based exclusively on the extreme values of these intervals indicating that the true age of the dated material is more recent than the lower extreme value of the 2σ interval and, independently, it is more ancient than the upper extreme value of the 2σ interval (see e.g. Zilhão 2001). Dates calculated from calibration (cal) are given as 'CE' or 'BCE', CE being 'current era' and BCE 'before current era'.

Radiocarbon samples from species that obtain their carbon from a source (or reservoir) different to atmospheric carbon, such as seabirds, will yield radiocarbon dates excessively old and require the application of a correction factor that varies with location due to complexities in ocean circulation. This regional difference from the average global marine reservoir correction is designated as ΔR and is assumed to be a constant for a given region and is calculated from the difference in ^{14}C years of known age marine samples and the marine model age for that calendar age (Stuiver and Braziunas 1993). The ages were calibrated using OxCal v.4.4 (Bronk Ramsey 2009) and a marine calibration curve (Marine20) (Heaton *et al.* 2020). Other calibrations were performed with a reservoir correction of ΔR = 18 ± 141 for a sample from Porto Santo (Madeira Archipelago), and ΔR = 38 ± 139 for two samples from Pico (Azores). Reservoir corrections were obtained from the 20 samples from the coast of mainland Portugal closest to the dated samples using the Marine Reservoir Correction Database (http://calib.org/marine/).

RESULTS

Systematic palaeontology

Order Procellariiformes Fürbringer, 1888

Family Procellariidae Leach, 1820

Genus *Pterodroma* Bonaparte, 1856

The material presented herein is included in the genus *Pterodroma* because of the following combination of characters: the dorsal distal outline of the premaxilla shows a deep concave kink in lateral view, the lachrymal is perfectly fused to the frontal and ectethmoid without any noticeable remaining suture between them forming part of the anterior wall of the eye socket (Warham 1996).

The bones are larger than Hydrobatidae and Oceanitidae with different proportions to those of Oceanitidae as they have short, stout humeri, ulnae, and femora, and greatly elongated tibiotarsi and tarsometatarsi (Olson 1985). These bones show no tendency toward the deep-diving adaptations of *Puffinus* or *Pelecanoides* in either the wing (flattened humerus and ulna) or hindlimbs (enlargement of crista cnemialis of the tibiotarsi and flattened tarsometatarsi) (Warham 1996). The cranium lacks the elongation of the area between the ectethmoid and the nasofrontal hinge with anterior elongation of the lacrimal typical of Oceanitidae (Olson and James 1991).

The fusion of the lachrymal to the frontal and ectethmoid is absent in most Procellariformes (Olson 1975b, Wharham 1996), but is present in the close genus *Lugensa*. The present material can be differentiated from *Lugensa* by the presence of a fenestrated fossa glandulae nasalis in the latter (Maurício 2014).

The shape of the fossil humeri also differs from the very slender and cylindrical humeri of *Bulweria* (Kuroda, 1983). In addition, the shape of these bones and the limb proportions are like other *Pterodroma* species (*Pt. madeira*, *Pt. feae*, *Pt. cahow*, and *Pt. deserta*) and different from those of *Bulweria* (Olson, 1975b).

These anatomical features have been checked with skeletons of *Pt. madeira*, *Pt. feae*, *Pt. cahow*, and *Pt. deserta*, *Puffinus puffinus* (Brünnich, 1764), *Pu. baroli* Bonaparte, 1856, and *Bulweria bulwerii* (Jardine and Selby, 1828) (Procellariidae), *Pelagodroma marina* (Latham, 1790) (Oceanitidae), and *Hydrobates pelagicus* (Linnaeus, 1758) (Hydrobatidae).

Pterodroma zinorum **Rando *et al.* sp. nov.**

urn:lsid:zoobank.org:act:69B8A7C7-875A-4D23-B3E8-414785A6EED4.

Holotype: MCMa 23020.023, a partial associated skeleton, including almost complete skull with premaxilla lacking palatinum and pterygoideum, left and right quadratum, 16 vertebrae, synsacrum, clavicula, a proximal fragment of the sternum, left and right coracoids, left and right scapula lacking distal part, right humerus, left and right ulna, left and right radius, right carpometacarpus, left phalanx proximalis digiti majoris, left phalanx distalis digiti majoris, left femur, distal fragment of right femur, proximal fragment of the right tibiotarsus, left tibiotarsus, left tarsometatarsus, and four pedal phalanges (Fig. 2; Supporting Information, Figs S1–S8).

Measurements of the holotype (mm): skull length: 66.3; skull height: 19.7; interorbital width: 8.7; culmen length: 16.5; coracoid length: 26; coracoid width: 17.4; right humerus length: 74.2; left ulna length: 76.5; right carpometacarpus length: 37; left femur length: 27; left tibiotarsus length: 49; left tarsometatarsus length: 30.2.

Type locality: Furna das Torres, Pico Island (Azores).

Horizon: Late Quaternary–Recent.

Distribution: The Azores archipelago (at least the islands of Graciosa, São Jorge, Pico, Terceira, and São Miguel).

Status: Extinct.

Etymology: The species' name honours both the late Paul Alexander Zino and his son Francis Zino for their effort and contributions to the knowledge and conservation of *Pterodroma* species from Macaronesia.

Paratypes: MCMa 23021.023, a partial associated skeleton including an almost complete skull with premaxilla lacking palatinum and pterygoideum, three fragments of the mandible, eight vertebrae, incomplete sternum, right humerus, left ulna, left radius, a proximal fragment of right radius, right carpometacarpus, left phalanx proximalis digiti majoris, right femur, right tibiotarsus, right tarsometatarsus, and two pedal phalanges.

MCMa 23022.023, a partial associated skeleton, including an almost complete skull with premaxilla lacking pterygoideum, left quadratum, three vertebrae, synsacrum, a proximal fragment of the sternum, left coracoid, a distal fragment of the right coracoid,

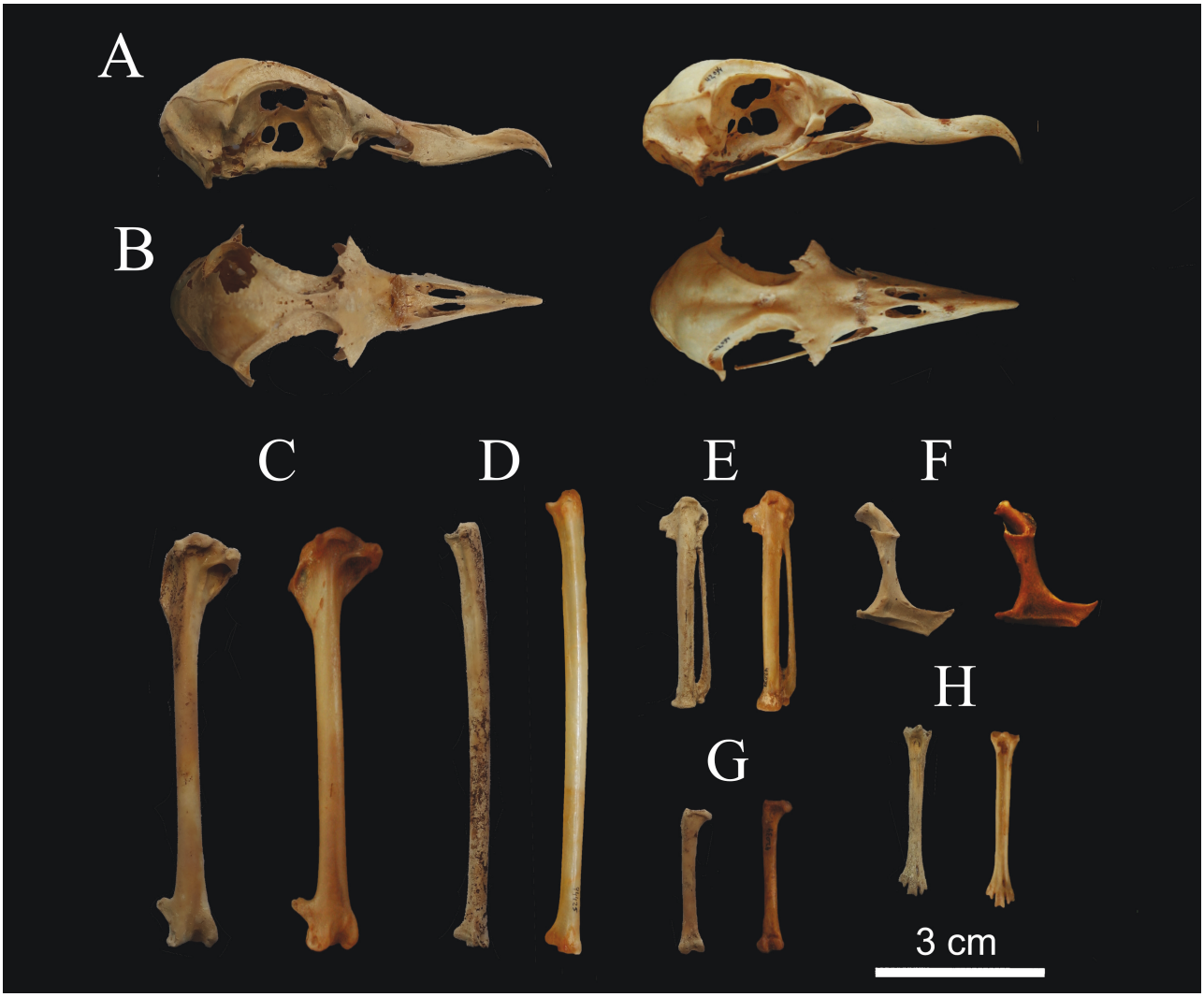

Figure 2. Bones of *Pterodroma zinorum* holotype from Pico Island (Azores) (left) and *Pt. madeira* from Madeira island (right). A, skull right lateral view. B, skull dorsal view. C, humerus, caudal view. D, ulna, dorsal view. E, carpometacarpus, dorsal view. F, coracoid, dorsal view. G, femur, caudal view. H, tarsometatarsus, dorsal view. All paired bones are of the left side except D. A-H (right series) MMF 42034; A-D, F (left) MCMa 23020.023; E, H (left) MCMa 23021.023; G (left) MCMa 23022.023.

left scapula, right humerus, right ulna, a distal fragment of the left ulna, a distal fragment of the left radius, right carpometacarpus, a distal fragment of the left carpometacarpus, right femur, left tibiotarsus, a distal fragment of the right tibiotarsus, left tarsometatarsus, and a proximal fragment of the right tarsometatarsus.

Other material belonging to Pterodroma zinorum: See Supporting Information, Table S1.

Suggested English name: Azorean Little Gadfly Petrel.

Suggested Portuguese name: Freira pequena dos Açores.

Diagnosis: A small species of *Pterodroma* similar in size to *Pt. madeira* from Madeira Island but with shorter forelimb bones (specially the ulna) and tarsometatarsus, but with a wider fossa glandulae nasalis in *Pt. zinorum* than in *Pt. madeira*. In addition, the distal extreme of the rostri maxillae of the new species shows a dorsal side higher and more curved than in *Pt. madeira* (Fig. 2).

Much smaller than the other Atlantic species of this genus (Tables 2–4; Figs 2–7; Supporting Information, S1–S8), including the South Atlantic *Pt. incerta* (Schlegel, 1863) (Carboneras *et al.* 2020a), but with a humerus longer than the small Pacific Ocean species of this genus, *Pt. pycrofti* Falla, 1933, *Pt. cookii* (Gray, 1843), *Pt. leucoptera* (Gould, 1844), *Pt. nigripennis* (Rothschild, 1893), and *Pt. axillaris* (Salvin, 1893) [see Table 3 and Cooper and Tennyson (2008)].

Remarks: The ^{14}C date of the complete right ulna of one specimen of *Pt. zinorum* sp. nov. from the type locality (RICH-21397) 1181 ± 30 BP was calibrated with 38 ± 139 (Δ R ± SD) providing the interval 1104–1672 CE (Table 1). Although there is overlap in the length of the hindlimb bones (femur, tibiotarsus, and tarsometatarsus) of *Pt. zinorum* and *Pt. madeira*, forelimb bones referable to the former (humerus, ulna, and carpometacarpus) are smaller than in *Pt. madeira* (Tables 2–4; Figs 2–4, 6, 7; Supporting Information, Figs S1–S8), so *Pt. zinorum* is the smallest Atlantic species of the genus. The morphology of the postcranial bones of the new species is similar to that of *Pt. madeira* with differences in the bone length between the two species. The ulna, tarsometatarsus (Wilk's

Table 1. Radiocarbon ages (yr BP) of gadfly petrels (genus *Pterodroma)* and two 2σ calibration intervals (cal BCE/cal CE). The two 2σ calibration intervals have been performed (i) using the Marine20 calibration curve and, (ii) using the Marine20 calibration curve with a Δ R ± SD calculated from the 20 closer samples to each archipelago (18 ± 141 for Madeira and 38 ± 139 for Azores) through the Marine Reservoir Correction Database (http://calib.org/marine/). (A), Azores; (M), Madeira Archipelago.

Lab code	Island	Sample	$\delta^{13}C$ (o/oo)	$\delta^{15}N$ (o/oo)	Radiocarbon age	2σ	2σ ΔR ± SD
RICH-21397	Pico (A)	*Pt. zinorum*	–13.8	+13.5	1181 ± 30 BP	1254–1467 cal CE	1104–1672 cal CE
RICH-21398	Pico (A)	*Pterodroma* sp. B	–14.0	+14.6	1654 ± 30 BP	760–1045 cal CE	665–1263 cal CE
WK-28566	Porto Santo (M)	*Pterodroma* sp. A	–13.4		7113 ± 37 BP	5607–5328 cal BCE	5739–5115 cal BCE

Table 2. Skull and mandible measurements of current species of *Pterodroma* (*Pt. madeira* from Madeira Island, *Pt. deserta* from Bugio Islet, Madeira Archipelago, *Pt. feae* from Cape Verde Archipelago, and *Pt. cahow* from Bermuda Island) and *Pt. zinorum* from Pico Island (Azores Archipelago), *Pterodroma* sp. A from North Dunes of Porto Santo (Madeira Archipelago), and *Pterodroma* sp. from Canary Islands. Sample size, mean length ± standard error (mm), and range are given. Measurements as in Rando (2002).

	Pt. madeira Madeira	*Pt. deserta* Bugio	*Pt. feae* Cape Verde	*Pt. cahow* Bermuda	*Pt. zinorum* sp. nov. Pico	*Pterodroma* sp. A Porto Santo	*Pterodroma* sp. Canary Islands
Skull							
Length	(1) 66.7	(3) 74.2 ± 1.5 76.3–72.7	(1) 71.3	(1) 71.7	(3) 64.8 ± 1.8 66.4–62.3	(1) 72.2	(1) 76.7
Height	(1) 19.7	(3) 20.4 ± 0.1 20.3–20.4	(1) 20.2	(1) 20.1	(5) 20.3 ± 0.2 20–20.4		(2) 23.1 ± 0.7 23.6–22.6
Width	(1) 26.7	(3) 29.5 ± 0.7 30.2–28.6	(1) 28	(1) 28.8	(1) 26.3		(1) 30.1
Interorbital width	(1) 9.6	(3) 10.1 ± 0.1 10.1–10	(1) 10.1	(1) 8.5	(5) 9.7 ± 0.6 10.3–8.7	(2) 9.6 ± 0.1 9.6–9.5	(2) 10 ± 0.9 9.3–10.7
Maxila dorsal length	(4) 32.6 ± 0.6 33.6–31.8	(3) 36.8 ± 0.4 37.1–36.2	(1) 35.3	(1) 35.2	(2) 31.4 ± 1.2 32.5–30.2	(1) 34.7	(1) 39.5
Maxilla length (from jugal articulation)	(3) 29.1 ± 0.4 29.6– 28.6	(3) 31.5 ± 1 32.9–30.8	(1) 31.6	(1) 30.9	(2) 26.2 ± 0.2 26.4–26	(1) 29.9	(1) 33.1
Culmen length (from anterior edge of narina)	(6) 18.5 ± 0.4 19.2–18	(3) 20.2 ± 0.8 21.2–19.5	(1) 19.6	(1) 19.6	(3) 16.9 ± 0.9 17.9–15.8	(1) 18.8	(1) 21.3
Culmen width	(3) 11.1 ± 0.7 11.8–10.1	(3) 13.2 ± 0.5 13.8–12.7	(1) 13		(1) 11.1		(2) 14 ± 0.5 14.4 –13.7
Width of the nasofrontal join	(4) 8.8 ± 0.4 9.1–8.1	(3) 10.8 ± 0.2 11–10.6	(1) 10.4	(1) 10.1	(5) 8.5 ± 0.3 8.9–8.1	(1) 8.9	(2) 11.6 11.6–11.6
Mandible							
Length	(1) 52.35	(3) 58.4 ± 0.6 59.2-57.6	(1) 56.9	(1) 60.2			-

Lambda = 0.203; d.f. = 4, 52; $P < .001$), and carpometacarpus (U = –2.683; $P < .007$, U = –2.761; $P < .006$) are smaller than *Pt. madeira* (tests performed between current bones of *Pt. madeira* and material from both Graciosa and Pico Islands, respectively). The new species has a shorter culmen (U = –2.121; $P = .034$) and a narrower nasofrontal joint (U = –2.236; $P = .025$) (tests performed between current bones of *Pt. madeira* and material from Pico) (Tables 2–4; Fig. 2).

Pterodroma deserta

Material and collection information: IMEDEA 109596, fragmented humerus. IMEDEA 109597, left complete ulna. IMEDEA 109595, right complete tarsometarsus.

Horizon: Holocene–Recent.

Distribution: Bugio Islet (Desertas Islands, Madeira Archipelago).

Remarks: The material, probably very recent, is biometrically and morphologically indistinguishable from those of the current population of *Pt. deserta* that breed on this small islet.

Pterodroma sp. A

The fossil bones included under this name are slightly larger than those of current *Pt. madeira*, specifically the skull length (Tables 2, 4). This fact, together with its breeding habitat in sand dunes close to the coast, which is very different from that of *Pt. madeira* that breeds inland 1600 m above sea level on Madeira Island (Carboneras *et al.* 2020b), suggests that it could be a new species. However, its ascription of these materials to other current species cannot be ruled out due to the close morphology and

Table 3. Measurements of *Pterodroma* long bones from the Azores. Data of *Pterodroma zinorum* and *Pterodroma* sp. B from the islands of Graciosa, São Jorge, Pico, São Miguel and Terceria. Sample size, mean length ± standard error (mm), and range are given. Measurements as in Rando (2002).

	Pt. zinorum **Graciosa**	***Pt. zinorum*** **São Jorge**	***Pt. zinorum*** **Pico**	***Pt. zinorum*** **São Miguel**	***Pt. zinorum*** **Terceira**	***Pterodroma* sp. B** **Graciosa**	***Pterodroma* sp. B** ***São Jorge***	***Pterodroma* sp. B** **Pico**	***Pterodroma* sp. B** **São Miguel**	***Pterodroma* sp. B** **Terceira**
Humerus length	(23) 74.3 ± 1.9 78.0–70.1		(22) 72.9 ± 1.2 75.8–70.5	(1) 74.1	(1) 73.9	(8) 84.9 ± 1.8 87.2–81.4	(3) 88.4 ± 0.9 89.4–87.3	(4) 88.4 ± 0.6 89.0–87.4	(3) 89.6 ± 0 89.7–89.6	(1) 89.9
Ulna length	(9) 76.0 ± 1.8 77.8–72.2	(1) 72.7	(13) 75.5 ± 1.6 78.7–72.8	(1) 76.8	(1) 75.5	(5) 86.4 ± 1.9 89.7–84.0		(6) 92.1 ± 0.8 93.3–91.0	(4) 92.4 ± 1 94.1–91.3	(2) 92.5 ± 1.2 93.7–91.3
Carpometacarpus length	(16) 37.3 ± 0.7 38.2–35.2		(22) 36.6 ± 0.8 38.3–35.3	(1) 37.5	(2) 37.9 ± 0.1 37.9–37.8	(19) 42.3 ± 1 44.8–40.7	(3) 44.1 ± 1.1 45.5–4 2.8	(8) 44.2 ± 0.5 44.9–43.3	(2) 44.9 ± 0.3 45.2–44.6	(2) 44.5 ± 1.4 45.9–43.1
Femur length	(16) 27.6 ± 0.8 29.2–26.1		(10) 26.6 ± 0.7 27.5–25.6			(2) 31.6 ± 0.3 32.0–31.3	(1) 30.4	(2) 32.5 ± 0.4 32.9–32.1		(1) 29.9
Tibiotarsus length	(5) 50.7 ± 0.9 52.3–49.5		(11) 49.3 ± 1.2 51.9–47.4			(3) 56.7 ± 1.4 58.2–54.8		(1) 57.6	(1) 56.7	(1) 56.1
Tarsometatarsus length	(13) 30.2 ± 0.6 31.3–28.7		(13) 29.7 ± 0.5 30.7–28.5	(1) 31.3		(2) 37.5 ± 0.5 38.0–37.0	(1) 37.3	(2) 36.7 ± 0.3 37.0–36.4	(1) 34.3	

Table 4. Measurements of *Pterodroma* long bones from the Madeiran Archipelago. *Pterodroma madeira* from Madeira Island (material of current specimens), *Pterodroma* sp. A and B from Madeira Island and Porto Santo (Madeira Archipelago) (fossil material), *Pt. deserta* from Bugio (Madeira Archipelago) (current and fossil material), *Pt. feae* from Cape Verde (material of current specimens), *Pt. cahow* from Bermuda (material of current specimens), and *Pterodroma* sp. from Canary Islands (fossil material). Sample size, mean length ± standard error (mm), and range are given. Measurements as in Rando (2002).

	Pt. madeira **Madeira current**	***Pterodroma* sp. B** **Madeira**	***Pterodroma* sp. B** **Porto Santo** ***Porto Frades***	***Pterodroma* sp. A** **Porto Santo North Dunes**	***Pterodroma* sp. A** **Porto Santo Fonte da Areia**	***Pt. deserta*** **Bugio current**	***Pt. deserta*** **Bugio fossil**	***Pt. feae*** **C.Verde current**	***Pt. cahow*** **Bermuda current**	***Pterodroma* sp.** **Canary Islands**
Humerus length	(2) 79.3 ± 3.3 82.6–75.9	(22) 83.2 ± 1.8 86.4–79.3	(11) 87.5 ± 1.8 90.4–84.2	(6) 82.4 ± 2.2 85.1–79.6	(12) 82.2 ± 1.4 85.7–80.0	(4) 85.5 ± 1.4 87.6–83.9	(1) 84.6	(1) 84.9	(4) 86.6 ± 0.9 87.8–85.3	(2) 87.9 ± 0.3 88.2–87.7
Ulna length	(8) 83.6 ± 2.6 88.2–80	(27) 86.7 ± 1.8 89.4–82.7	(13) 89.4 ± 2.5 93.9–83.4	(6) 85.0 ± 2 87.8–81.8	(5) 84.4 ± 0.5 85–83.7	(4) 88.4 ± 1 90.2–87.5	(1) 89.1	(1) 87.3	(4) 88.6 ± 2.7 91.9–84.3	(2) 90.6 ± 0.5 91.2–90.1
Carpometacarpus length	(3) 40.1 ± 1 41.2–38.7	(34) 41.9 ± 1.1 43.5–39.2	(36) 43.8 ± 1 46–41.5	(12) 41.9 ± 1.1 43.6–39.9	(19) 42.2 ± 0.8 43.7–41	(4) 44.2 ± 0.5 45–43.6		(1) 40.7	(4) 43.3 ± 1.9 46.1–41.0	(3) 44.5 ± 0.5 45.1–44.0
Femur Length	(1) 27.1	(12) 29.5 ± 1 30.9–27.6	(8) 29.6 ± 0.4 30.3–29	(1) 29.1	(11) 28.6 ± 0.6 29.5–27.5	(3) 30.4 ± 0.5 30.9–29.8		(1) 30.8	(3) 29.5 ± 0.9 30.8–28.8	(1) 32.3
Tibiotarsus length	(1) 49.9	(5) 54.0 ± 2.3 56.5–51.2	(9) 54.9 ± 0.7 55.8–53.5	(3) 51.7 ± 0.6 52.5–51.2	(8) 52.9 ± 0.9 54.4–51.2	(3) 54.5 ± 1.1 55.7–53.0		(1) 55.3	(3) 56.5 ± 1 57.4–55.2	(1) 56
Tarsometatarsus length	(12) 31.9 ± 0.6 33.0–30.7	(11) 35.3 ± 0.9 36.1–33.3	(18) 34.3 ± 0.9 35.9–32.1	(3) 32.7 ± 0.9 33.7–31.5	(14) 33.7 ± 0.8 34.6–32.1	(3) 35.2 ± 0.9 36.4–34.3	(1) 35.2		(3) 35.3 ± 0.8 36.3–34.3	(1) 35.4

Figure 3. Forelimb bones of *Pterodroma*. Humeri (caudal view), ulnae (ventral view) and carpometacarpi (ventral view), upper (u), middle (m) and lower (l) row respectively. Current species: *Pt. cahow* from Bermuda (A), *Pt. feae* from Cape Verde (B), *Pt. deserta* from Bugio (Madeira Archipelago) (C) and *Pt. madeira* from Madeira Island (D). Fossil material from Macaronesia: *Pterodroma* sp. A from Porto Santo (Madeira Archipelago) (E), and *Pt. zinorum* from Azores Islands, São Miguel (F), Graciosa (G), Pico (H) and Terceira (I), *Pterodroma* sp. B from Madeira Island (J), Porto Santo (K), and Azores Islands, São Miguel (L), Graciosa (M), Pico (N) and Terceira (O). Bones A (u), C (u), D (u), K (u), M (u), O (u), B (m), E (m), F (m), H (m), I (m), J (m), K (m), L (m), N (m), O (m), A (l), B (l), C (l), F (l), H (l), I (l) and M (l) are from the right side, the other are from the left. A, IMEDEA 94430; B, IMEDEA 103568; C, IMEDEA 94424; D (u and l) MMF 42034, D (m) IMEDEA 94425; E (u) MHMN 45597, E (m) MHMN 45466, E (l) MHMN 45644; F (u) MCMa 2271.017, F (m) MCMa 2270.017, F (l) MCMa 2263.017; G (u) MCMa 2011.017, G (m) MCMa 2037.017, G (l) MCMa 2062.017; H (u) MCMa 23021.023, H (m) MCMa 2302.017, H (l) MCMa 2306.017; I (u) MCMa 2258.017, I (m) MCMa 2260.017, I (l) 2260.017; J (u) MMF 45261, J (m) MMF 45333, J (l) MMF 45305; K (u) MHMN 46087, K (m) MHMN 46061, K (l) MHMN 46022; L (u and m) MCMa 2265017, L (l) MCMa 2264.017; M (u) MCMa 2287.017, M (m) MCMa 2171.017, M (l) MCMa 2184.017; N (u) MCMa 2282.017, N (m) MCMa 2287.017, N (l) MCMa 2283.017; O (u) MCMa 2255.017, O (m) MCMa 2254.017, O (l) McMa 2253.017.

size that show the species inside this genus (Figs 3–7; Tables 2, 4; Supporting Information, Figs S1–S8).

Material and collection information: See Supporting Information, Table S1.

Horizon: Quaternary–Recent.

Distribution: Sandy sites of Porto Santo (Fonte da Areia and North Dunes) (Madeira Archipelago).

Remarks: The ^{14}C date of the left ulna, radius, and carpometacarpus of one specimen of *Pterodroma* sp. A from North Dunes (WK-28566, 7113 ± 37 BP) was calibrated with 18 ± 141 (Δ R ± SD) to provide the interval 5739–5115 cal BCE (Table 1). Some of the material overlaps with several extant North Atlantic species of *Pterodroma* (Tables 2, 4) but is closer to those of *Pt. madeira* than to the other species of bigger size (Fig. 3). No differences were found between ulna lengths from the current *Pt. madeira* and from North Dunes (U = –0.645; P = .519) and from Fonte da Areia (U = 0; P = 1) but the carpometacarpus length of the current *Pt. madeira* is smaller than those of North Dunes (U = –2.021 P = .043) and Fonte da Areia (U = –2.44 P = .015).

Material from Fonte da Areia and North Dunes (humerus, ulna, carpometacarpus, femur, tibiotarsus, and tarsometatarsus) is longer than those of *Pt. zinorum* from the Azores (Wilk's

Figure 4. Hindlimb bones of *Pterodroma*. Femora (caudal view), tibiotarsi (cranial view) and tarsometatarsi (dorsal view), upper (u), middle (m) and lower (l) row respectively. Current species: *Pt. cahow* from Bermuda (A), *Pt. feae* from Cape Verde (B), *Pt. deserta* from Bugio (Madeira Archipelago) (C) and *Pt. madeira* from Madeira Island (D). Fossil material from Macaronesia: *Pterodroma*. sp. A from Porto Santo (E), *Pt. zinorum* from Azores Islands, São Miguel (F), Graciosa (G), Pico (H), *Pterodroma* sp. B from Madeira Island (J), Porto Santo (K), and the Azores São Miguel (L), Graciosa (M), Pico (N) and Terceira (O). Bones B (u), F (u), G (u), H (u), M (u), N (u), A (m), G (m), H (m), J (m), L (m), N (m), C (l), E (l), F (l), G (l), H (l), J (l), M (l) and N (l) are from the right side, the other are from the left. A, IMEDEA 94430; B, IMEDEA 103568; C IMEDEA 94424; D MMF 42034; E (u) MHMN 45781, E (m) MHMN 45981, E (l) MHMN 45611; F (u) MCMa 2270.017, F (l) MCMa 2270.017; G (u) MCMa 2114.017, G (m) MCMa 2127.017, G (l) MCMa 2137.017; H (u, m and l) MCMa 23020.023; J (u) MMF 45282, J (m) MMF 45423, J (l) MMF 45323; K (u) MMF 46151, K (m) MMF 46074, K (l) MMF 46153; L (m and l) MCMa 2273.017; M (u) MCMa 2209.017, M (m) MCMa 2210.017, M (l) MCMa 2214.017; N (u, m and l) MCMa 2292.017; O (u and m) MCMa 2253.017.

Lambda = 0.53; d.f. = 6, 17; $P < .001$) but many are smaller than those of *Pt. deserta* and *Pt. cahow* (Nichols and Mowbray, 1916) (humerus and ulna, Wilk's Lambda = 0.28; d.f. = 4, 30; $P = .001$; tibiotarsus, U = –2.102; $P = .036$ and U = –2.57; $P = .01$; and tarsometatarsus, U = –2.488; $P = .013$ in both tests).

The MANOVA performed with the humerus, ulna and carpometacarpus lengths from Porto Santo (Fonte da Areia and North Dunes) and fossil material from Madeira revealed differences (Wilk's Lambda = 0.455; d.f. = 6, 36; $P = .021$) with the ulnae from the Madeiran fossils being longer than those from North Dunes ($P = .009$) and Fonte da Areia ($P = .002$). However, there were no differences between the humerus ($P = .644$ and $P = .881$) and carpometacarpus ($P = .571$ and $P = .276$) of fossil material from Madeira and these sites of Porto Santo. The ANOVA performed between the femur length of fossil material from Madeira and Fonte da Areia indicates a longer size of the former ($F_{1,21} = 6.154$; $P = .022$). The tibiotarsus length of the Madeira fossils is similar to those from Fonte da Areia ($F_{1,11} = 1.283$; $P = .281$) and North Dunes (U = -1.043; $P = .297$), whereas the tarsometatarsus is longer in the fossil material from Madeira than Fonte da Areia ($F_{1,23} = 32.55$; $P < .001$) and North Dunes (U = –2.413; $P = .016$).

The bones from the Porto dos Frades site (Porto Santo) are longer than those from Fonte da Areia and North Dunes.

Figure 5. Articulated skeleton of *Pterodroma* sp. A. from North Dunes site in Porto Santo (Madeira Archipelago). Note the remains of an egg in the posterior side of the bird, documenting that *Pterodroma* sp. A was a burrow nesting species. Specimen exposed at Museu de História Natural do Jardim Botânico da Madeira, Funchal (without collection number).

The MANOVA performed with the humerus, ulna, and carpometacarpus lengths from North Dunes, Fonte da Areia, and Porto dos Frades (all sites from Porto Santo) show differences (Wilk's Lambda = 0.194; d.f. = 6, 34; $P < .001$) between the material from Porto dos Frades and Fonte da Areia ($P < .001$) and between Porto dos Frades and North Dunes ($P < .001$). The femurs from Porto dos Frades are longer than those of Fonte da Areia ($F_{1,17} = 14.63$; $P = .001$). The tibiotarsus from Porto dos Frades are longer than both from North dunes (U = –2,49; $P = .013$) and Fonte da Areia ($F_{1,15} = 23.25$; $P < .001$), like the tarsometarsus (U = –2211; $P = .027$, and $F_{1,30} = 10.12$; $P < .003$, respectively).

The material from Fonte da Areia and North Dunes is smaller than those from the Azores (excluding those of *Pt. zinorum* n. sp.) (see Figs 3, 4, 6, 7; Tables 2–4). In addition, the *Pterodroma* bones from El Hierro (Canary Islands) are larger than those from Fonte da Areia (U = –2727; $P = .006$) and North Dunes (U = –2598; $P = .009$) (test performed with carpometacarpus lengths).

Pterodroma sp. B

This name includes material that is similar in morphology and close in size to those of the current *Pt. deserta*, *Pt. feae*, and *Pt. cahow*, so they could be included in any of these species.

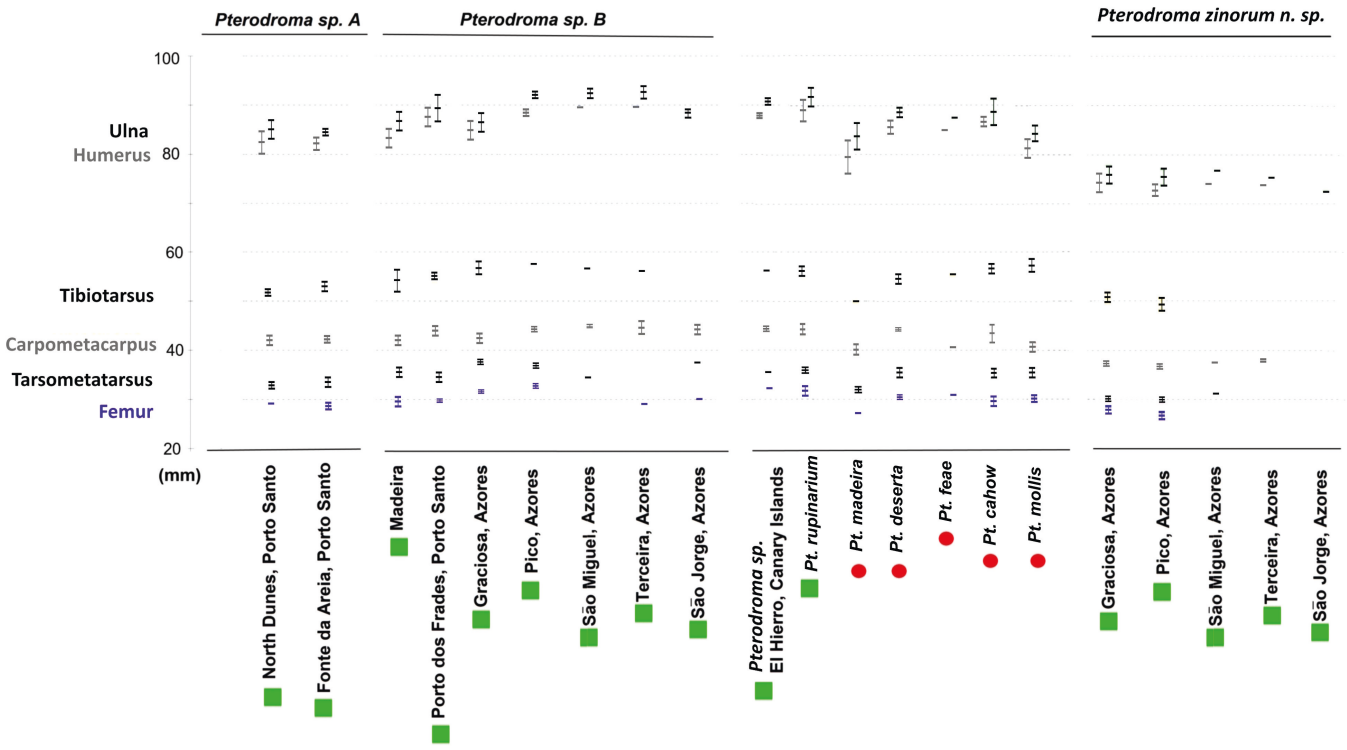

Figure 6. Plot of mean ± SD of forelimb bones length (humerus, ulna and carpometacarpus) and hindlimb bones length (femur, tibiotarsus and tarsometatarsus) of *Pterodroma* found in the fossil record of the Macaronesian islands (Pt. zinorum, *Pterodroma* sp. A, *Pterodroma* sp. B and *Pterodroma* sp. from El Hierro, Canary Islands. Green squares) and of current species (*Pt. madeira*, *Pt. deserta*, *Pt. feae*, *Pt. cahow* and *Pt. mollis*. Red circles). In the case of the material from Porto Santo (Madeira Archipelago) information about the site is indicated, for the other fossil material information on the island and archipelago is given. Data from Tables 3 and 4. Measurements of *Pt. rupinarum* and *Pt. mollis* are from Olson (1975) and Cooper & Tennyson (2008) respectively.

Nevertheless, it also remains possible (even probable) that they represent one or more cryptic unknown species (Figs 3, 4, 6, 7; Tables 2, 3, 4; Supporting Information, Figs S1–S8).

Material and collection information: See Supporting Information, Table S1.

Horizon: Late Quaternary–Recent.

Distribution: Porto dos Frades (Porto Santo, Madeira Archipelago), Madeira Island, and the Azores (São Miguel, Terceira, Graciosa, São Jorge, and Pico).

Remarks: The ^{14}C date of two fragments of ulna (proximal right and distal left) of one specimen of *Pterodroma* sp. B from Furna das Torres, Pico (Azores): RICH-21398 and 1654 ± 30 BP, was calibrated with 38 ± 139 (Δ R ± SD) providing the interval 665–1263 CE (Table 1). These bones are longer than those of the current *Pt. madeira* (Tables 2–4; Figs 3, 4, 6, 7). The ANOVA performed with the ulna lengths of the current *Pt. madeira* and those from these material [from Madeira Island, Porto dos Frades (Porto Santo), and Graciosa, Pico, and São Miguel (Azores)] indicate a smaller size of *Pt. madeira* bones ($F_{5,62}$ = 18 526; P < .001). The carpometacarpus from Madeira Island, Porto dos Frades (Porto Santo), Graciosa, and Pico are longer than those of the current *Pt. madeira* (U = –2.170; P = .03, U = –2.846; P = .004, U = –2.536; P = .011, and U = –2.449; P = .014, respectively). In addition, the ANOVA performed with the tarsometatarsus lengths of the current *Pt. madeira* and those of *Pterodroma* sp. B from the island of Madeira sites and from Porto Santo (Porto dos Frades) indicate a small size of the former ($F_{2,41}$ = 53 326; P < .001).

The material of this genus found in the Canary Islands (El Hierro) (Rando 2002) is of a similar size to those of this group (Tables 2, 4; Figs 3, 4, 6, 7). No differences were found in the carpometacarpus lengths between the fossil bones from El Hierro, the fossils from Pico (U = –0,816; P = .414), São Jorge (U = –0,655; P = .513), Porto dos Frades (U = –1528; P = .126), and the bones of the current specimens of *Pt. cahow* (U = –1061; P = .289) and *Pt. deserta* (U = –0,707; P = .48).

DISCUSSION

The material from Macaronesia and the fossil and archaeological records from northern Europe (Serjeantson 2005) and Gibraltar (Cooper 2005) indicate a previous wider distribution of *Pterodroma* in the North Atlantic Ocean. These records show at least two species of *Pterodroma* co-inhabiting several Macaronesian islands (Madeira, Porto Santo, São Miguel, Terceira, Pico, Faial, São Jorge, and Graciosa) in contrast to the current situation where the living species are the only one of this genus in the islands where they bred (Ramos *et al.* 2016).

Some current species of *Pterodroma* are impossible to discriminate through morphometric characters of their bones. For instance, the MANOVA of the humerus, ulna, and carpometacarpus

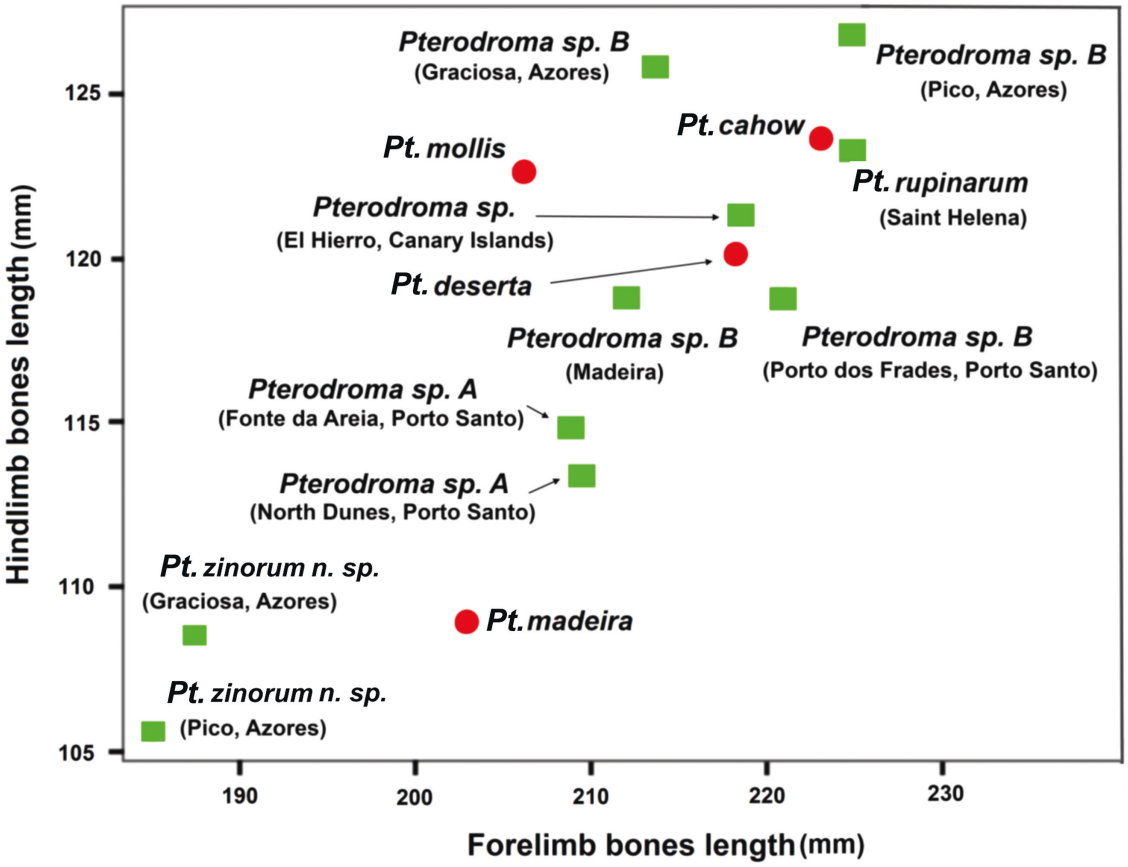

Figure 7. Plot of forelimb bones length (humerus+ulna+carpometacarpus) vs. hindlimb bones length (femur+tibiotarsus+tarsometatarsus) of *Pterodroma* found in the fossil record of the Macaronesian islands (*Pt. zinorum*, *Pterodroma* sp. A and *Pterodroma* sp. B., green squares) and of current species (*Pt. madeira*, *Pt. deserta*, *Pt. feae*, *Pt. cahow* and *Pt. mollis*, red circles). In the case of the material from Porto Santo (Madeira Archipelago) information about the site is given, for the other fossil material information on the island and archipelago is given in brackets. Data from Tables 3 and 4. Measurements of *Pt. rupinarum* and *Pt. mollis* are from Olson (1975) and Cooper & Tennyson (2008) respectively.

lengths of *Pt. deserta* (Bugio Islet, Madeira Archipelago) and *Pt. cahow* (Bermuda) did not reveal any differences (Wilk's Lambda = 0.376; d.f. = 3, 4; $P = .23$). Also, the femur ($U = -1.091$; $P = .275$), the tibiotarsus ($U = -1.528$; $P = .127$), and the tarsometatarsus lengths ($U = -0.218$; $P = .827$) of these species are not different. In addition, the lengths of limb bones of the solely available specimen of *Pt. feae* (Fogo, Cape Verde islands) fall inside, or close to, the range of variation of both species (Table 2, 4), thus it is difficult to determine the original diversity of this genus in the Atlantic through bone biometry. Nonetheless, the fossil records of *Pterodroma* in Macaronesia indicate the extinction of at least one species and a former much wider distribution of this genus in the Atlantic Ocean.

Considering that the fossil remains obtained of each identified entity (*Pterodroma* sp. A, *Pterodroma* sp. B, and *Pt. zinorum*) on each island document at least an ancient population, at least 11 populations of this genus have disappeared from the Azores: *Pt. zinorum* and *Pterodroma* sp. B in São Miguel, Terceira, Pico, São Jorge, and Graciosa, plus another population of *Pterodroma* sp. B in Faial. One population has disappeared from the island of Madeira (*Pterodroma* sp. B) plus two from Porto Santo (*Pterodroma* sp. A and B), whereas in the Canary Islands and in the Selvagens the *Pterodroma* fossils have been found only in one island on each archipelago (Rando 2002, Gangloff *et al.* 2013). The current *Pterodroma* species are present on six Macaronesian islands (Ramos *et al.* 2016) (Fig. 1). The data indicate that of the 22 former populations of *Pterodroma* in four archipelagos, only six populations (27%) survive today in two archipelagos (Cape Verde and Madeira). This approach is very conservative, so it is probable that both the number of extinct populations and species is higher.

Due to their breeding-site fidelity (Ramos *et al.* 2016), the extinction of many populations indicates a loss of an important part of the original genetic diversity of *Pterodroma* in Macaronesia in contrast to *Calonectris*, another Procellariform genus that breeds on all Macaronesian islands (Gómez-Díaz *et al.* 2006). In the Canary Islands, *C. borealis* (Cory, 1881) exhibits high values of genetic diversity with similarities between the ancient and the modern populations (Ramírez *et al.* 2013).

Gadfly petrels are currently absent as breeders in latitudes above 33°N (Madeira archipelago) (Fig. 1) showing a gap in its distribution in the North Atlantic Ocean (Ramos *et al.* 2017), so *Pterodroma* species may either have been exterminated by introduced predators or overlooked in the Azores, especially if they nest, as they often do elsewhere, in the winter (Bourne 1965, 1983). In 1990, a living *Pterodroma* was caught in a seabird colony in the Azores with similar measurements to those found on Bugio (*Pt. deserta*) but with a longer tail more like that of *Pt. cahow* and

a moderately developed brood patch, so it seems quite likely that this bird breeds in the Azores (Bibby and Nevo 1991). In 1993, another *Pterodroma* caught on an islet was identified as *Pt. feae* either as a vagrant from Bugio (currently *Pt. deserta*) or the Cape Verde Islands or as an Azores' bird from an unknown breeding population (Monteiro and Furness 1995). This bird was closely similar in measurements to the specimen caught by Bibby and Nevo (1991), except for a shorter tail length similar to that of the birds of Bugio (Monteiro and Furness 1995). The authors obtained a louse, identified as *Halipeurus theresae* Timmermann, 1969, from this bird. This species has been previously found in *Pterodroma* from Bugio (Zonfrillo 1993), so it is possible that the Azores' population of *Pterodroma*, if it exists, may already be close to extinction as a consequence of rats (Monteiro and Furness 1995). The dimensions of the two birds from the Azores are larger than *Pt. madeira* and similar to *Pt. deserta*, *Pt. feae*, and *Pt. cahow*. The *Pterodroma* sp. B. remains from the Azores are similar to the latter three species (Figs 6, 7) so these captures may represent a vestigial population of this taxon from islets where rodents have not been introduced.

Within the genus *Pterodroma*, the current Macaronesian species are a monophyletic clade (Jesus *et al.* 2009), *Pt. madeira* the ancestral taxon, and *Pt. feae* and *Pt. deserta* sister-taxa that diverged later (Gangloff *et al.* 2013). The divergence of the three populations occurred without gene flow and very recently, the split between *Pt. feae–Pt. deserta* was estimated at 32 Kya (9–153 Kya) and the split between the ancestor *Pt. feae–Pt. deserta* and *Pt. madeira* occurred at 153 Kya (47–359 Kya). The populations of Madeira and Bugio Islands in the Madeira Archipelago (the closest populations) (Fig. 1) have been intensively monitored over the last three decades with no interbreeding between *Pt. madeira* and *Pt. deserta* observed (Gangloff *et al.* 2013).

Additionally, mitochondrial DNA sequences from *Pterodroma* bones from the Hebrides (Scotland), and from *Pt. rupinarum* from the island of Saint Helena indicate that both are part of a very young evolutionary radiation with a former wider distribution during the last millennia (Serjeantson 2005, Brace *et al.* 2014, Welch *et al.* 2014).

The bones of *Pt. feae* and *Pt. deserta* are similar morphologically but *Pt. madeira* is smaller ($F_{1,10}$ = 10.36, P = .009 for ulna; U = –2.121, P = .034 for carpometacarpus; and U = –2.598, P = .009 for tarsometatarsus lengths) (Tables 2, 4; Figs 3, 4; Supporting Information, Figs S1–S8). The findings of recent extinct populations of *Pterodroma* close in size to both *Pt. feae–deserta*, and *Pt. madeira*, and the new species *Pt. zinorum*, smaller than *Pt. madeira*, show a more complex scenario in the phylogeography of this genus in Macaronesia.

The fossil record of *Pterodroma* in the Azores, with at least two species, seems to parallel the current situation in the Madeira archipelago where two current species of different sizes are breeding (*Pt. madeira* and *Pt. deserta* breeding on Madeira and Bugio Islands, respectively). As in the Madeira archipelago, the Azores were inhabited by gadfy petrels of two different body sizes. Both size classes are close in both archipelagos, so it is possible a close phylogenetic relationship between the species belonging to the same size class, like occur between the petrels of Bugio (*Pt. deserta*) and Cape Verde (*Pt. feae*) (Jesus *et al.* 2009, Gangloff *et al.* 2013). If this hypothesis is true, the larger petrels from the Azores could be part of the recent radiation *Pt. deserta–Pt. feae* in the Atlantic (Brace *et al.* 2014, Welch *et al.* 2014), and *Pt. zinorum* could be a sister-taxon of the smaller *Pt. madeira*; only through ancient DNA techniques will it be possible to validate this hypothesis.

Radiocarbon data indicate that *Pt. zinorum* survived, at least, until the 12th century (Table 1), thus this species is the third extinct seabird during the last millennium in the western Palaearctic, together with the great auk *Pinguinus impennis* (Linnaeus, 1758) (Thomas *et al.* 2019) and the lava shearwater *Puffinus olsoni* McMinn *et al.*, 1990 (Rando and Alcover 2008). The 2σ calibration interval, of the dated bones of *Pt. zinorum* performed using the Marine20 calibration curve with 38 ± 139 (Δ R ± SD) (1104–1672 cal CE) overlaps with the Portuguese presence on the archipelago in the first half of the 15th century (Newitt 2005). The other radiocarbon dates of *Pterodroma* bones from Macaronesia indicate a late last record for *Pterodroma* sp. B from Pico (665–1263 cal CE) and a Mid-Holocene (5739–5115 cal BCE) last record for *Pterodroma* sp. A from Porto Santo (Madeira). These recent dates, especially the two former, point to historical events linked to human activities and to the introduction of alien mammals as the most probable cause for the extinction, like other Procellariiformes in Macaronesia and other islands around the world (Blackburn *et al.* 2004, Rando and Alcover 2008, 2010, Scofield 2009).

SUPPLEMENTARY DATA

Supplementary data are available at *Zoological Journal of the Linnean Society* online.

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AUTHOR CONTRIBUTIONS

Fieldwork and material curation J.C.R, H.P, F.P, E.TR, and J.A.A; data analysis and writing original draft J.C.R and J.A.A; review and editing J.C.R, H.P, F.P, E.TR, and J.A.A; project administration J.A.A.. All authors approved the final submitted version for publication.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest in relation to this work.

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DATA AVAILABILITY

Data will be made available on reasonably request.

APPENDIX

CURRENT COMPARATIVE MATERIAL EXAMINED

Pterodroma madeira (most of the available material are partial skeletons of birds depredated by rats and collected in breeding areas on the Island of Madeira): MMF 26304 (1–4), 26306, 30500, 31492, 31596, 31599, 31600, 31603 (1–2), 42033, 42034, 42037 (1–5), 42038, 42039, 42041, 42042.

Pterodroma deserta (Bugio Islet, Madeiran Archielago): MMF 33794; IMEDEA 94424, 94426, 94427.

Pterodroma feae (Fogo Island, Cape Verde): IMEDEA 103568.

Pterodroma cahow (partial skeletons from Bermuda Island): MMF 2922-2; IMEDEA 94430 (1-30).

Pelagodroma marina (Selvagens Islands): DZUL 2396, 2397, 2405.

Hydrobates pelagicus (Canary Islands): DZUL 2843, 2847, 2849.

Bulweria bulwerii (Canary Islands): DZUL 393, 1379, 1832.

Puffinus puffinus (Canary Islands): DZUL 392, 2756.

Puffinus baroli (Canary Islands): DZUL 384, 826, 2255.

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