

# Unforeseen diversity of quails (Galliformes: Phasianidae: *Coturnix*) in oceanic islands provided by the fossil record of Macaronesia

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The original bird fauna of most oceanic islands has been affected by recent extinction processes associated with human arrival and its subsequent impacts. In the volcanic Macaronesian archipelagos (Azores, Madeira, Selvagens, Canary Islands and Cape Verde), in the North Atlantic, the Late Quaternary fossil record indicates that there was formerly a higher avian diversity, including a high number of now extinct endemic species. This assemblage of extinct birds includes endemic insular quails (Galliformes: Phasianidae). In this study, we describe three newly discovered extinct species of quails, two of which inhabited the archipelago of Madeira (*Coturnix lignorum* sp. nov. from Madeira Island and *Coturnix alabrevis* sp. nov. from Porto Santo Island) and one from Cape Verde (*Coturnix centensis* sp. nov.). The fossil record also indicates the presence of additional species of extinct endemic quails on other Macaronesian islands. These birds plus the extinct Canary Island quail (*Coturnix gomerae*) indicate a high former endemic diversity of this genus in Macaronesia, a feature unique among oceanic archipelagos. Anatomical traits show that the new taxa were flightless ground dwellers, making them vulnerable to human interference, with their extinction being linked to human arrival and subsequent habitat alterations and the introduction of invasive species.

**ADDITIONAL KEYWORDS:** anatomy – extinction – fossil birds – island biogeography – morphometrics – Quaternary.

## INTRODUCTION

The extant autochthonous biotas of most oceanic islands are only a subset of the original ones. Birds

are one of the most impoverished groups on oceanic islands owing to recent extinction processes (e.g. Olson & James, 1982; Worthy & Holdaway, 2002; Blackburn *et al.*, 2004; Steadman, 2006; Turvey, 2009; Hume & Walters, 2012; Duncan *et al.*, 2013). The loss of avian species has been dramatic in many archipelagos. For instance, in Hawaii > 70% of the original Holocene avifauna is now extinct (Boyer, 2008), and ≥ 41% of the endemic species of birds of New Zealand became

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extinct after human arrival (Worthy & Holdaway, 2002). Steadman (1995) estimated that ~2000 species of birds, mainly flightless rails, have been lost in Oceania since human expansion across the region, although this might be an overestimation (Livezey, 2003). A new approach, 'conservative but crude', was presented by Steadman (2006), who estimated that between 559 and 1696 species of non-passerine landbirds and 82 species of passerines have been lost since human arrival in Oceania (excluding the Hawaiian Islands and New Zealand), although < 10% of this figure has currently been described. An independent approach using a different methodology estimated ~1200 extinct species of Pacific landbirds (Curnutt & Pimm, 2001). The total number of bird extinctions (i.e. adding seabirds) is higher (Duncan *et al.*, 2013). Knowledge of the original diversity and distribution of insular birds is necessary to understand the current state of ecosystems and, in addition, could help to drive future restoration and conservation programmes (Steadman, 2006; Barnosky *et al.*, 2017).

During the Quaternary, most extinction episodes on archipelagos are correlated with the arrival of humans and their subsequent impacts, such as habitat alterations, hunting and the introduction of alien species, parasites and diseases (Olson & James, 1982; Worthy & Holdaway, 2002; Blackburn *et al.*, 2004; Steadman, 2006; Turvey, 2009; Hume & Walters, 2012). In many archipelagos, at least two waves (one prehistorical and one historical) of human settlement occurred, whereas other archipelagos were populated only in historical times (Wood *et al.*, 2017).

The volcanic Macaronesian archipelagos (the Azores, Madeira, Selvagens, Canary Islands and Cape Verde) are located in the North Atlantic Ocean (15°–39°N and 10°–30°W), between ~100 km (Canary Islands) and ~1350 km (Azores) from the mainland (Africa and Europe, respectively) (Fig. 1). On the Canary Islands, two waves of human settlement took place, the first before 313 of the Current Era (CE) (Alcover *et al.*, 2009) and the second from the 14<sup>th</sup> century onwards (Aznar *et al.*, 2006). In contrast, the Azores, Madeira and Cape Verde islands did not harbour aboriginal populations and were first settled permanently by people from Portugal during 15<sup>th</sup> century (Newitt, 2005), although Madeira, and probably the Azores, seem to have been visited by Viking sailors about four centuries earlier, who might have been responsible for the early introduction of the house mouse (*Mus musculus* Linnaeus, 1758) there (Rando *et al.*, 2014b; Gabriel *et al.*, 2015). The small archipelago of Selvagens, although historically visited by fishermen and shearwater hunters, was never settled permanently by humans.

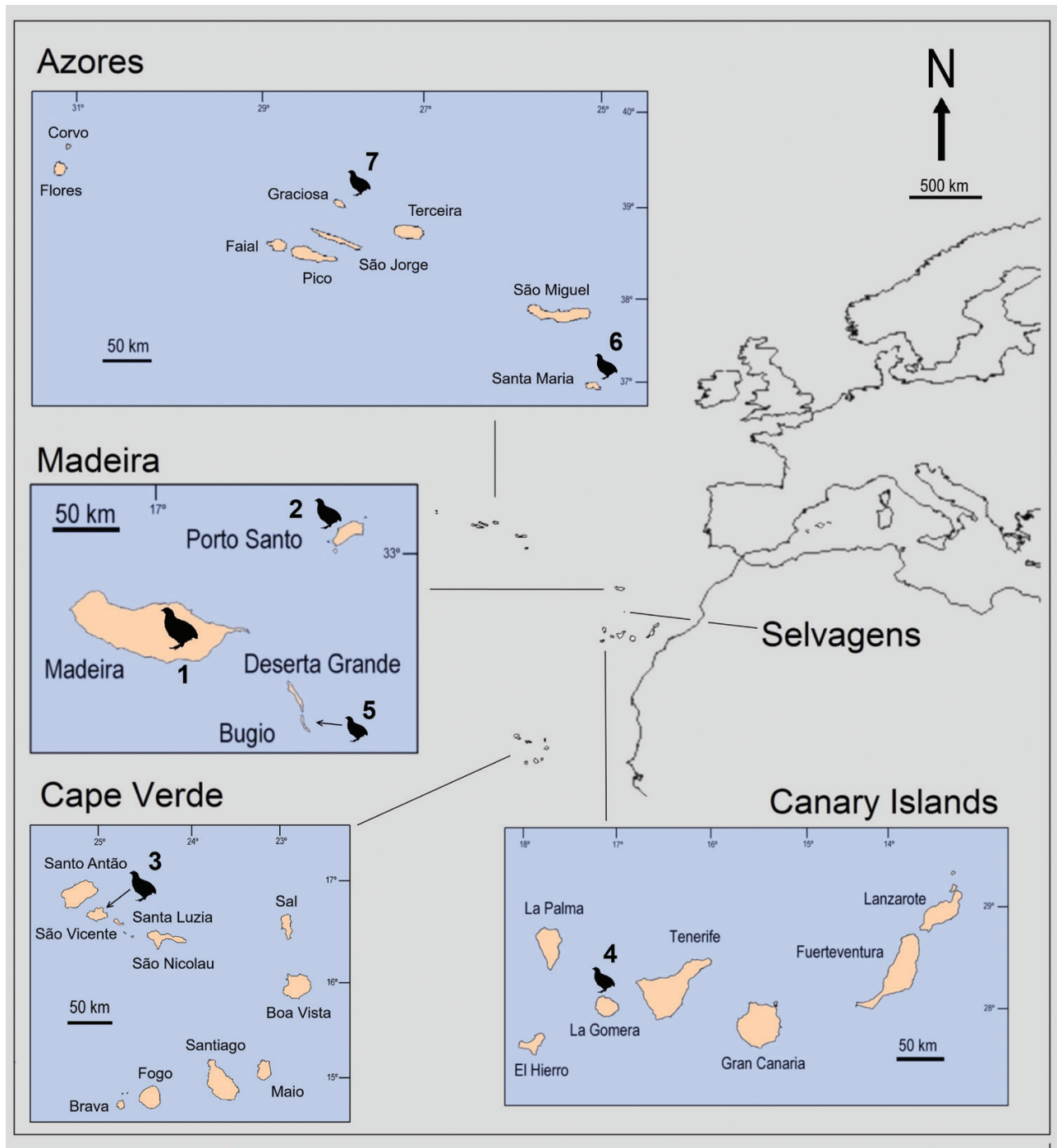
Although the fossil record (in the sense of Steadman, 2006: 92) of the Selvagens and Cape Verde

is not well known, the Late Quaternary record of the Azores, Madeira and Canary Islands indicates a high former avian diversity, including a high number of endemic species (Illera *et al.*, 2012, 2016). So far, in the Azores five endemic extinct species have been described (three rails, a scops owl and a bullfinch; Rando *et al.*, 2013, 2017; Alcover *et al.*, 2015), in the Canary Islands seven extinct species are known (two shearwaters, a quail, an oystercatcher and three passerines; Alcover & Florit, 1987; McMinn *et al.*, 1990; Walker *et al.*, 1990; Jaume *et al.*, 1993; Rando *et al.*, 1999, 2010; Martín & Lorenzo 2001) and in Madeira three extinct species were reported (two rails and one scops owl; Rando *et al.*, 2012b; Alcover *et al.*, 2015). Other rail and scops owl fossils have been obtained on these archipelagos and, although they most probably represent undescribed endemic species (the rails of Terceira, Graciosa and Santa Maria in the Azores, and the scops owl of Porto Santo), they remain unnamed because of insufficient material (Rando *et al.*, 2012b; Alcover *et al.*, 2015). Remains of more extinct species are indicated from the Madeiran archipelago, among which are quails and passerines (Pieper, 1985).

The anatomical traits and behaviour of many of these species indicate that they were probably vulnerable to human impact, including the introduction of alien mammals. In addition, the radiocarbon ages of bones of some of these extinct species (Rando & Alcover, 2008, 2010; Rando *et al.*, 2013; Alcover *et al.*, 2015) indicate that they were still in existence close to or until the first human presence in each archipelago. All these data implicate human arrival as the main factor triggering the extinctions in these archipelagos.

The common quail, *Coturnix coturnix* (Linnaeus, 1758), currently inhabits Macaronesian islands. According to McGowan *et al.* (2019), *Coturnix coturnix confisa* Hartert, 1917 is present in Azores, Madeira and Canary Islands and *Coturnix coturnix inopinata* Hartert, 1917 in Cape Verde. However, some authors consider these populations as belonging to the nominal form (e.g. Puigcerver, 1990; Fontoura & Gonçalves, 1995; Puigcerver *et al.*, 2001).

The genus *Coturnix* is placed in the family Phasianidae, which is the largest family of Galliformes. Species of this family are noted to be poorly suited for dispersal across oceanic barriers. *Coturnix* is the sole Palaearctic Phasianidae that has been recorded in Upper Pleistocene avifaunas of Mediterranean islands (e.g. Alcover *et al.*, 1992). This Upper Pleistocene fossil record suggests that the remaining western Palaearctic Phasianidae are virtually unable to colonize islands, even those separated by narrow channels from the mainland. The limitation of Phasianidae to cross oceanic barriers is also evidenced by their virtual



**Figure 1.** Map of the Macaronesian Islands. Silhouettes indicate specimen records discussed in this paper: (1) *Coturnix lignorum*; (2) *Coturnix alabrevis*; (3) *Coturnix centensis*; (4) *C. gomerae*; and (5–7) *Coturnix* sp.

absence from islands placed to the east of Wallace's line. Only a few Australasian oceanic islands harbour species such as the Asian blue quail *Synoicus chinensis* (Linnaeus, 1766), the brown quail *Synoicus ypsilophorus* (Bosc, 1792) and the New Zealand quail

*Coturnix novaezelandiae* Quoy & Gaimard, 1830, all of which are related clearly to the Eurasian *Coturnix* (e.g. Eo *et al.* 2009; Seabrook-Davison *et al.*, 2009), which is the sole genus of Phasianidae with truly migratory forms among its members. Seemingly, the

snow mountains quail *Anurophasis monorhonyx* Van Oort, 1910 from the New Guinean highlands and the Madagascan partridge, *Margaroperdix madagarensis* (Scopoli, 1787), from Madagascar are also derived from *Coturnix*, as established through morphological (Olson, 1980) and genetic (Hosner *et al.*, 2017) criteria.

Until now, the Canary Islands quail, *Coturnix gomerae* Jaume *et al.*, 1993, was the only extinct endemic insular species of quail reported to occur in the Atlantic Ocean. It was initially described from bones found at La Gomera (Jaume *et al.*, 1993), but subsequent records indicate that this bird was present on almost all the islands of the archipelago (Rando, 2003). *Coturnix gomerae* was more heavily built and had a more robust synsacrum and hindlimbs and slightly shorter wings than its congener, the common quail, *C. coturnix*. It was certainly a sedentary species with reduced flying capabilities compared with *C. coturnix* (Jaume *et al.*, 1993).

Here, we report and discuss the presence of insular endemic quails (Galliformes: Phasianidae: *Coturnix*) in Macaronesia. Our findings provide an unexpected and distinctive quail diversity, which sheds light on the diversification processes of this avian family in island ecosystems. In this paper, we describe three new species of extinct quails from the archipelagos of Madeira and Cape Verde. This is the first endemic extinct bird reported from Cape Verde. We discuss their peculiar morphological traits and present a chronology and possible causes for their extinction.

## MATERIAL AND METHODS

Palaeontological surveys in the Madeira archipelago between 1979 and 1994 produced a great number of bird bones (Pieper, 1985), some of them belonging to the genus *Coturnix*. Subsequent fieldwork provided new bones of this genus in the Azores, Madeira and Cape Verde archipelagos. Bones of quails were found in the Madeiran archipelago on the islands of Madeira (three sites in Ponta de São Lourenço; eolian sand deposits with black volcanic sands, probably redeposited by colluviation), Porto Santo (Fonte da Areia and Porto dos Frades; eolianites) and on Bugio Islet (surface findings at the top of the islet). In the Azores, quail bones were found on Santa Maria Island (Praia; eolian sand deposit affected by colluviation) and Graciosa (Furna do Calcinhas; sediments inside a cave) and on Cape Verde on the south side of Monte Verde (sediment infilling a fissure) in São Vicente Island (Fig. 1). All

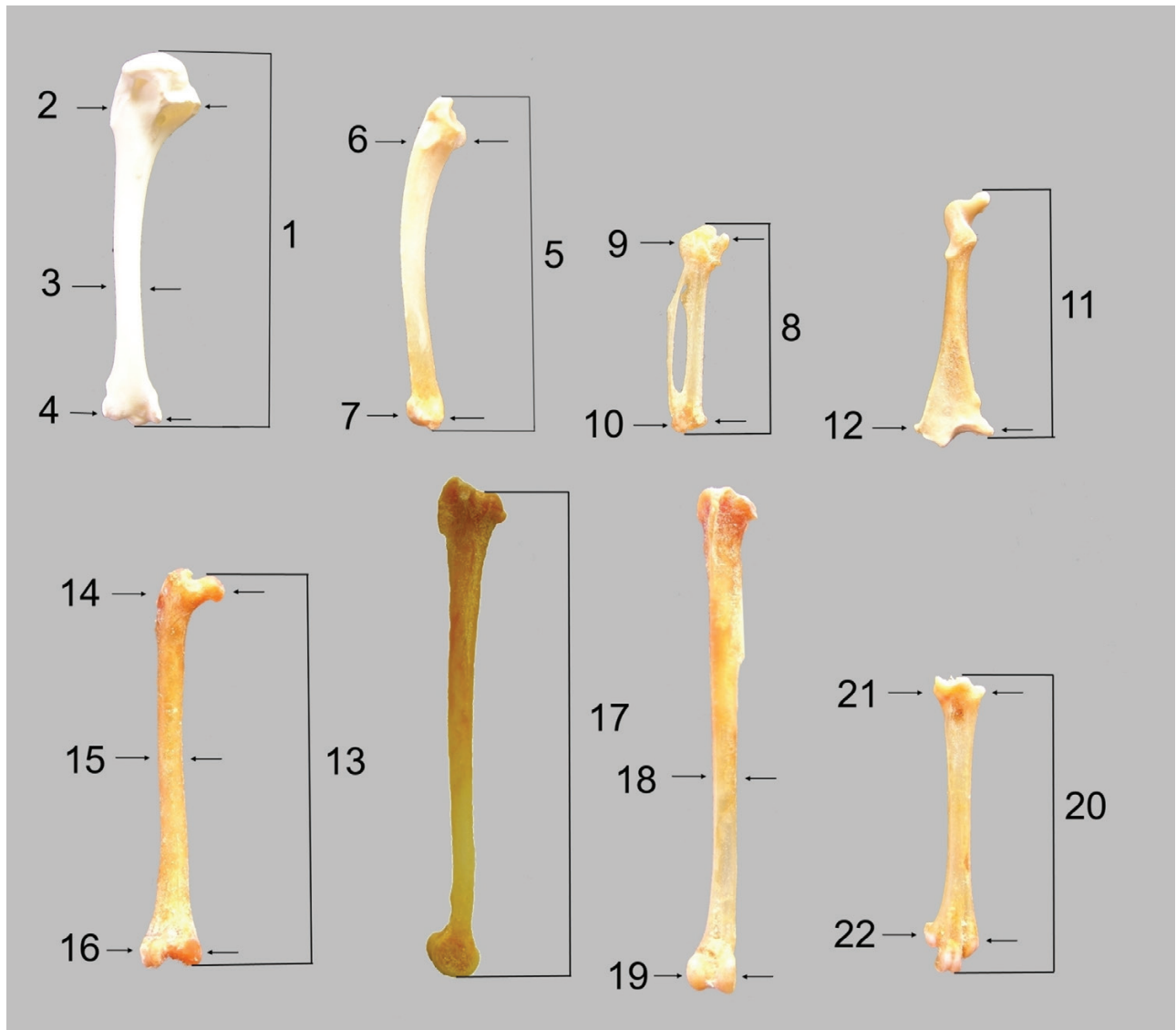
the obtained fossils consist of unarticulated bones (i.e. non-associated skeletons).

Bone measurements (Fig. 2) were taken with digital callipers returning an accuracy of 0.1 mm. The anatomical terminology follows Livezey & Zusi (2006). To summarize the segregation of taxa and to explore morphological patterns in relationship to bone proportions, we performed a principal components analysis. Differences in bone lengths among quails were evaluated using a multivariate analysis of variance (MANOVA) on femur, tibiotarsus and tarsometatarsus lengths (traits 13, 17 and 20). Other comparisons were made with ANOVA using Tukey's post hoc test and a non-parametric test (Mann–Whitney *U*-test). We performed all statistical analyses with SPSS v.19 software. The percentages of the differences among the measurements of the different species provided in the text were calculated with the arithmetical means presented in Table 1.

To estimate the weight and wing loading of the new taxa, we used the expression  $Y = 1.05X^{0.326}$ , where the tibiotarsus length is the dependent variable (*Y*) and the estimated weight of the bird (*X*) the independent variable (Olmos *et al.*, 1996). The lengths of wing bones of extinct taxa are used here as a conservative proxy to estimate wing surface area, because it is known that the shape of the wing of extant flightless birds tends to become more rounded distally through a differential increased shortening of the remiges (e.g. Livezey, 2003). The flight capability of the new taxa was assessed through: (1) the humerus length to femur length ratio (Livezey, 2003); and (2) using the ratio of combined humerus + ulna + carpometacarpus length to femur length (Millener, 1989; Millener & Worthy, 1991; Rando *et al.*, 1999, 2010). We calculated the mean for each bone length and used them as a proxy for the size of each bone, calculating the previous indexes and describing the different island quails, assuming their representativeness.

Two samples of bones were dated through accelerator mass spectrometry at the Radiocarbon Dating Laboratory of the Royal Institute for Cultural Heritage (Brussels). The accelerator mass spectrometry radiocarbon dates, given in years BP, are conventional radiocarbon ages with the standard error, where BP is before present (the year 1950), following standard reporting procedures. Radiocarbon calibrations were performed using the software OXCAL v.4.3 (Bronk Ramsey, 2009) and the IntCal13 dataset (Reimer *et al.*, 2013). Dates calculated from calibration are expressed as 2σ intervals (95.4% confidence interval) and given as 'cal CE' or 'cal BCE' (CE being Current Era and BCE, Before Current Era).





**Figure 2.** Measurements are as follows: (1) humerus length; (2) proximal humerus width; (3) humerus width of shaft at midpoint; (4) humerus distal width; (5) ulna length; (6) ulna proximal width; (7) ulna distal width; (8) carpometacarpus length; (9) carpometacarpus proximal width; (10) carpometacarpus distal width; (11) coracoid length; (12) coracoid width; (13) femur length; (14) femur proximal width; (15) femur width of shaft at midpoint; (16) femur distal width; (17) tibiotarsus length; (18) tibiotarsus width of shaft at midpoint; (19) tibiotarsus maximum width of the distal end; (20) tarsometatarsus length; (21) tarsometatarsus proximal width; (22) tarsometatarsus distal width.

#### ABBREVIATIONS

Institutional abbreviations: DZUL, Departamento de Zoología, Universidad de La Laguna, Tenerife, Canary Islands; IMEDEA, Institut Mediterrani d'Estudis Avançats, Mallorca, Balearic Islands; MCMa, Museu Carlos Machado, Ponta Delgada, São Miguel, Azores; MMF, Museu de História Natural do Funchal, Funchal,

Madeira; ULPGC, Universidad de Las Palmas de Gran Canaria.

Anatomical abbreviations: cmc, carpometacarpus; cor, coracoid; dis, distal; fem, femur; frag, fragment/fragmented; hum, humerus; L, left; pmx, premaxilla; prox, proximal; R, right; rad, radius; sca, scapula; ste, sternum; syn, synsacrum; tbt, tibiotarsus; tmt, tarsometatarsus; uln, ulna.

**Table 1.** Measurements (1–22) of the extinct *Coturnix lignorum*, *Coturnix alabrevis*, *Coturnix gomerae*, two samples of *Coturnix coturnix* (current specimens from several localities and fossil specimens from Es Pouàs, a Late Quaternary site from Eivissa, Balearic Islands) and of quail bones *Coturnix* sp. A from Bugio (Desertas, Madeira archipelago) and *Coturnix* sp. C from Graciosa (Azores Islands)

|                    | <i>Coturnix lignorum</i> ,<br>Madeira | <i>Coturnix alabrevis</i> ,<br>Porto Santo | <i>Coturnix</i> sp. A,<br>Bugio | <i>Coturnix</i> sp. C,<br>Graciosa | <i>Coturnix centensis</i> ,<br>São Vicente | <i>Coturnix gomerae</i> ,<br>La Gomera | <i>Coturnix coturnix</i> ,<br>current | <i>Coturnix coturnix</i> ,<br>Eivissa |
|--------------------|---------------------------------------|--|---------------------------------|------------------------------------|--|--|---------------------------------------|---------------------------------------|
| Humerus            |                                       |  |                                 |                                    |  |  |                                       |                                       |
| 1. Length          | (13) 34.6 ± 0.7<br>[33.2–35.5]        | (18) 30.5 ± 1.1<br>[28.4–32.5]             | (1) 33.9                        | (1) 32.7                           | (8) 30.2 ± 1.2<br>[28.7–32.5]              | (4) 35.4 ± 1.1<br>[33.6–36.3]          | (14) 34.6 ± 1.2<br>[32.6–36.7]        | (32) 34.7 ± 0.6<br>[32.0–33.6]        |
| 2. Proximal width  | (13) 7.8 ± 0.1<br>[7.5–8.0]           | (16) 6.8 ± 0.2<br>[6.4–7.1]                | (1) 7.3                         | (2) 7.3 ± 0.1<br>[7.2–7.3]         | (8) 6.9 ± 0.4<br>[6.5–7.5]                 | (4) 7.8 ± 0.1<br>[7.75–8.00]           | (16) 8.1 ± 0.4<br>[7.5–8.8]           | (32) 8.2 ± 0.3<br>[7.7–8.9]           |
| 3. Shaft width     | (13) 2.6 ± 0.1<br>[2.5–2.7]           | (18) 2.1 ± 0.1<br>[2.0–2.2]                | (1) 2.4                         | (1) 2.5                            | (8) 2.1 ± 0.2<br>[1.9–2.4]                 | (4) 2.5 ± 0.1<br>[2.5–2.6]             | (15) 2.6 ± 0.1<br>[2.3–2.8]           | (32) 2.7 ± 0.1<br>[2.5–3.1]           |
| 4. Distal width    | (13) 5.7 ± 0.2<br>[5.5–6.0]           | (17) 5 ± 0.2<br>[4.8–5.4]                  | (1) 5.3                         | (1) 5.3                            | (8) 4.9 ± 0.2<br>[4.7–5.4]                 | (4) 5.3 ± 0.3<br>[5.0–5.8]             | (16) 5.5 ± 0.2<br>[5.0–5.9]           | (32) 5.6 ± 0.2<br>[5.2–6.1]           |
| Ulna               |                                       |  |                                 |                                    |  |  |                                       |                                       |
| 5. Length          | (4) 27.3 ± 1.2<br>[25.5–28.5]         | (7) 24.6 ± 1.1<br>[22.6–25.9]              | –                               | (1) 28.3                           | (3) 24.6 ± 0.7<br>[23.7–25.5]              | (3) 28.7 ± 0.7<br>[27.8–29.5]          | (15) 30.3 ± 1<br>[28.6–31.7]          | (39) 29.9 ± 1<br>[27.5–32.6]          |
| 6. Proximal width  | (5) 4.6 ± 0.2<br>[4.2–4.8]            | (7) 4.1 ± 0.2<br>[3.9–4.3]                 | –                               | (4) 3.4 ± 0.1<br>[3.3–3.5]         | (2) 3.9 ± 0.1<br>[3.9–4]                   | (3) 4.5 ± 0.2<br>[4.2–4.7]             | (15) 3.9 ± 0.4<br>[3.5–4.7]           | (39) 3.7 ± 0.2<br>[3.3–4]             |
| 7. Distal width    | (5) 3.8 ± 0.1<br>[3.7–3.9]            | (7) 3.5 ± 0.1<br>[3.3–3.6]                 | –                               | (4) 3.5 ± 0.1<br>[3.4–3.6]         | (3) 3.3 ± 0.1<br>[3.2–3.5]                 | (3) 3.9 ± 0.1<br>[3.7–4.0]             | (15) 3.8 ± 0.1<br>[3.6–4.0]           | (39) 3.8 ± 0.2<br>[3.5–4.2]           |
| Carpometacarpus    |                                       |  |                                 |                                    |  |  |                                       |                                       |
| 8. Length          | (3) 19.1 ± 0.7<br>[18.5–20.0]         | (9) 16.1 ± 0.3<br>[15.7–16.4]              | (1) 18.7                        | –                                  | (3) 16 ± 0.4<br>[15.4–16.4]                | –                                      | (14) 19.4 ± 0.6<br>[18.4–20.5]        | (38) 19 ± 0.5<br>[17.8–20.4]          |
| 9. Proximal width  | (3) 4.8 ± 0.2<br>[4.5–5.1]            | (9) 4.5 ± 0.2<br>[4.2–4.8]                 | (1) 4.64                        | –                                  | (3) 4.2 ± 0.4<br>[4.1–4.3]                 | –                                      | (14) 4.7 ± 0.2<br>[4.3–5.0]           | (38) 4.7 ± 0.2<br>[4.3–5.5]           |
| 10. Distal width   | (2) 3.8 ± 0.4<br>[3.3–4.2]            | (8) 3.1 ± 0.1<br>[2.9–3.3]                 | (1) 3.41                        | –                                  | (3) 2.7 ± 0.2<br>[2.5–3.0]                 | –                                      | (14) 3.3 ± 0.2<br>[3.1–3.7]           | (38) 3.1 ± 0.2<br>[2.6–3.5]           |
| Coracoid           |                                       |  |                                 |                                    |  |  |                                       |                                       |
| 11. Length         | (9) 22.6 ± 0.6<br>[21.6–23.5]         | (5) 19.8 ± 0.5<br>[19.2–20.6]              | (1) 23                          | (4) 22.8 ± 0.4<br>[22.1–23.1]      | –  | (1) 22.4                               | (15) 23 ± 0.8<br>[21.9–24.6]          | (13) 22.9 ± 0.6<br>[21.7–24.1]        |
| 12. Width          | (6) 8.4 ± 0.4<br>[8.1–9.1]            | –  | –                               | (1) 7.3                            | –  | –                                      | (12) 7.6 ± 0.2<br>[7.1–7.9]           | (13) 7.8 ± 0.3<br>[7.1–8.4]           |
| Femur              |                                       |  |                                 |                                    |  |  |                                       |                                       |
| 13. Length         | (11) 43.8 ± 0.9<br>[42.1–45.1]        | (13) 37.5 ± 0.7<br>[36.4–39.0]             | (3) 39.8 ± 0.9<br>[38.5–40.7]   | (1) 34.3                           | (5) 36.8 ± 0.6<br>[36.1–37.7]              | (12) 38.7 ± 0.9<br>[37.2–40.0]         | (14) 35.1 ± 1<br>[33.1–37.0]          | (18) 36.1 ± 1<br>[34.2–38.2]          |
| 14. Proximal width | (10) 7.9 ± 0.2<br>[7.6–8.2]           | (12) 6.9 ± 0.3<br>[6.5–7.4]                | (1) 7.2                         | (1) 5.7                            | (1) 6.7                                    | (12) 7.1 ± 0.2<br>[6.8–7.4]            | (14) 6 ± 0.4<br>[5.1–6.4]             | (18) 6.3 ± 0.3<br>[5.6–6.9]           |

Table 1. Continued

|                    | <i>Coturnix<br/>ignorum</i> ,<br>Madeira | <i>Coturnix<br/>alabrevis</i> ,<br>Porto Santo | <i>Coturnix</i> sp. A,<br>Bugio | <i>Coturnix</i> sp. C,<br>Graciosa | <i>Coturnix<br/>centensis</i> ,<br>São Vicente | <i>Coturnix<br/>gomeræ</i> ,<br>La Gomera | <i>Coturnix<br/>coturnix</i> ,<br>current | <i>Coturnix<br/>coturnix</i> ,<br>Eivissa |
|--------------------|--|--|---------------------------------|------------------------------------|--|---|---|---|
| 15. Shaft width    | (12) 3.4 ± 0.2<br>[3.1–3.7]              | (13) 3 ± 0.1<br>[2.9–3.1]                      | (3) 3 ± 0.1<br>[2.9–3.1]        | (1) 2.4                            | (5) 2.8 ± 0.1<br>[2.7–2.9]                     | (12) 3 ± 0.1<br>[2.8–3.2]                 | (14) 2.4 ± 0.2<br>[2.2–2.9]               | (18) 2.6 ± 0.2<br>[2.2–2.8]               |
| 16. Distal width   | (12) 7.6 ± 0.3<br>[7.2–8.2]              | (13) 6.5 ± 0.2<br>[6.1–6.8]                    | (3) 6.5 ± 0.2<br>[6.4–6.7]      | (1) 5.2                            | (5) 6.1 ± 0.3<br>[5.7–6.6]                     | (11) 6.4 ± 0.2<br>[6.0–6.8]               | (15) 5.4 ± 0.2<br>[5.0–5.7]               | (18) 5.5 ± 0.2<br>[5.1–5.9]               |
| Tibiotarsus        |  |  |                                 |                                    |  |   |   |   |
| 17. Length         | (8) 57.7 ± 1.5<br>[54.7–59.9]            | (12) 49.1 ± 1.3<br>[46.2–50.7]                 | (2) 50.2 ± 1.7<br>[48.5–51.9]   | –                                  | (3) 46.5 ± 0.8<br>[45.5–47.5]                  | (4) 48.3 ± 0.8<br>[47.1–49.4]             | (15) 44.3 ± 1.3<br>[41.7–46.4]            | (11) 44.5 ± 1.1<br>[42.4–47.0]            |
| 18. Shaft width    | (8) 3 ± 0.1<br>[2.7–3.1]                 | (12) 2.4 ± 0.1<br>[2.1–2.6]                    | (4) 2.5<br>[2.5–2.6]            | –                                  | (4) 2.5 ± 0.1<br>[2.4–2.7]                     | (4) 2.5 ± 0.1<br>[2.4–2.7]                | (15) 2.2 ± 0.2<br>[2.0–2.6]               | (11) 2.3 ± 0.2<br>[2.0–2.8]               |
| 19. Distal width   | (8) 5.9 ± 0.3<br>[5.5–6.3]               | (11) 5.3 ± 0.2<br>[4.9–5.5]                    | (4) 5.1 ± 0.1<br>[4.9–5.3]      | –                                  | (4) 5 ± 0.2<br>[4.8–5.2]                       | (3) 4.7 ± 0.2<br>[4.4–4.8]                | (15) 4.4 ± 0.2<br>[4.0–4.8]               | (11) 4.5 ± 0.1<br>4.2–4.8                 |
| Tarsometatarsus    |  |  |                                 |                                    |  |   |   |   |
| 20. Length         | (14) 32.2 ± 0.9<br>[30.4–34.4]           | (22) 28.2 ± 0.9<br>[26.0–30.4]                 | (1) 28.8                        | (2) 25.2<br>[25.2–25.2]            | (7) 26.2 ± 0.5<br>[25.2–26.9]                  | (4) 27.7 ± 0.4<br>[27.3–28.4]             | (12) 27.6 ± 1.1<br>[25.7–29.7]            | (68) 26.9 ± 0.9<br>[24.2–29.0]            |
| 21. Proximal width | (13) 6.5 ± 0.2<br>[6.0–6.9]              | (21) 5.8 ± 0.2<br>[5.4–6.2]                    | (1) 5.65                        | (2) 4.7<br>[4.7–4.7]               | (5) 5.5 ± 0.1<br>[5.3–5.6]                     | (3) 5.5 ± 0.1<br>[5.4–5.6]                | (12) 4.8 ± 0.2<br>[4.5–5.1]               | (68) 4.8 ± 0.2<br>[4.5–5.3]               |
| 22. Distal width   | (14) 7.2 ± 0.3<br>[6.5–7.7]              | (21) 6.3 ± 0.2<br>[5.6–6.7]                    | (1) 6.3                         | (2) 5.1 ± 0.1<br>[5.0–5.2]         | (7) 5.9 ± 0.2<br>[5.7–6.1]                     | (4) 6 ± 0.1<br>[5.9–6.2]                  | (12) 5.1 ± 0.3<br>[4.5–5.5]               | (68) 5.1 ± 0.2<br>[4.7–5.7]               |

Measurements are as in Figure 2, given as: (sample size), mean length ± SEM [range] (in millimetres).

## RESULTS

## SYSTEMATIC PALAEONTOLOGY

GALLIFORMES Temminck, 1820

PHASIANIDAE Horsfield, 1821

*COTURNIX* Garsault, 1764

The fossils are referred to *Coturnix* rather than to other genera of Galliformes, because of their size (this genus includes the sole small-sized Galliformes from the western Palaearctic and north-western tropical regions) and the characters listed by Holman (1964), Olson (1976), Fitzgerald (1969) and Dyke *et al.* (2003), such as the characteristically short and slightly curved premaxilla, with great apertura nasi ossea, the well-developed secondary fossa pneumotricipitalis on the proximal end of humerus, the characteristically flat and curved ulnae, the reduced processus pisiformis at the carpometacarpus, the femur relatively long and slightly curved, and the size of the crista cnemialis cranialis with respect to the crista cnemialis lateralis. All the bones here studied agree with the morphology of bones of *Coturnix*, detailed by Fitzgerald (1969), although they differ from *C. coturnix* in size and proportions.

The new fossil bones of quail from the Macaronesian islands were compared with common quail (*C. coturnix*) bones from extant specimens and with unarticulated fossils from Es Pouàs (Late Quaternary, Eivissa, Balearic Islands) (Supporting Information, Table S1), and with bones of the Canary Island extinct quail (*C. gomeræ*) (specimens of type series from Bujero del Silo, La Gomera). The Afrotropical harlequin quail, *Coturnix delegorguei* Delegorgue, 1847, has bones of similar size to those of *C. coturnix* (measurements of the sole available skeleton are given by Jaume *et al.*, 1993).

## EXTINCT MACARONESIAN QUAILS

***Coturnix lignorum*** Rando, Alcover, Pieper, Olson, Hernández & López-Jurado **sp. nov.**

(Figs 3–7)

urn:lsid:zoobank.org:act:6DBF0A7A-DED2-4568-A4E1-98EF5E11B47E

**Holotype:** MMF 47266, complete right tibiotarsus (Figs 5, 6) collected by H. Pieper and O. Runze in 1994.

**Measurements of holotype:** Length, 58 mm; shaft width, 2.9 mm; distal width, 6.3 mm.

**Type locality:** Ponta de São Lourenço (Prainha II site), Madeira Island, Madeira, Portugal.

**Distribution:** Madeira Island.

**Age:** Holocene; 1021–806 cal BCE is the age of a sample consisting of an associated femur, tibiotarsus and a fragment of tarsometatarsus of the new species (Lab-Code KIA- 47430: 2755 ± 55 BP) from Ribeira Groh (Ponta de São Lourenço).

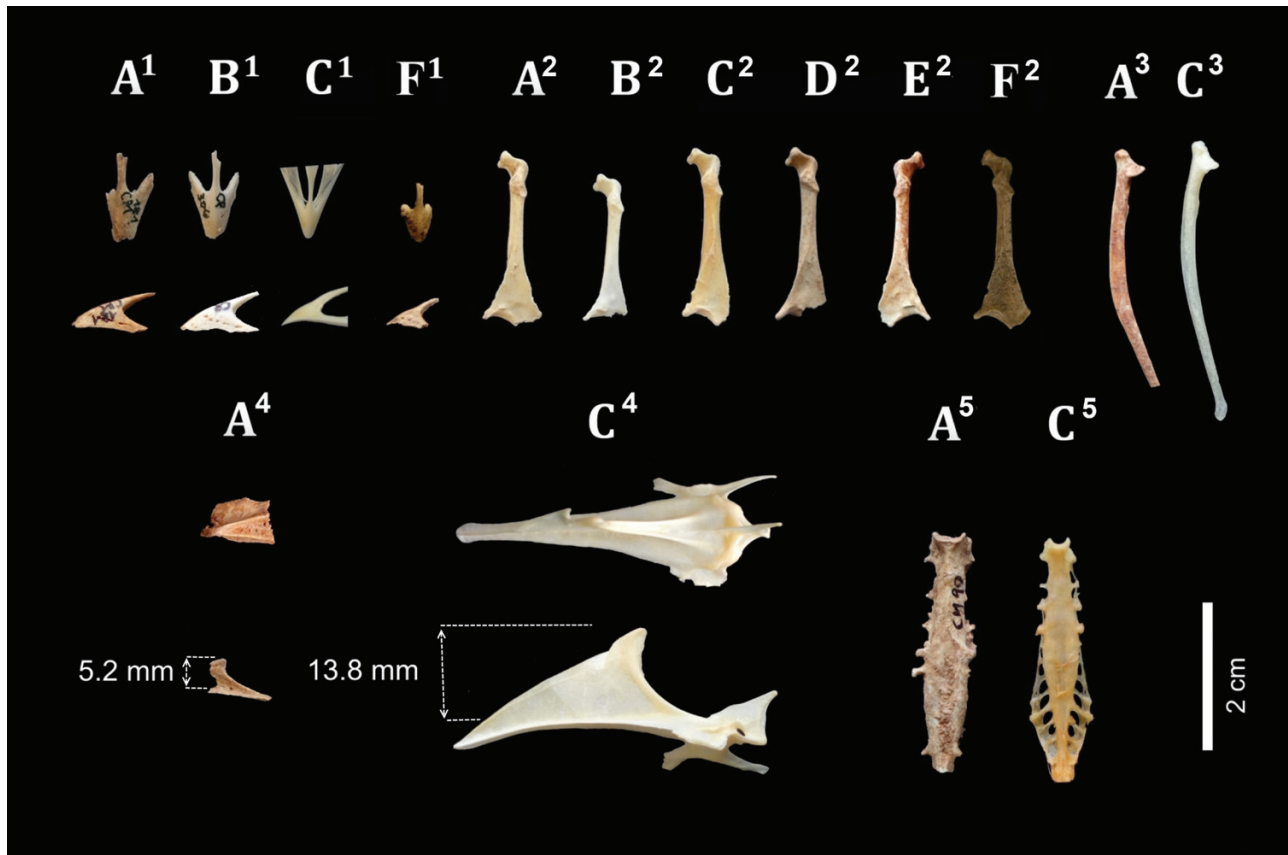
**Status:** Extinct.

**Etymology:** The specific name *lignorum* is derived from the Latin genitive plural of *lignum*, wood, a direct translation of the Portuguese *madeira*.

**Paratypes:** Complete or near-complete bones collected, separately or jointly, by H. Pieper, O. Runze and Klaus Groh. Prainha II site: MMF 47267, L tbt; MMF 47271, R tbt; MMF 47272, R tbt; MMF 47274, R tbt; MMF 47282, R fem; MMF 47286, L tmt; MMF 47290, R tmt; MMF 47294, R tmt; MMF 47300, L hum; MMF 47309, R hum; MMF 47311, L uln; MMF 47314 R uln; MMF 47316, L cmc; MMF 47321, L cor; MMF 47322, L cor; MMF 47327, syn; MMF 47328, frag ste; MMF 47329, pmx; MMF 47330, L sca; IMEDEA 106875, R fem; IMEDEA 106876, R tmt. Prainha I site: MMF 47313, R uln. Main Sand Place site: MMF 47268, R tbt; MMF 47270, L tbt; MMF 47276, R fem; MMF 47277, R fem; MMF 47278, L fem; MMF 47283, L fem; MMF 47284, L fem; MMF 47285, L tmt; MMF 47287 L tmt; MMF 47288, L tmt; MMF 47291, R tmt; MMF 47292, R tmt; MMF 47293, R tmt; MMF 47295, R tmt; MMF 47297, R tmt; MMF 47298, L hum; MMF 47299, L hum; MMF 47301, L hum; MMF 47302, L hum; MMF 47303, L hum; MMF 47305, R hum; MMF 47306, R hum; MMF 47307, R hum; MMF 47308, R hum; MMF 47312, L uln; MMF 47315, L cmc; MMF 47317, R cmc; MMF 47318, L cor; MMF 47319, L cor; MMF 47320, L cor; MMF 47323, L cor; MMF 47324, L cor; MMF 47325, R cor; MMF 47326, R cor. Ribeira Groh site: MMF 47269, L tbt; MMF 47273, R tbt; MMF 47275, R fem; MMF 47279, R fem; MMF 47280, R fem; MMF 47281, L fem; MMF 47289, R tmt; MMF 47296, R tmt; MMF 47304, R hum; MMF 47310, R hum; IMEDEA 106877, R hum; IMEDEA 106878, L cor.

**Diagnosis:** Larger than the extant *C. coturnix* and the extinct *C. gomeræ* from the Canary Islands, with different proportions. *Coturnix lignorum* has the hindlimb bones (femur, tibiotarsus and tarsometatarsus) more robust and longer than in *C. coturnix* or *C. gomeræ*; the coracoid and the humerus are about the same size, but the ulna is shorter than in those species. The carpometacarpus is about the same size as in *C. coturnix*. All bones of *C. lignorum* are larger than *Coturnix* bones from Porto Santo (Madeira archipelago) and São Vicente (Cape Verde) (Figs 3–5; Table 1).





**Figure 3.** Premaxilla, coracoid, scapula, sternum and synsacrum of *Coturnix lignorum* from Madeira (A<sup>1</sup>–A<sup>5</sup>), *Coturnix alabrevis* from Porto Santo (B<sup>1</sup>, B<sup>2</sup>), *Coturnix coturnix* (C<sup>1</sup>–C<sup>5</sup>), *Coturnix gomerae* from La Gomera (D<sup>2</sup>), *Coturnix* sp. A from Bugio (E<sup>2</sup>) and *Coturnix* sp. C from Graciosa (F<sup>2</sup>). A<sup>1</sup>–C<sup>1</sup>, premaxilla dorsal view (top) and left lateral view (bottom). A<sup>2</sup>–F<sup>2</sup>, coracoid, dorsal view. A<sup>3</sup>, C<sup>3</sup>, scapula, left lateral view. A<sup>4</sup>, C<sup>4</sup>, sternum ventral view (top) and left lateral view (bottom) (the high of apex carinae is shown). A<sup>5</sup>, C<sup>5</sup>, synsacrum ventral view. Scapulas and coracoids are from the left side, except for E<sup>2</sup>. A<sup>1</sup>, MMF 47329; B<sup>1</sup>, MMF 47413; C<sup>1</sup>, IMEDEA 106905; F<sup>1</sup>, MCMa 2354.018; A<sup>2</sup>, MMF 47325; B<sup>2</sup>, MMF 47411; C<sup>2</sup>, IMEDEA 106904; D<sup>2</sup>, DZUL 1830; E<sup>2</sup>, MMF 47416; F<sup>2</sup>, MCMa FC-1368; A<sup>3</sup>, MMF 47330; C<sup>3</sup>, IMEDEA 106907; A<sup>4</sup>, MMF 47328; C<sup>4</sup>, IMEDEA 106905; A<sup>5</sup>, MMF 47327; C<sup>5</sup>, IMEDEA 106906.

**Description and comparisons:** Some characteristic features in comparison with *C. coturnix* can be identified: a longer and stouter premaxilla; ulna with the cotyla ventralis oval shaped, more elongated and with impressio musculi brachialis more developed; coracoid more slender in its distal part and main axis with a shorter labrum internum coracoidei; femur with a deeper fossa poplitea and crista tibiofibularis more prominent and with larger condylus lateralis and medialis; tibiotarsus with a higher crista patellaris, crista cnemialis lateralis and crista cnemialis cranialis more prominent, prominent facies articularis lateralis and fossa retrocristalis wider and deeper; tarsometatarsus with cotyla medialis and cotyla lateralis wider and deeper, and larger trochlea metatarsi II, III and IV. All limb bones are stouter in *C. lignorum* than in *C. coturnix*, giving a peculiar

shape to the hindlimb and suggesting that this species was a robust bird (Fig. 5).

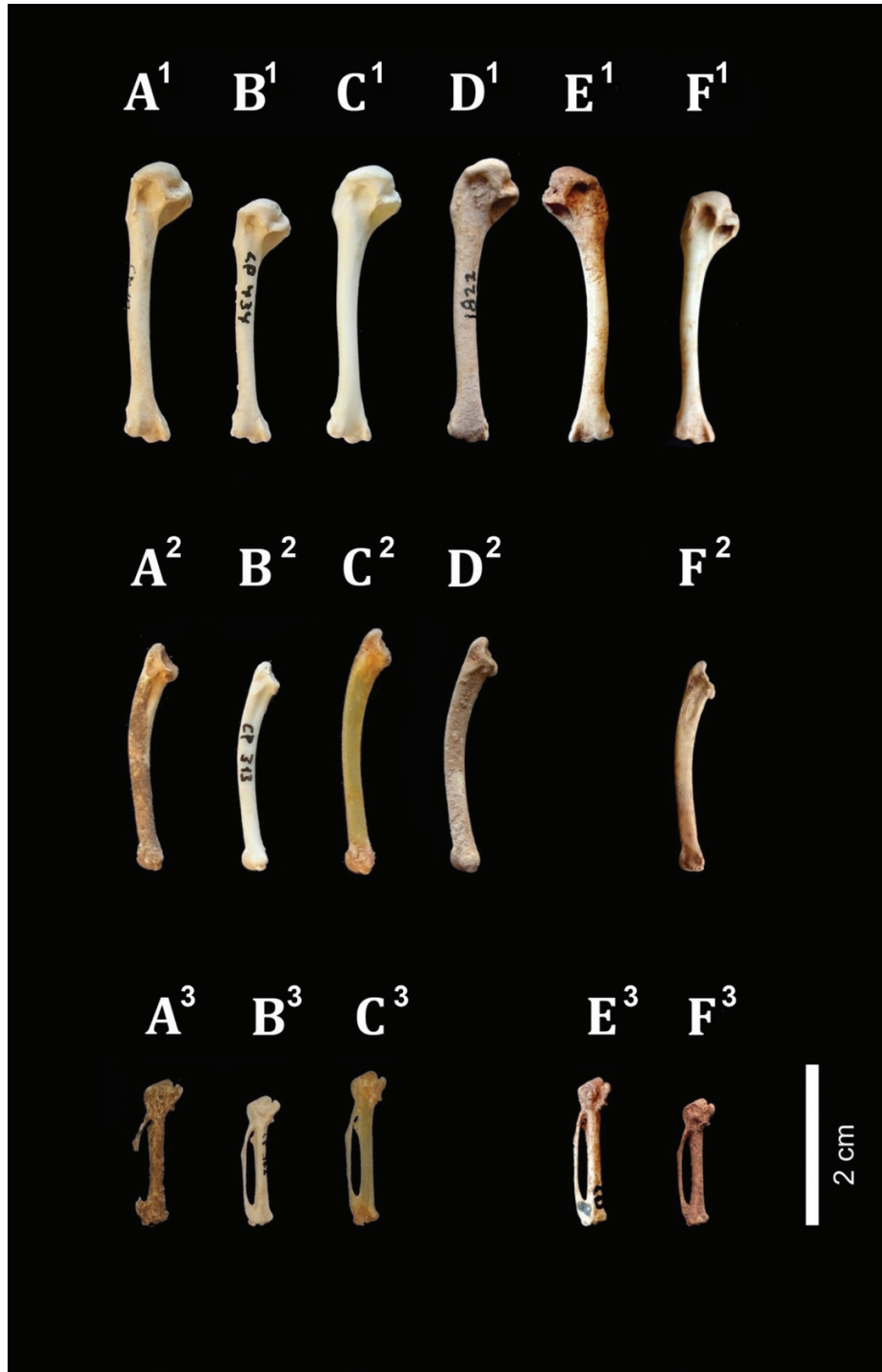
***Coturnix alabrevis*** Rando, Alcover, Pieper, Olson, Hernández & López-Jurado **sp. nov.**

(Figs 3–7)

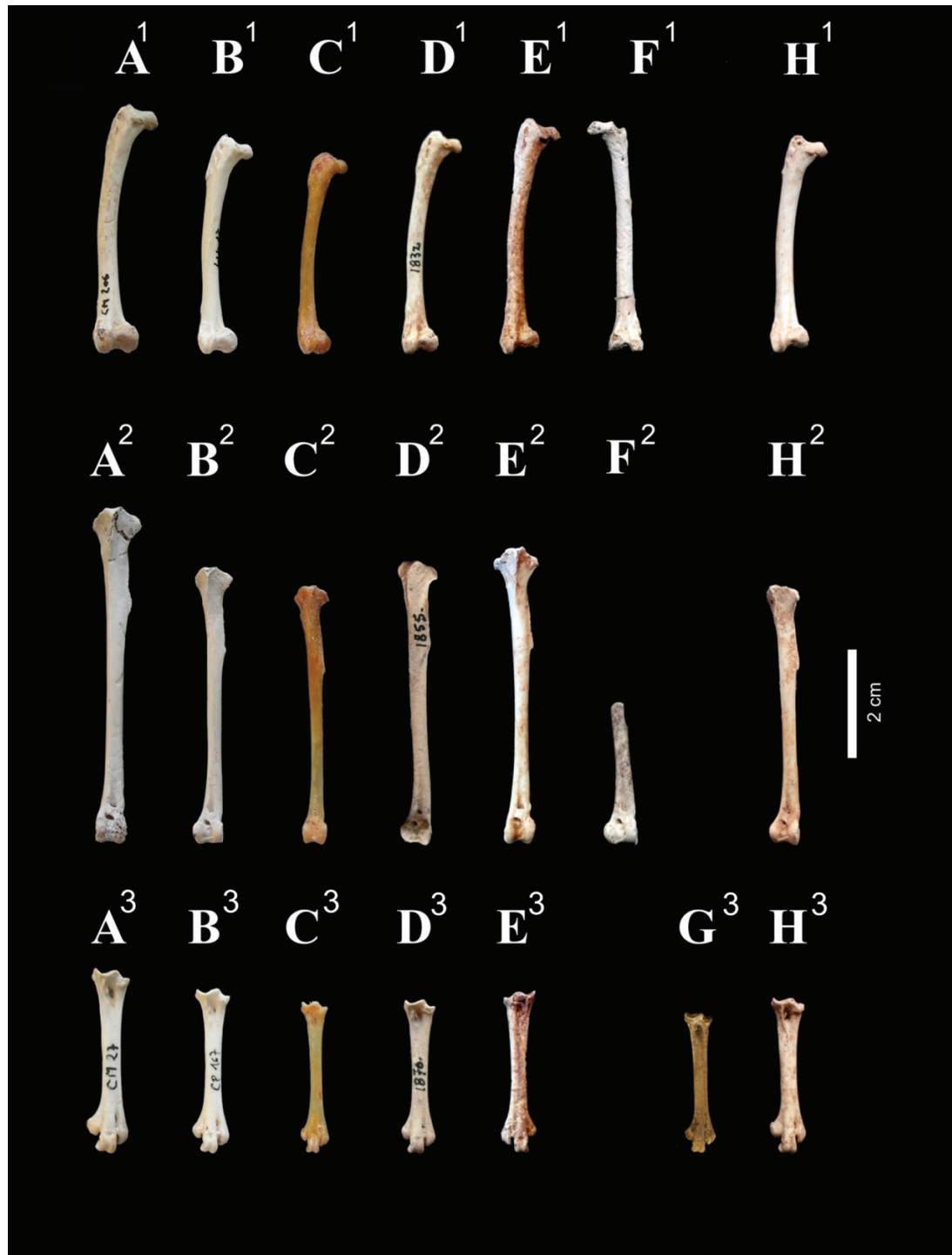
urn:lsid:zoobank.org:act:6FE8D8BE-6112-4ACC-A6E0-A55E9E9BD8A6

**Holotype:** MMF 47331, complete left tibiotarsus (Fig. 6) collected by H. Pieper, O. Runze and K. Groh in May 1992.

**Measurements of holotype:** Length, 48.5 mm; shaft width, 2.4 mm; distal width, 5.3 mm.



**Figure 4.** Forelimb bones of *Coturnix lignorum* from Madeira (A<sup>1</sup>–A<sup>3</sup>), *Coturnix alabrevis* from Porto Santo (B<sup>1</sup>–B<sup>3</sup>), *Coturnix coturnix* (C<sup>1</sup>–C<sup>3</sup>), *Coturnix gomerae* from La Gomera (D<sup>1</sup>, D<sup>2</sup>), *Coturnix* sp. A from Bugio (E<sup>1</sup>, E<sup>3</sup>) and *Coturnix centensis* from São Vicente (F<sup>1</sup>–F<sup>3</sup>). A<sup>1</sup>–F<sup>1</sup>, humerus, caudal view. A<sup>2</sup>–F<sup>2</sup>, ulna, ventral view. A<sup>3</sup>–F<sup>3</sup>, carpometacarpus, ventral view. All bones are from the left side except for E<sup>1</sup>. A<sup>1</sup>, MMF 47301; B<sup>1</sup>, MMF 47381; C<sup>1</sup>, IMEDEA106904; D<sup>1</sup>, DZUL 1822; E<sup>1</sup>, MMF 47417; F<sup>1</sup>, ULPGC-A8; A<sup>2</sup>, MMF 47311; B<sup>2</sup>, MMF 47390; C<sup>2</sup>, IMEDEA106904; D<sup>2</sup>, DZUL 1826; F<sup>2</sup>, ULPGC-A11; A<sup>3</sup>, MMF 47315; B<sup>3</sup>, MMF 47399; C<sup>3</sup>, IMEDEA106904; E<sup>3</sup>, MMF 47423; F<sup>3</sup>, ULPGC-A15.

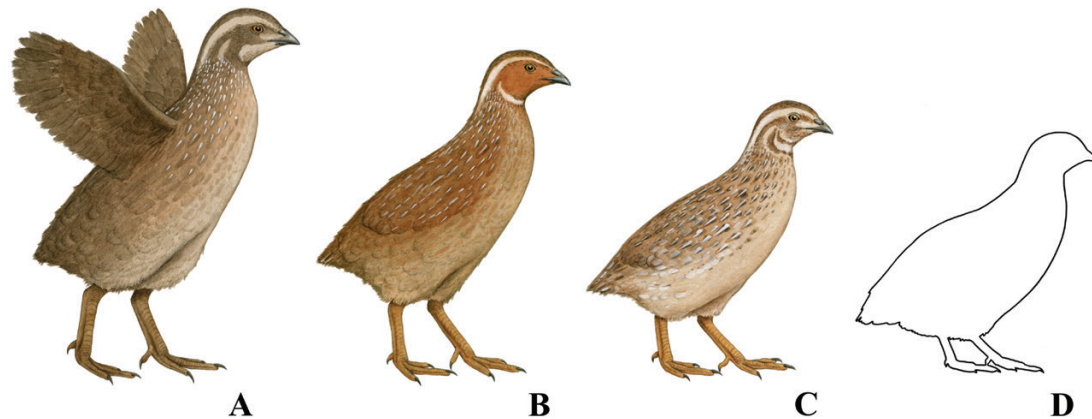


**Figure 5.** Hindlimb bones of *Coturnix lignorum* from Madeira (A<sup>1</sup>–A<sup>3</sup>), *Coturnix alabrevis* from Porto Santo (B<sup>1</sup>–B<sup>3</sup>), *Coturnix coturnix* (C<sup>1</sup>–C<sup>3</sup>), *Coturnix gomerae* from Canary Islands (D<sup>1</sup>–D<sup>3</sup>), *Coturnix* sp. A from Bugio (E<sup>1</sup>–E<sup>3</sup>), *Coturnix* sp. B from Santa Maria (F<sup>1</sup>, F<sup>2</sup>), *Coturnix* sp. C from Graciosa (G<sup>3</sup>) and *Coturnix centensis* from São Vicente (H<sup>1</sup>–H<sup>3</sup>). A<sup>1</sup>–H<sup>1</sup>, femur, caudal view. A<sup>2</sup>–H<sup>2</sup>, tibiotarsus, cranial view. A<sup>3</sup>–E<sup>3</sup>, tarsometatarsus, dorsal view. All bones are from the left side except for F<sup>1</sup> and E<sup>3</sup>. A<sup>1</sup>, MMF 47281; B<sup>1</sup>, MMF 47345; C<sup>1</sup>, IMEDEA 106904; D<sup>1</sup>, DZUL 1832; E<sup>1</sup>, MMF 47420; F<sup>1</sup>, MCMa 2320.018; H<sup>1</sup>, ULPGC-A16; A<sup>2</sup>, MMF 47268; B<sup>2</sup>, MMF 47331; C<sup>2</sup>, IMEDEA 106904; D<sup>2</sup>, DZUL 1855; E<sup>2</sup>, MMF 47425; F<sup>2</sup>, MCMa 2321.018; H<sup>2</sup>, ULPGC-A21; A<sup>3</sup>, MMF 47285; B<sup>3</sup>, MMF 47358; C<sup>3</sup>, IMEDEA 106904; D<sup>3</sup>, DZUL 1870; E<sup>3</sup>, MMF 47419; G<sup>3</sup>, MCMa 2323.018; H<sup>3</sup>, ULPGC-A25.



**Figure 6.** Holotypes (tibiotarsus) of: A, *Coturnix lignorum* from Madeira Island (MMF 47266); B, *Coturnix alabrevis* from Porto Santo (MMF 47331); C, *Coturnix centensis* from São Vicente Island (Cape Verde) (ULPGC-A21); and D, the same bone of a current specimen of *Coturnix coturnix* from Madeira (IMEDEA 106904). From top to bottom, the figure shows the cranial, lateral and caudal views.





**Figure 7.** Artistic reconstruction of: A, *Coturnix lignorum*; B, *Coturnix alabrevis*; C, *Coturnix centensis*; and D, the silhouette of the common quail for comparison, based on bone measurements, when available (wing and leg bones of the three species, sternum of *C. lignorum*, and premaxillae of *C. lignorum* and *Coturnix alabrevis*). Colours are speculative. All drawings are depicted at the same scale. Artwork by Pau Oliver.

**Type locality:** Fonte da Areia site, Porto Santo Island, Madeira, Portugal.

**Distribution:** Porto Santo Island.

**Age:** Late Quaternary.

**Status:** Extinct.

**Etymology:** From Latin *ala*, wing, and *brevis*, short, in reference to the small size of the forelimb (wing) bones.

**Paratypes:** Complete or near-complete bones collected, separately or jointly, by H. Pieper, O. Runze and K. Groh. Porto dos Frades site: MMF 47332, L tbt; MMF 47333, L tbt; MMF 47334, L tbt; MMF 47335, L tbt; MMF 47336, R tbt; MMF 47337, R tbt; MMF 47339, R tbt; MMF 47340, R tbt; MMF 47341, R tbt; MMF 47342, R tbt; MMF 47343, L fem; MMF 47344, L fem; MMF 47345, L fem; MMF 47346, L fem; MMF 47347, R fem; MMF 47349, R fem; MMF 47350, R fem; MMF 47351, R fem; MMF 47352, R fem; MMF 47353, R fem; MMF 47354, R fem; MMF 47355, L tmt; MMF 47357, L tmt; MMF 47358, L tmt; MMF 47359, L tmt; MMF 47360, L tmt; MMF 47361, L tmt; MMF 47362, L tmt; MMF 47363, L tmt; MMF 47364, R tmt; MMF 47365, R tmt; MMF 47366, R tmt; MMF 47367, R tmt; MMF 47368, R tmt; MMF 47369, R tmt; MMF 47370, R tmt; MMF 47371, R tmt; MMF 47372, R tmt; MMF 47373, R tmt; MMF 47374, L hum; MMF 47375, L hum; MMF 47376, L hum; MMF 47377, L hum; MMF 47378, L hum; MMF 47379, L hum; MMF 47380, L hum; MMF 47381, L hum; MMF 47383, R hum; MMF 47384, R hum; MMF 47385, R hum; MMF 47386, R hum; MMF 47387, R hum; MMF 47388, L uln; MMF

47389, L uln; MMF 47390, L uln; MMF 47391, L uln; MMF 47392, L uln; MMF 47393, R uln; MMF 47394, R uln; MMF 47395, R uln; MMF 47396, R uln; MMF 47397, R uln; MMF 47398, L cmc; MMF 47399, L cmc; MMF 47400, L cmc; MMF 47401, R cmc; MMF 47403, R cmc; MMF 47404, R cmc; MMF 47405, R cmc; MMF 47406, R cmc; MMF 47407, L cor; MMF 47409, L cor; MMF 47410, R cor; MMF 47411, R cor; MMF 47413, pmx; MMF 47414, pmx; MMF 47415, pmx; IMEDEA 106879, R fem; IMEDEA 106880, L tmt; IMEDEA 106881, L hum. Fonte da Areia site: MMF 47338, R tbt; MMF 47348, R fem; MMF 47356, L tmt; MMF 47382, R hum; MMF 47402, R cmc; MMF 47408, L cor; MMF 47412, R cor.

**Diagnosis:** All the bones of this species are much smaller than those of *C. lignorum* from the main island of Madeira. Hindlimb bones are close in size to those of *C. coturnix* and *C. gomeræ* (Table 1), but with smaller and more slender coracoid and forelimb bones (Fig. 3). *Coturnix alabrevis* shows similar bone lengths and proportions to the extinct quail from São Vicente (Cape Verde). All forelimb bones and the femur of both species are similar in size, but the tibiotarsus of *C. alabrevis* is longer and the tarsometatarsus slightly larger (Figs 3, 5).

**Description and comparisons:** In addition to the differences in length, some characteristic features in comparison with *C. coturnix* can be identified: a longer and stouter premaxilla; slender humerus with a less developed fossa pneumotricipitalis and crista deltopectoralis; slender ulna with a smaller cotyla dorsalis; slender coracoid with a small labrum internum coracoidei; a stouter femur with a deeper fossa poplitea and crista

tibiofibularis more prominent, and with the condylus lateralis and medialis more robust; stout tibiotarsus with a higher crista patellaris, crista cnemialis lateralis and crista cnemialis cranialis more prominent, and a deeper fossa retrocristalis; a more robust tarsometatarsus with cotyla medialis and cotyla lateralis wider and deeper, and bigger trochlea metatarsi II, III and IV.

***Coturnix centensis*** Rando, Alcover, Pieper, Olson, Hernández & López-Jurado **sp. nov.**

(FIGS 3–7)

urn:lsid:zoobank.org:act:C6911A9F-9FD2-4B60-9202-1C191B742BBA

**Holotype:** ULPGC-A21, complete left tibiotarsus collected by L. F. López-Jurado in November 1997.

**Measurements of holotype:** Length, 45.5 mm; shaft width, 2.5; distal width, 5 mm.

**Type locality:** Monte Verde, São Vicente Island, Cape Verde.

**Distribution:** São Vicente Island.

**Age:** Holocene; 1015–1155 cal CE is the age of a sample consisting of the assemblage of two fragments of femur, a tibiotarsus and a fragment of tarsometatarsus of this new species (Lab-Code RICH-25956:  $974 \pm 28$  BP) from Monte Verde.

**Status:** Extinct.

**Etymology:** In the Portuguese-based creole language spoken in Cape Verde, the island of São Vicente is called 'Son Cent'. We based our epithet on this, adding the Latin locative suffix *-ensis*.

**Paratypes:** Collected by L. F. López-Jurado. ULPGC-A1, R hum; ULPGC-A2, R hum; ULPGC-A3, R hum; ULPGC-A4, R hum; ULPGC-A5, R hum; ULPGC-A6, R hum; ULPGC-A7, L hum; ULPGC-A8, L hum; ULPGC-A9, R uln; ULPGC-A10, R uln; ULPGC-A11, L uln; ULPGC-A12, L uln; ULPGC-A13, R cmc; ULPGC-A14, L cmc; ULPGC-A15, L cmc; ULPGC-A16, L fem; ULPGC-A17, L fem; ULPGC-A18, R fem; ULPGC-A19, R fem; ULPGC-A20, R fem; ULPGC-A22, L tbt; ULPGC-A23, L tbt; ULPGC-A24, R tbt; ULPGC-A25, L tmt; ULPGC-A26, L tmt; ULPGC-A27, R tmt; ULPGC-A28, R tmt; ULPGC-A29, R tmt; ULPGC-A30, R tmt; ULPGC-A31, R tmt; ULPGC-A32, R tmt.

All the material for *C. centensis* is currently stored in the collection of the Department of Biology of the ULPGC. In the event that a scientific collection with

guaranteed security is established in Cape Verde, the holotype (ULPGC-A21) and different paratypes (ULPGC-A1–A4; A9–A10; A13; A19, A20; A21, A22; A29–A32) will be transferred to that collection.

**Diagnosis:** All the bones of *C. centensis* are much smaller than those of *C. lignorum*. The humerus and ulna are much smaller than in *C. gomeræ* or *C. coturnix*. The femur and the tibiotarsus are smaller than that of *C. gomeræ*, but the tarsometatarsus is about the same size. All hindlimb bones are close in size to *C. coturnix*. *Coturnix centensis* has similar bone lengths and proportions to *C. alabrevis* from Porto Santo. All forelimb bones and the femur of *C. centensis* are similar in size to those of *C. alabrevis*, but with the tibiotarsus shorter and the tarsometatarsus slightly smaller.

**Description and comparisons:** In addition to the differences in length, some characteristic features can be identified in comparison to *C. coturnix*; humerus slender, with a less developed fossa pneumotricipitalis and crista deltopectoralis; slender ulna with a smaller cotyla dorsalis; a stouter femur with a deeper fossa poplitea and the crista tibiofibularis more prominent, with the condylus lateralis and medialis more robust; tibiotarsus stout with crista cnemialis lateralis and crista cnemialis cranialis more prominent, and a larger and deeper fossa retrocristalis; a more robust tarsometatarsus with cotyla medialis and wider cotyla lateralis, and larger trochlea metatarsi II, III and IV.

#### OTHER MACARONESIAN QUAILS

##### COTURNIX SP. A

(FIGS 3–5)

Owing to the scarcity of material of this taxon, we refer to it as an unnamed species of *Coturnix*. The material from the island of Bugio (archipelago of Madeira; Fig. 1) consists of 25 bones (16 in fragmentary condition). All lengths of these bones are within or close to the range of variation of *C. gomeræ*, with the tibiotarsus being the only bone that seems to be slightly longer in the sample from Bugio (Fig. 4; Table 1). Significant differences were found between femur lengths of *Coturnix* from Bugio and *C. lignorum* ( $U = -2.569$ ;  $P = 0.01$ ), *C. alabrevis* ( $U = -2.354$ ;  $P = 0.019$ ) and *C. coturnix* ( $U = -2.569$ ;  $P = 0.01$ ), but not with those of *C. gomeræ* ( $U = -1.443$ ;  $P = 0.149$ ). The scarcity of material on Bugio does not rule out the possibility that these bones belong to the Canarian quail, but the poor flight ability of this species suggests the existence of an endemic extinct quail on this islet that was convergent with *C. gomeræ* and different from the geographically closer *C. lignorum* and *C. alabrevis* (Fig. 1).

*Distribution:* Bugio Islet, Desertas Islands, Madeira archipelago, Portugal.

*Age:* Late Quaternary.

*Status:* Extinct.

*Material:* All material was collected by Francis Zino. MMF 47416, L cor; MMF 47417 R hum; MMF 47418 R fem; MMF 47419, R tmt; MMF 47420, L fem; MMF 47421, L tbt dis frag; MMF 47422, R tmt dis frag; MMF 47423, L cmc; MMF 47424, L cor dis frag; MMF 47425, L tbt; MMF 47426, L tbt dis frag; MMF 47427, L cor dis frag; MMF 47428, R fem; MMF 47429, L fem prox frag; MMF 47430, R fem dis frag; MMF 47431, R tbt; MMF 47432, R tbt prox frag; MMF 47433, L tbt prox frag; MMF 47434, R tmt frag; MMF 47435, R hum frag; MMF 47436, L hum prox frag; MMF 47437, R cor dis frag; MMF 47438, R sca prox frag; MMF 47439, T tbt prox frag; MMF 47440, L tbt prox frag.

#### COTURNIX SP. B

(FIG. 5)

This material probably represents a new endemic extinct quail from Santa Maria, Azores, although the material is insufficient to confirm, define and name, and we refer to it with an open terminology as an unnamed species of *Coturnix*. The Santa Maria material consists of three bones (two distal fragments of tibiotarsus and one almost complete femur). The length of the femur (~41.6 mm) and the stouter conditions of all fragments indicate that this specimen cannot be assigned to *C. coturnix* (Fig. 4). The length of the femur is close to, but slightly longer than, those of *C. alabrevis* from Porto Santo (range 36.4–39 mm) and *C. gomeræ* from the Canary Islands (37.2–40 mm) and slightly shorter than those of *C. lignorum* of Madeira (42.1–45.1 mm) (Table 1).

*Distribution:* Santa Maria Island, Azores archipelago, Portugal.

*Age:* Late Quaternary.

*Status:* Extinct.

*Materials:* Collected by H. Pieper. MCMa 2320.018, R fem; MCMa 2321.018, L tbt dis frag; MCMa 2322.018, L tbt dis frag.

#### COTURNIX SP. C

(FIGS 3, 5)

The Graciosa material consists of 31 bones (complete and fragmented), but owing to the scarcity and poor condition

of the material of this quail, we refer to it as *Coturnix* sp. The long bone lengths are close to or fall inside the lower range of variation of *C. coturnix* (Table 1). The sole premaxilla found is stouter than in *C. coturnix* (Fig. 3).

*Distribution:* Graciosa Island, Azores archipelago, Portugal.

*Age:* Late Quaternary.

*Materials:* Collected by E. Torres, J. C. Illera, H. Pieper, J. C. Rando and J. A. Alcover at Forna do Calcinhas (Caldeira Volcano). MCMa 2323.018, L tmt; MCMa 2324.018, R tmt dis; MCMa 2325.018, R hum prox; MCMa 2326.018, R fem dis; MCMa 2327.018, R hum dis; MCMa 2328.018, L hum dis; MCMa 2329.018, L hum dis; MCMa 2330.018, L hum prox; MCMa 2331.018, R cor; MCMa 2332.018, R cor frag; MCMa 2333.018, R cor frag; MCMa 2334.018, L cor frag; MCMa 2335.018, R cor frag; MCMa 2336.018, L tbt frag; MCMa 2337.018, L tbt prox; MCMa 2338.018, R tbt frag; MCMa 2339.018, L tbt frag; MCMa 2340.018, L hum; MCMa 2341.018, L hum prox frag; MCMa 2342.018, L uln; MCMa 2343.018, L uln; MCMa 2344.018, R uln; MCMa 2345.018, R uln; MCMa 2346.018, L cor; MCMa 2347.018, L cor; MCMa 2348.018, L cor; MCMa 2349.018, MCMa 2350.018, L cor; MCMa 2351.018, L fem; MCMa 2352.018, R tmt; MCMa 2353.018, R tmt; MCMa 2354.018, pmx.

#### COTURNIX COTURNIX

A few bones that can be attributed to this species were found in the islands of Madeira (two ulnae and one tarsometatarsus) and Porto Santo (two humeri and one carpometacarpus), in the same sites where the bones of the endemic extinct quails were collected. All the traits that can be measured (1–10, 18 and 20–22) are within the range of variation of *C. coturnix*.

*Age:* Holocene–Recent.

*Status:* Extant.

*Material:* Collected by H. Pieper, O. Runze and K. Groh Main. Sand Place Site (Ponta de São Lourenço, Madeira Island): MMF 47441, R uln; MMF 47442, L uln. Ribeira Groh Site (Ponta de São Lourenço, Madeira Island): MMF 47443, L tmt. Fonte da Areia Site (Porto Santo Island): MMF 47444 L cmc; MMF 47445, L hum prox frag; MMF 47446 R hum.

#### COMPARATIVE MORPHOLOGY

The MANOVA performed with femur, tibiotarsus and tarsometatarsus lengths (traits 13, 17 and 20; Table 1)



of *C. lignorum*, *C. alabrevis*, *C. centensis*, *C. gomeræ* and both samples of *C. coturnix* identified significant morphological differences among quails (Wilks'  $\lambda = 0.02$ ; d.f. = 15, 105;  $P < 0.001$ ) for the three bones ( $F = 111$ ; d.f. = 5, 46;  $P < 0.001$  for the femur;  $F = 117$ ; d.f. = 5, 46;  $P < 0.001$  for the tibiotarsus; and  $F = 28$ ; d.f. = 5, 46;  $P < 0.001$  for the tarsometatarsus). *Coturnix lignorum* has the longest leg bones of the sample ( $P < 0.001$  in all comparisons). *Coturnix alabrevis* shows significant differences from *C. gomeræ* in the length of the femur ( $P = 0.001$ ), but not for the tibiotarsus ( $P = 0.26$ ) and tarsometatarsus ( $P = 0.45$ ). *Coturnix alabrevis* shows no significant differences from *C. centensis* in the length of the femur ( $P = 0.2$ ), but the quail from Cape Verde had a smaller tibiotarsus ( $P < 0.001$ ) and tarsometatarsus ( $P = 0.005$ ). In addition, *C. alabrevis* shows no significant differences from either sample of *C. coturnix*, current ( $P = 0.21$ ) and Late Quaternary specimens from Eivissa ( $P = 0.054$ ), in tarsometatarsus length. However, both samples of *C. coturnix* have significantly shorter femurs ( $P < 0.001$ ) and tibiotarsi ( $P < 0.001$ ) than *C. alabrevis*. In contrast, *C. gomeræ* shows significantly longer femurs ( $P < 0.001$ ) and tibiotarsi ( $P < 0.001$ ) than in any sample of *C. coturnix*, but the tarsometatarsus is of similar size ( $P > 0.35$ ). No significant differences were found between current and Late Quaternary samples of *C. coturnix* ( $P = 0.17$  for femur;  $P = 0.62$  for tibiotarsus; and  $P = 0.38$  for tarsometatarsus length). *Coturnix centensis* shows a smaller femur ( $P < 0.001$ ) and tibiotarsus ( $P = 0.028$ ) than *C. gomeræ*, but the tarsometatarsus is of the same size ( $P = 0.074$ ).

Despite *C. lignorum* having longer and stouter hindlimb bones (Fig. 4), it has a humerus of similar size to that of *C. gomeræ* ( $U = -1.698$ ;  $P = 0.89$ ) and *C. coturnix* ( $U = -0.34$ ;  $P = 0.734$ ) but significantly longer than *C. alabrevis* ( $U = -4.684$ ;  $P < 0.001$ ). The ANOVA performed with the humerus lengths of this last species and those of *C. gomeræ*, *C. centensis* and *C. coturnix* identified significant morphological differences ( $F_{4,76} = 77.57$ ,  $P < 0.001$ ). *Coturnix alabrevis* has a shorter humerus than *C. gomeræ* or *C. coturnix* ( $P < 0.001$  for both cases), but the humerus is of the same size as those of *C. centensis* ( $P = 0.976$ ). *Coturnix coturnix* and *C. gomeræ* have a humerus of similar size ( $P > 0.7$ ).

The ANOVA performed with the ulna lengths of *C. lignorum*, *C. alabrevis* and *C. coturnix* identified significant differences ( $F_{2,23} = 59.987$ ,  $P < 0.001$ ). The ulna of *C. coturnix* is significantly longer than those of *C. lignorum* ( $P = 0.001$ ) and *C. alabrevis* ( $P < 0.001$ ). The ulna of *C. lignorum* is significantly longer than those of *C. alabrevis* ( $P = 0.004$ ). The ulna of *C. gomeræ* is of similar size to those of *C. coturnix* ( $U = -1.955$ ;  $P = 0.051$ ). In addition, the ulna of *C. centensis* is

significantly shorter than in *C. lignorum* ( $U = -2.12$ ;  $P = 0.034$ ) or *C. coturnix* ( $U = -2.67$ ;  $P = 0.08$ ), but of the same size as in *C. alabrevis* ( $U = -0.61$ ;  $P = 0.54$ ).

The carpometacarpus is of similar length in *C. lignorum* and *C. coturnix* ( $U = -0.378$ ;  $P < 0.705$ ), but in *C. alabrevis* it is significantly shorter than in *C. lignorum* ( $U = -2.501$ ;  $P = 0.012$ ) or *C. coturnix* ( $U = -3.971$ ;  $P < 0.001$ ). In addition, the carpometacarpus of *C. centensis* is of the same size as that of *C. alabrevis* ( $U = -0.93$ ;  $P = 0.926$ ).

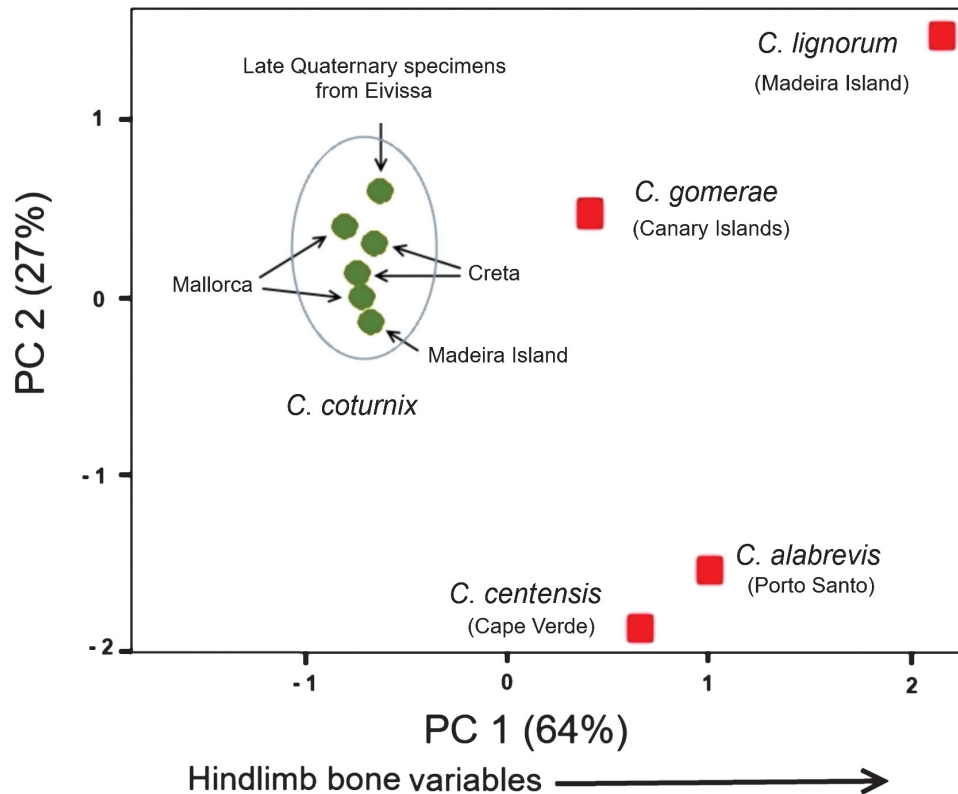
The ANOVA performed with coracoid lengths ( $F_{2,26} = 37.601$ ,  $P < 0.001$ ) shows the same pattern, with similar length in *C. lignorum* and *C. coturnix* ( $P = 0.370$ ), but significantly shorter in *C. alabrevis* than in *C. lignorum* or *C. coturnix* ( $P < 0.001$  in both cases).

The principal components analysis performed with variables 1–5, 13 and 15–22 (Table 1; Fig. 8) produced two principal components explaining 91% of the total variance; 64% is explained by principal component 1, which shows a high positive weighting for variables of hindlimb bones (traits 13 and 15–22) and a negative weighting for variables of forelimb bones (traits 1–5). Principal component 2 explains 27% of the variance and shows a high positive weighting for variables of forelimb bones and a moderate or low positive weighting for variables of hindlimb bones. The four species of extinct quails from Macaronesia score values higher than zero on principal component 1, whereas all specimens of *C. coturnix* score below zero in the same axis. This finding is in direct relationship with differences in the length of their legs, which probably reflect different habits for extinct and extant species.

To check the validity of the method to calculate the weight of quails, we applied the equation to current quails (Olmos *et al.*, 1996). The estimated weight for *C. coturnix* is  $97 \pm 8$  g ( $N = 15$ ), the range being 80–111 g. Both the mean weight and the range are close to the data for this species. The mean weight recorded for extant males is 90 g, for females 103 g (mean for males and females, ~96.5 g) and the range 76–122 g (Dunning, 2008). With the same equation, we estimated the weight of *C. lignorum* to be  $218 \pm 17$  g ( $N = 8$ ), for *C. alabrevis*  $133 \pm 11$  g ( $N = 12$ ), for *C. centensis*  $110 \pm 6$  g ( $N = 4$ ) and for *C. gomeræ*  $126 \pm 6$  g ( $N = 4$ ).

Taking into account that *C. lignorum* has forelimb bones similar in size to those of *C. coturnix* (Fig. 9; no significant differences were found for humerus and carpometacarpus length, and the ulna is a little shorter in *C. lignorum*), both taxa probably had wings of a similar size. Given that the estimated weight of *C. lignorum* (218 g) is more than twice that of *C. coturnix* (96.5 g average of extant specimens, 97 g estimated), the wing loading of the former is probably about twice





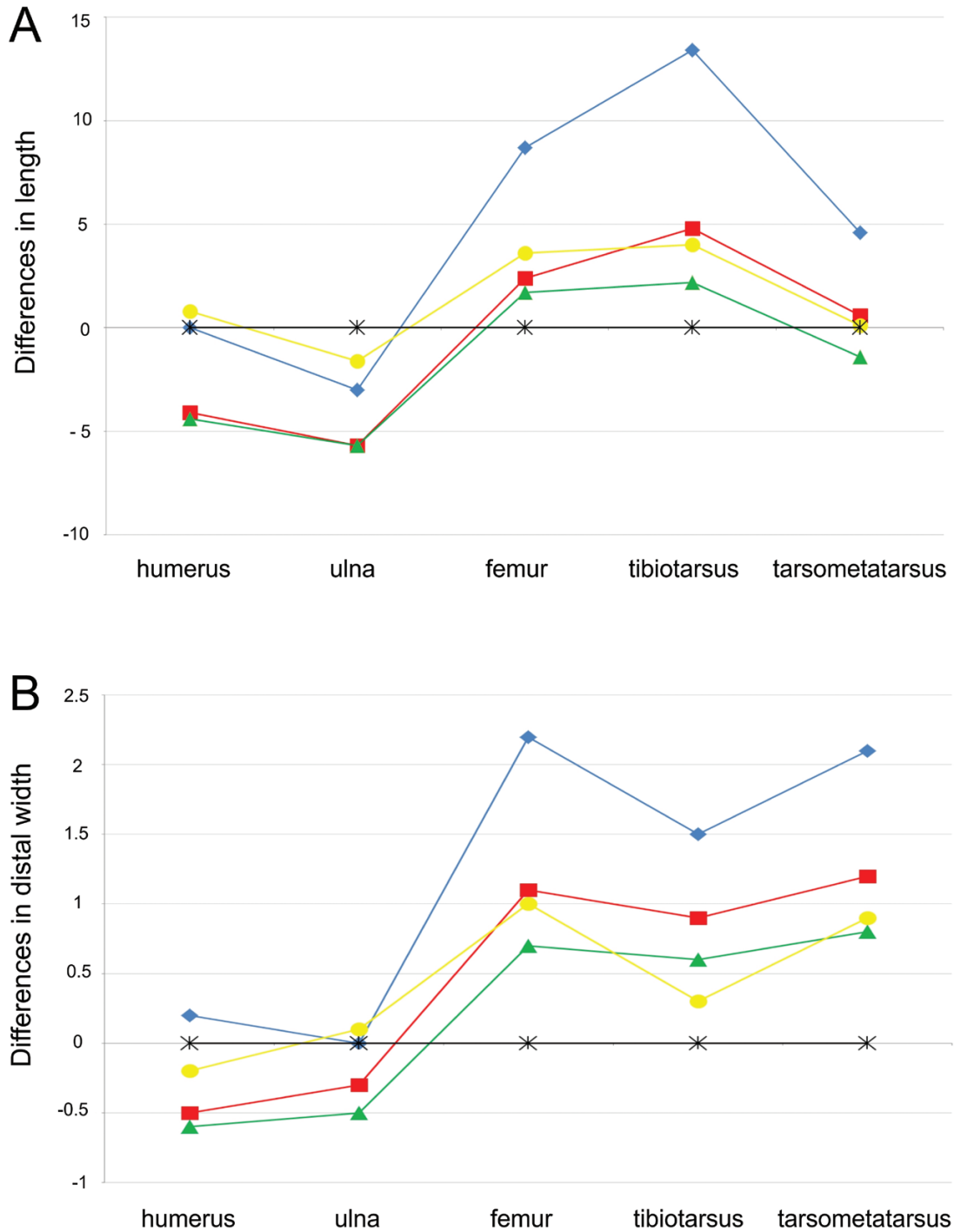
**Figure 8.** Principal components analysis plot for the two principal components (PC 1 and PC 2) obtained from variables 1–5, 13 and 15–22 (Table 1; Fig. 2) of extinct Macaronesian quails (squares), current specimens of common quail from different localities and fossil bones of common quail from Es Pouàs (Late Quaternary, Eivissa, Balearic Islands) (circles).

as great. These data suggest that *C. lignorum* was a flightless species. This is supported by its reduced carina sterni, the bone where the main flight muscles attach. A fragment of this bone, including the apex carinae, shows an apex 62% lower in *C. lignorum* than in *C. coturnix* (5.2 vs. 13.8 mm; Fig. 3).

The estimated weight for *C. alabrevis* is ~37% higher than that of *C. coturnix* (133 vs. 97 g), but the former had a notable reduction (~16%) in the wing elements (humerus + ulna + carpometacarpus = 71.2 mm) compared with the second (84.3 mm) (Fig. 4), meaning that the length and surface area of the wing of *C. alabrevis* is considerably lesser than in *C. coturnix*. These data seem to indicate that *C. alabrevis*, like *C. lignorum*, was flightless owing to the high wing loading. The similar size of the forelimb bones of *C. centensis* and *C. alabrevis* (humerus and ulna; Fig. 9) indicates a similar reduction in the wing length compared with *C. coturnix*. The estimated weight of *C. centensis* is ~13% higher than those of *C. coturnix* (110 vs. 97 g). These data seem to indicate that the extinct quail from São Vicente was also a flightless bird. This is supported by the ratio of humerus length to femur length being 0.79 for *C. lignorum*, 0.81 for

*C. alabrevis* and 0.82 for *C. centensis*. These ratios are similar to those of other flightless birds, such as rails (0.78 in *Rallus lowei* Alcover *et al.*, 2015, 0.85 in *Rallus adolfocesaris* Alcover *et al.*, 2015, 0.76 in *Rallus carvaensis* Alcover *et al.*, 2015 and 0.84 in *Rallus nanus*; Alcover *et al.*, 2015), but smaller than those of good flying birds, such as *C. coturnix* (0.99) and *Rallus aquaticus* Linnaeus, 1758 (0.94). The ratio of humerus + ulna + carpometacarpus length to femur length behaves in a similar manner. It is 1.8 for *C. lignorum*, 1.9 for *C. alabrevis* and *C. centensis* and 1.8 for *R. nanus*, whereas it is 2.3 in *C. coturnix* and 2.2 in *R. aquaticus*.

The estimated weight for the extinct *C. gomerae* from the Canary Islands is ~30% higher than that of *C. coturnix* (126 vs. 97 g). Taking into account that both species have wings of similar size (no differences were found between the humerus and ulna of either species; Fig. 4), the wing load for *C. gomerae* was probably ~30% higher than in *C. coturnix*, meaning that the extinct Canary Islands quail was probably a weak flying bird. This is supported by the ratio of humerus length to femur length for this species (0.91), which falls between the good flying and the flightless birds.



**Figure 9.** Differences (in millimetres), calculated using the mean for each element (Table 1), in the length (A) and distal width (B) of the main bones among endemic extinct Macaronesian quails and common quail: *Coturnix lignorum* from Madeira Island, rhombus (blue); *Coturnix alabrevis* from Porto Santo, squares (red); *Coturnix centensis* from São Vicente Island (Cape Verde), triangles (green); *Coturnix gomeræ* from the Canary Islands, circles (yellow); *Coturnix coturnix*, asterisks (black).

## DISCUSSION

*Coturnix* is the sole Palaearctic Phasianidae genus with truly migratory members (Olson, 1980), and it is the sole genus of this family that has been able to colonize islands without human agency. The extinct quails of Macaronesia, a diversified group of endemic birds with anatomical traits evidencing ground-dwelling habits, confer to the pristine bird communities of these islands a uniqueness not found in any other archipelago studied thus far.

Although the same allometric trends (i.e. hindlimb bones longer and stouter, but forelimb bones of the same size or smaller than in the common quail) are shared by all extinct species of Macaronesian quails, they are more accentuated in Madeira (hindlimb bones elongate and stout), Porto Santo and São Vicente (forelimb bones shorter and slenderer) than in the Canary Islands (Figs 3–5, 9).

This parallelism is most striking in *C. alabrevis* from Porto Santo Island (Madeira archipelago) and *C. centensis* from São Vicente Island (Cape Verde) (Figs 3–5, 9), two far distant islands located ~2000 km apart. Both species are similar in size and flightless, have short wings and display stouter hindlimb bones than the remaining species. Such a pattern suggests that both species are likely to have occurred in comparable island niches on Madeira and Cape Verde, experienced similar selective pressures and responded in a similar way.

The proportions and anatomical traits shared by the extinct quails of Macaronesia suggest that they exhibited more terrestrial habits than common quails, which have a greater capacity for flight than the extinct species described in the present study; therefore, it is plausible that the extinct species occupied habitats different from the open ones preferred by the common quail (McGowan *et al.*, 2019). This circumstance, together with their presumed low reproductive rate (a characteristic of insular species; Ricklefs, 1980; Crowell & Rothstein, 1981), could explain the differential extinction of these endemic quails compared with the common quail. In addition, the migratory condition of the common quail could be a key factor in explaining its survival.

Radiocarbon dating performed directly on the collagen of bones of *C. lignorum* (1021–806 cal BCE) and on bones of other terrestrial birds obtained at the sites where the bones of *C. alabrevis*, *C. gomeræ* and the fossil quails from Azores were recovered, indicates a Late Holocene age for the extinction of these quails. Likewise, the extinction of the Cape Verde quail postdates the first millennium of the Current Era. The most significant environmental alteration that took place during that period in these archipelagos was the arrival of humans. The European presence on Macaronesia began from the 14–15<sup>th</sup> centuries onwards (Newitt, 2005; Aznar *et al.*,

2006) and involved huge habitat alterations and the introduction of many invasive species, although humans had arrived in these archipelagos many centuries before. Aborigines arrived at the Canary Islands from north-west Africa before the year 313 CE (Alcover *et al.*, 2009), whereas Viking sailors reached Madeira around one millennium ago (Rando *et al.*, 2014b), and they probably also reached the Azores (Gabriel *et al.*, 2015). These early arrivals facilitated the introduction of the house mouse (*Mus musculus*) in these archipelagos, which is among the worst pest species introduced to island ecosystems (Angel *et al.*, 2009; Harris, 2009). After their introduction, the house mouse could have reached high population densities owing to its fast reproductive rate, particularly in the absence of rats (*Rattus* spp.) and given the scarcity or absence of predators. In such a situation, a wide range of the native biota could have been impacted, and the magnitude of the impact would have been devastating, as described for islands harbouring mice but no rats (Angel *et al.*, 2009; Wanless *et al.*, 2012; Bolton *et al.*, 2014; Davies *et al.*, 2015).

In the Canary Islands, the extinction of some endemic vertebrates has already been linked to aboriginal arrival or to European colonization. The extinction of the giant rat of Tenerife, *Canariomys bravi* Crusafont & Peter, 1964 (Rando *et al.*, 2014a), and the dune shearwater, *Puffinus holeae* (Walker *et al.*, 1990) (Rando & Alcover, 2010), was probably triggered by aboriginal arrival on the islands, whereas the extinction of the lava mouse, *Malpaisomys insularis* Hutterer, López-Martínez & Michaux, 1988 (Rando *et al.*, 2012a), and of the lava shearwater, *Puffinus olsoni* McMinn *et al.*, 1990 (Rando & Alcover, 2008), were linked to the first European colonization and subsequent environmental alterations associated with it.

In the case of the endemic quails of the Azores, Madeira and Canary Islands, if they survived the early impact of the house mouse, they would have gone extinct shortly afterwards with the introduction of other alien species, such as rats, cats and livestock, and the alterations to the habitat caused by the first European colonizers. A similar process has been suggested to explain the extinction of *C. novaezelandiae*, an endemic quail from New Zealand that vanished at the end of the 19<sup>th</sup> century, probably as a result of the spread of alien mammals (Worthy & Holdaway, 2002; Hume & Walters, 2012).

Finally, there is no trace of early human presence on Cape Verde. Only three centuries separate the upper limit of the 2 $\sigma$  interval (1015–1155 cal CE) of the dated bones of *C. centensis* from the 15<sup>th</sup> century European colonization of the islands (Newitt, 2005). Thus, this endemic quail probably survived until European colonization, disappearing subsequently as a result of the alterations produced by human settlers.

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## REFERENCES

- Alcover JA, Florit F. 1987.** Una nueva especie de *Carduelis* (Fringillidae) de La Palma. *Vieraea* **17**: 75–86.
- Alcover JA, Florit F, Mourer-Chauviré C, Weesie PDM. 1992.** The avifaunas of the isolated Mediterranean Islands during the middle and upper Pleistocene. In: Campbell KE, ed. *Papers in avian ornithology honoring Pierce Brodkorb. Science series*. Los Angeles: Natural History Museum of Los Angeles County, 273–283.
- Alcover JA, Pieper H, Pereira F, Rando JC. 2015.** Five new extinct species of rails (Aves: Gruiformes: Rallidae) from the Macaronesian Islands (North Atlantic Ocean). *Zootaxa* **4057**: 151–190.
- Alcover JA, Rando JC, García-Talavera F, Hutterer R, Michaux J, Trias M, Navarro JF. 2009.** A reappraisal of the stratigraphy of Cueva del Llano (Fuerteventura) and the chronology of the house mouse (*Mus musculus*) introduction into the Canary Islands. *Palaeogeography, Palaeoclimatology, Palaeoecology* **277**: 184–190.
- Angel A, Wanless RM, Cooper J. 2009.** Review of impacts of the introduced house mouse on islands in the Southern Ocean: are mice equivalent to rats? *Biological Invasions* **11**: 1743–1754.
- Aznar E, Corbella D, Pico B, Tejera A. 2006.** *Le Canarien. Retrato de dos mundos. I. Textos*. Santa Cruz de Tenerife: Instituto de Estudios Canario.
- Barnosky AD, Hadly EA, Gonzalez P, Head J, Polly PD, Lawing AM, Eronen JT, Ackerly DD, Alex K, Biber E, Blois J, Brashares J, Ceballos G, Davis E, Dietl GP, Dirzo R, Doremus H, Fortelius M, Greene HW, Hellmann J, Hickler T, Jackson ST, Kemp M, Koch PL, Kremen C, Lindsey EL, Looy C, Marshall CR, Mendenhall C, Mulch A, Mychajliw AM, Nowak C, Ramakrishnan U, Schnitzler J, Shrestha K, Solari K, Stegner L, Stegner MA, Stenseth NC, Wake MH, Zhang Z. 2017.** Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science* **355**: eaah4787.
- Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ. 2004.** Avian extinction and mammalian introductions on oceanic islands. *Science* **305**: 1955–1958.
- Bolton M, Stanbury A, Baylis AM, Cuthbert R. 2014.** Impact of introduced house mice (*Mus musculus*) on burrowing seabirds on Steeple Jason and Grand Jason Islands, Falklands, South Atlantic. *Polar Biology* **37**: 1659–1668.
- Boyer AG. 2008.** Extinction patterns in the avifauna of the Hawaiian Islands. *Diversity and Distributions* **14**: 509–517.
- Bronk Ramsey C. 2009.** Bayesian analysis of radiocarbon dates. *Radiocarbon* **51**: 337–360.
- Crowell KL, Rothstein SI. 1981.** Clutch sizes and breeding strategies among Bermudan and North American passerines. *Ibis* **123**: 42–50.
- Curnutt J, Pimm SL. 2001.** How many bird species in Hawai'i and the central Pacific before first contact? *Studies in Avian Biology* **22**: 15–30.
- Davies D, Dilley BJ, Bond AL, Cuthbert RJ, Ryan PG. 2015.** Trends and tactics of mouse predation on Tristan albatross *Diomedea dabbenena* chicks at Gough Island, South Atlantic Ocean. *Avian Conservation and Ecology* **10**: 5.
- Duncan RP, Boyer AG, Blackburn TM. 2013.** Magnitude and variation of prehistoric bird extinctions in the Pacific. *Proceedings of the National Academy of Sciences of the United States of America* **110**: 6436–6441.
- Dunning JB. 2008.** *CRC handbook of avian body mass*, 2nd edn. Boca Raton: CRC Press.
- Dyke GJ, Gulas BE, Crowe TM. 2003.** Suprageneric relationships of galliform birds (Aves, Galliformes): a cladistic analysis of morphological characters. *Zoological Journal of the Linnean Society* **137**: 227–244.
- Eo SH, Bininda-Emonds ORP, Carroll JP. 2009.** A phylogenetic supertree of the fowls (Galloanserae, Aves). *Zoologica Scripta* **38**: 465–481.
- Fitzgerald TC. 1969.** *The Coturnix quail. Anatomy and histology*. Ames: The Iowa State University Press.
- Fontoura AP, Gonçalves D. 1995.** *Coturnix coturnix confisa* Hartet 1917 (Aves: Phasianidae), a real endemic subspecies or an artifact of science? *Boletim do Museu Municipal do Funchal Suplemento* **4**: 277–284.
- Gabriel SI, Mathias ML, Searle JB. 2015.** Of mice and the 'Age of Discovery': the complex history of colonization of the Azorean archipelago by the house mouse (*Mus musculus*) as revealed by mitochondrial DNA variation. *Evolutionary Biology* **28**: 130–145.
- Harris DB. 2009.** Review of negative effects of introduced rodents on small mammals on islands. *Biological Invasions* **11**: 1611–1630.
- Holman JA. 1964.** Osteology of Gallinaceous birds. *Quarterly Journal of the Florida Academy of Sciences* **27**: 230–252.
- Hosner PA, Tobias JA, Braun EL, Kimball RT. 2017.** How do seemingly non-vagile clades accomplish trans-marine



- dispersal? Trait and dispersal evolution in the landfowl (Aves: Galliformes). *Proceedings of the Royal Society B: Biological Sciences* **284**: 20170210.
- Hume JP, Walters M. 2012.** *Extinct birds*. London: T & AD Poyser.
- Illera JC, Rando JC, Richardson DS, Emerson BC. 2012.** Age, origin and extinctions of the avifauna of Macaronesia: a synthesis of phylogenetic and fossil information. *Quaternary Science Reviews* **50**: 14–22.
- Illera JC, Spurgin LG, Rodriguez-Exposito E, Nogales M, Rando JC. 2016.** What are we learning about speciation and extinction from the Canary Islands? *Ardeola* **63**: 15–33.
- Jaume D, McMinn M, Alcover JA. 1993.** Fossil birds from the Bujero del Silo, La Gomera (Canary Islands), with a description of a new species of quail (Galliformes: Phasianidae). *Boletim do Museu Municipal do Funchal* **2**: 147–165.
- Livezey BC. 2003.** Evolution of flightlessness in rails (Gruiformes: Rallidae): phylogenetic, ecomorphological, and ontogenetic perspectives. *Ornithological Monographs* **53**: 1–654.
- Livezey BC, Zusi RL. 2006.** Phylogeny of Neornithes. *Bulletin of the Carnegie Museum of Natural History* **37**: 1–544.
- Martín A, Lorenzo JA. 2001.** *Aves del Archipiélago Canario*. La Laguna: Francisco Lemus Publisher.
- McGowan PJK, Kirwan GM, de Juana E, Boesman P. 2019.** Common quail (*Coturnix coturnix*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E, eds. *Handbook of the birds of the world alive*. Barcelona: Lynx Edicions. Available at: <https://www.hbw.com/node/53434>
- McMinn M, Jaume D, Alcover JA. 1990.** *Puffinus olsoni* n. sp.: nova espècie de baldritja recentment extinguida provinent de depòsits espeleològics de Fuerteventura i Lanzarote (Illes Canàries, Atlàntic Oriental). *Endins* **16**: 63–71.
- Millener PR. 1989.** The only flightless passerine; the Stephens Island wren (*Traversia lyalli*: Acanthisittidae). *Notornis* **36**: 280–284.
- Millener PR, Worthy TH. 1991.** Contribution to New Zealand's Late Quaternary avifauna. II: *Dendroscansor recurvirostris*, a new genus and species of wren (Aves: Acanthisittidae). *Journal of the Royal Society of New Zealand* **21**: 179–200.
- Newitt M. 2005.** *A history of Portuguese overseas expansion, 1400–1668*. London: Routledge.
- Olmos M, Casinos A, Cubo J. 1996.** Limb allometry in birds. *Annales des Sciences Naturelles Zoologie* **17**: 39–49.
- Olson SL. 1976.** Fossil woodcocks: an extinct species from Puerto Rico and an invalid species from Malta (Aves: Scolopacidae). *Proceedings of the Biological Society of Washington* **89**: 265–274.
- Olson SL. 1980.** The significance of the distribution of Megapodidae. *Emu* **80**: 21–24.
- Olson SL, James HF. 1982.** Fossil birds from the Hawaiian Islands: evidence for a wholesale extinction by man before western contact. *Science* **217**: 633–635.
- Pieper H. 1985.** The fossil land birds of Madeira and Porto Santo. *Bocagiana* **88**: 1–6.
- Puigcerver M. 1990.** *Contribución al conocimiento de la biología y ecoetología de la codorniz (Coturnix coturnix)*. Unpublished D. Phil. Thesis, Universitat de Barcelona.
- Puigcerver M, Rodriguez-Teijeiro JD, Gallego S. 2001.** The problem of the subspecies in *Coturnix coturnix* quail. *Game Wildlife Science* **18**: 561–571.
- Rando JC. 2003.** Protagonistas de una catástrofe silenciosa. Los vertebrados extintos de Canarias. *El Indiferente* **14**: 3–15.
- Rando JC, Alcover JA. 2008.** Evidence for a second western Palaearctic seabird extinction during the last millennium: the lava shearwater *Puffinus olsoni*. *Ibis* **150**: 188–192.
- Rando JC, Alcover JA. 2010.** On the extinction of the dune shearwater (*Puffinus holeae*) from the Canary Islands. *Journal of Ornithology* **151**: 365–369.
- Rando JC, Alcover JA, Galván B, Navarro JA. 2014a.** Reappraisal of the extinction of *Canariomys bravoii*, the giant rat from Tenerife (Canary Islands). *Quaternary Science Reviews* **94**: 22–27.
- Rando JC, Alcover JA, Illera JC. 2010.** Disentangling ancient interactions: a new extinct passerine provides insights on character displacement among extinct and extant island finches. *PLoS ONE* **5**: e12956.
- Rando JC, Alcover JA, Michaux J, Hutterer R, Navarro JF. 2012a.** Late-Holocene asynchronous extinction of endemic mammals on the eastern Canary Islands. *The Holocene* **22**: 801–808.
- Rando JC, Alcover JA, Olson SL, Pieper H. 2013.** A new species of extinct scops owl (Aves: Strigiformes: Strigidae: *Otus*) from São Miguel Island (archipelago of Azores, North Atlantic Ocean). *Zootaxa* **3647**: 343–357.
- Rando JC, López M, Segué B. 1999.** A new species of extinct flightless passerine (Emberizidae: *Emberiza*) from the Canary Islands. *The Condor* **101**: 1–13.
- Rando JC, Pieper H, Alcover JA. 2014b.** Radiocarbon evidence for house mouse presence on Madeira Island (North Atlantic) one millennium ago. *Proceedings of the Royal Society B: Biological Sciences* **281**: 20133126.
- Rando JC, Pieper H, Alcover JA, Olson SL. 2012b.** A new species of extinct fossil scops owl (Aves: Strigiformes: *Otus*) from the archipelago of Madeira (North Atlantic Ocean). *Zootaxa* **3182**: 29–42.
- Rando JC, Pieper H, Olson SL, Pereira F, Alcover JA. 2017.** A new extinct species of large bullfinch (Aves: Fringillidae: *Pyrrhula*) from Graciosa Island (Azores, North Atlantic Ocean). *Zootaxa* **4282**: 567–583.
- Reimer PJ, Bard E, Bayliss A, Beck JW, Blackwell PG, Bronk Ramsey C, Grootes PM, Guilderson TP, Haflidason H, Hajdas I, Hatt C, Heaton TJ, Hoffmann DL, Hogg AG, Hughen KA, Kaiser KF, Kromer B, Manning SW, Niu M, Reimer RW, Richards DA, Scott EM, Southon JR, Staff RA, Turney CSM, Van der Plicht J. 2013.** IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* **55**: 1869–1888.

- Ricklefs RE. 1980.** Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *The Auk* **97**: 38–49.
- Seabrook-Davison M, Huynen L, Lambert DM, Brunton DH. 2009.** Ancient DNA resolves identity and phylogeny of New Zealand's extinct and living quail (*Coturnix* sp.). *PLoS ONE* **4**: e6400.
- Steadman DW. 1995.** Extinctions of birds on tropical Pacific islands. In: Steadman DW, Mead JI, Martin PS, eds. *Late Quaternary environments and deep history: a tribute to Paul S. Martin*. Hot Springs: Mammoth Site of Hot Springs, South Dakota, Inc.
- Steadman DW. 2006.** *Extinction and biogeography of tropical Pacific birds*. Chicago and London: The University of Chicago Press.
- Turvey ST. 2009.** *Holocene extinctions*. Oxford: Oxford University Press.
- Walker CA, Wragg GM, Harrison CJO. 1990.** A new shearwater from the Pleistocene of the Canary Islands and its bearing on the evolution of certain *Puffinus* shearwaters. *Historical Biology* **3**: 203–224.
- Wanless RM, Ratcliffe N, Angel A, Bowie BC, Cita K, Hilton GM, Kritzinger P, Ryan PG, Slabber M. 2012.** Predation of Atlantic petrel chicks by house mice on Gough Island. *Animal Conservation* **15**: 472–479.
- Wood J, Alcover JA, Blackburn T, Bover P, Duncan R, Hume JP, Louys J, Meijer HJM, Rando JC, Wilmshurst J. 2017.** Island extinctions: processes, patterns, and potential for ecosystem restoration. *Environmental Conservation* **44**: 348–358.
- Worthy TH, Holdaway RH. 2002.** *The lost world of the moa: prehistoric life of New Zealand*. Bloomington: Indiana University Press.

### SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Table S1.** Comparative material examined (recent skeletons and Late Quaternary material from Eivissa, Balearic Island).