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# A new extinct species of large bullfinch (Aves: Fringillidae: *Pyrrhula*) from Graciosa Island (Azores, North Atlantic Ocean)

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## Summary

A new species of extinct bullfinch, *Pyrrhula crassa* **n. sp.**, is described from bones found in Furna do Calcinhas, a small cave situated at Caldeira, a volcano located in the southeastern portion of the Graciosa Island (Azores archipelago, North Atlantic Ocean). It is the first extinct passerine bird to be described from this archipelago. Both skull and post-cranial bones are larger in the new species than in its relatives, the Eurasian Bullfinch (*P. pyrrhula*) and the Azores Bullfinch or "Priolo" from São Miguel Island (*P. murina*), the new species being the largest known in this genus. The morphology of its humerus and the estimated wing length and surface area seem to indicate a flying ability similar to that of the extant *P. murina*. The possible sources of colonization of the genus into Azores, causes and chronology of extinction of the new species are discussed

## Resumo

Uma nova espécie extinta de *Pyrrhula*, *P. crassa* n.sp., é descrita a partir de ossos encontrados em a Furna do Calcinhas, uma pequena caverna situada na Caldeira, vulcão localizado no sudoeste da ilha Graciosa (Arquipélago dos Açores, Atlântico Norte). É a primeira ave Passeriforme extinta descrita neste arquipélago. Tanto o crânio e os ossos do seu esqueleto pós-craniano são maiores que os dos seus parentes, o dom-fafe *Pyrrhula pyrrhula* e o priolo *Pyrrhula murina*. A nova espécie é a maior do gênero. A morfologia do úmero e o tamanho estimado das suas asas indica uma capacidade para o voo semelhante a o priolo. As possíveis fontes de colonização dos Açores por *Pyrrhula* e as causas e cronologia da extinção da espécie nova são discutidas.

**Key words:** Azores, Bullfinch, extinction, evolution, Graciosa Island, Macaronesia, *Pyrrhula crassa* n. sp., *Pyrrhula murina*, Quaternary

## Introduction

Many species of island birds have gone extinct during the last millennium. The Macaronesian Islands (archipelagos of Azores, Madeira, Selvagens, Canaries and Cape Verde) are no exception. Bone remains indicate the extinctions of many endemic species among Procellariidae, Phasianidae, Rallidae, Strigidae, Turdidae, Emberizidae and Fringillidae on these archipelagos (see Illera *et al.* 2012).

Until now three extinct endemic passerines have been described from the fossil record in the Canary Islands: *Carduelis triasi* Alcover & Florit, 1987, *C. aurelioi* Rando, Alcover, & Illera, 2010 and *Emberiza alcoveri* Rando, López, & Seguí, 1999. In addition, extinctions of passerines have been reported for the archipelago of Madeira

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(Pieper 1985), but until now not for Azores. The Canarian extinct passerines lived in the forest, were flightless or weak flyers, and very probably bred on or very close to the ground. Their extinction seems to be directly related to the introduction of alien mammals (Alcover & Florit 1987; Rando *et al.* 1999, 2010).

According to these data, the current communities of forest passerines from the Canary Islands have lost endemic elements only since human arrival. The aboriginal peoples arrived in the eastern Canary Islands from North Africa before 313 AD (Alcover *et al.* 2009). Similar impacts on Madeira and Azores should have occurred later, because these islands were populated during the 13th century by people from Portugal, although early visits of Vikings on both archipelagos, around one millennium ago, seem to have taken place (Rando *et al.* 2014; Gabriel *et al.* 2015).

Currently, two genera of granivorous passerines inhabit the forest of the Canary Islands, Madeira, and Azores (*Fringilla* and *Pyrrhula*). They are represented by at least four species: the Priolo in São Miguel, Azores (*P. murina*), the Blue Chaffinches (*F. teydea* and *F. polatzeki*, in Tenerife and Gran Canaria respectively) in the Canary Islands, and the Common Chaffinch (*F. coelebs*) in all three archipelagos, *F. c. moreletti* in Azores, *F. c. maderensis* in Madeira, and *F. c. canariensis*, *F. c. palmae* and *F. c. ombriosa* in the Canary Islands. According to some authors (e.g., Illera *et al.* 2016), the Common Chaffinches of each archipelago are better treated as full species (i.e., *F. moreletti*, *F. maderensis* and *F. canariensis*). Two of these birds, the Blue Chaffinch of Gran Canaria and the Priolo, are threatened species, the former being the rarest songbird in Europe (Sangster *et al.* 2015; BirdLife International 2013). In addition, the three extinct known passerines of the Canary Islands were granivorous, and in Madeira the extinction of at least two species (*Coccothraustes coccothraustes* and one or several species related probably to *Acanthis*) has been reported (Pieper 1985). Taking into account the limited knowledge of Quaternary extinctions in the Azores, the current diversity of these birds seems to be only a small part of the original, which is supported by recent palaeornithological explorations (started in 2001 by one of us, H.P., and resumed from 2012 onwards). These have led to the discovery in Graciosa Island (Azores) of remains of at least two new species of extinct Fringillidae. Based on the bill morphology, one of these birds is an extinct new bullfinch (genus *Pyrrhula*), the largest so far known species in the genus. The aim of this paper is to describe this new bird, discuss its probable relatives, habitat, life style, causes and chronology of its extinction.

## Locality and methods

Graciosa is one of the younger (2.5 My) and smaller (62 km$^2$) islands of the Azores. It is located in the north of the central group of islands (Figure 1). The material studied here was found inside Furna do Calcinhas, a small cave situated in Caldeira, a volcano 1650 m wide and 350 m high located in the southeast of the island (Figure 1) that has an age of 12,000 years (França *et al.* 2003). The bones were collected directly from the surface of bare rock as well as from sediment. In a crevice that drains into the cave, we found a carcass of a recent Common Chaffinch (*Fringilla coelebs*), indicating that the cave still works today as a trap and a place for accumulation of bones.

The fossil series of *Pyrrhula* consists mainly of cranial material (premaxilla, quadrate and mandible), because many isolated postcranial bones of Fringillidae in the fossil sites could not be confidently identified beyond family. The bones in question are from a fringillid that was markedly larger and more robust than any species of *Fringilla* but agreeing well with the configuration of cranial bones in the genus *Pyrrhula*.

We compared the fossil material with the two European species of *Pyrrhula*, *P. pyrrhula* and *P. murina*, and with the Himalayan *P. erythaca*. We also made comparisons with all the skeletons of European Fringillidae in the IMEDEA collection, especially with *Coccothraustes coccothraustes*, *Pinicola enucleator, Loxia curvirostra* and *Loxia pityopsittacus*. See Appendix.

The available sample of *P. pyrrhula* skeletons contains specimens of different geographic origin, presumably belonging to different subspecies. Unfortunately, no information on the subspecies of the specimens exists. The "Northern Bullfinch" (i.e., *P. pyrrhula pyrrhula* from Northern Europe) is known to be larger than its southern counterparts. The specimens from Spain and Portugal should belong to the subspecies *P. pyrrhula iberiae*, and the specimen from England should represent *P. pyrrhula pileata*, both of which subspecies are quite sedentary. The specimens from Sweden and Poland (the largest male and the female of the available series) probably belong to *P. pyrrhula pyrrhula*. The specimens from Greece probably belong also to *P. pyrrhula pyrrhula*, although they are smaller than the northern specimens. Given the lack of precise subspecific information, all the specimens of *P. pyrrhula* have been considered as a single sample, as were those of *P. erythaca*.

**FIGURE 1.** Geographic position of Macaronesia in eastern Atlantic Ocean, showing the Azores Archipelago and the location of Furna do Calcinhas (spot) inside Caldeira volcano in Graciosa Island.

We selected osteological measurements (Figure 2) that allow comparisons with the fragmented and scarce fossil material obtained. The cranial and postcranial measurements of all available specimens of the genus *Pyrrhula* are summarized in Tables 1 and 2.

Measurements were taken with digital callipers and rounded to the nearest 0.1 mm. The terminology of premaxilla, mandible and long bones follows Livezey & Zusi (2006), while for the quadrate we follow Nuijens & Zweers (1997) and Genbrugge *et al.* (2011).

We performed two Principal Component Analyses (PCA) on premaxilla and mandible proportions among bullfinches. Length differences between *P. pyrrhula* and the new species were evaluated using a multivariate analysis of variance (MANOVA) on ventral length of premaxilla, nostril length, premaxilla width, premaxilla height, and symphyseal length (traits 3, 4, 7, 8, and 10). Elements known only from three specimens (carpometacarpus length; trait 21) were compared with a nonparametric test (Mann–Whitney U tests). The percentages of the differences among the measurements of the different species provided in the text were calculated on the arithmetical means presented in Tables 1 and 2.

We derived an approximate weight of the new species using the formula $Y = 1.05\ X^{0.326}$ (Olmos *et al.* 1996), where tibiotarsus length was the dependent variable (Y), and the estimated mass of the bird (X) the independent variable.

In order to evaluate the flight capability of the new species we performed two linear regressions, using data from fresh specimens of Fringillidae (Rando *et al.* 2010): (1) $Y = 3.357\ X + 23.6722$ ($p < 0.001$; $r^2 = 0.98$; $n = 7$), humerus length versus wing length, with wing length as the dependent variable, and (2) $Y = 306.554\ X - 1837.995$ ($p = 0{,}011$; $r^2 = 0.752$; $n = 7$), humerus length versus wing area, with wing area as the dependent variable.

All the fossil specimens described herein are deposited in Museu Carlos Machado (MCMa) in São Miguel Island (Azores).

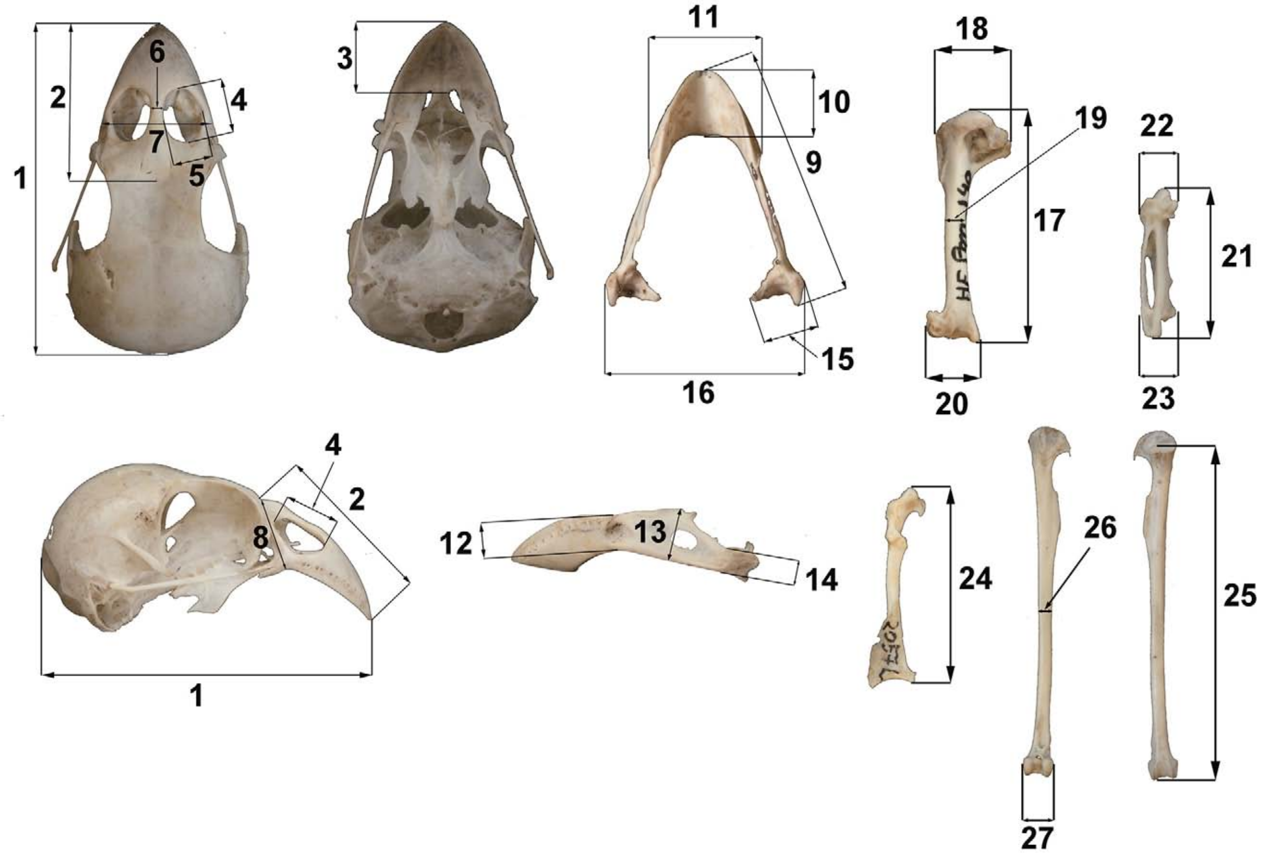

**FIGURE 2**. Measurements. 1: cranium length, from the apex of the premaxilla to the end of the cranium; 2: dorsal length of the premaxilla, from the nasofrontal hinge to the premaxillary apex; 3: ventral length of the premaxilla, from the palatine notch to the premaxillary apex; 4: nostril length, 5: nostril width; 6: processus dorsonarialis width; 7: premaxilla width; 8: premaxilla height; 9: mandible length; 10: length of the mandibular symphysis; 11: maximum width of the symphysis; 12: minimum height of mandibular ramus; 13: maximum mandibular height; 14: minimal mandibular height at the lateral cotyla; 15: length of the lateral cotyla; 16: maximum width of the mandible; 17: humerus length, from the *caput humeris* to the end of *processus flexorius*; 18: proximal humerus width; 19: humerus width of shaft at midpoint; 20: humerus distal width; 21: carpometacarpus length; 22: carpometacarpus proximal width; 23: carpometacarpus distal width; 24: coracoid length, from the *processus acrocoracoideus* to the *angulus medialis coracoidei*. 25: tibiotarsus length from the apex of the *facies articularis medialis* to the distal part of the distal condyles; 26: tibiotarsus width of shaft at midpoint; and 27: tibiotarsus maximum width of the distal end.

## Systematic paleontology

### Order Passeriformes Linnaeus, 1758

### Family Fringillidae (Vigors, 1825)

### Subfamily Carduelinae Vigors, 1825

### Tribe Pyrrhulini

### Genus *Pyrrhula* Brisson, 1760

The bones described here are referred to *Pyrrhula* by the following characteristics. The bill is characteristically short and wide, the nostrils are large and subquadrangular and the pars symphysialis of the mandible is short compared with other Fringillidae, such as *Fringilla*, *Carduelis*, *Serinus,* or *Coccothraustes* (e.g., Moreno 1984). In addition, the quadrate of *Pyrrhula* has the condylus medialis relatively larger compared with other Fringillidae. The comparisons are focused on the new taxon's closest relatives so we have not compared it with other extant or extinct insular large billed finches.

### ***Pyrrhula crassa* n.sp.**

(Figures 3, 4, 5, and supplementary figures in Appendix 2)

**Holotype. MCMa 2002.016**: fragmentary mandible, with a near complete right half, without processus medialis mandibulae and a fragment of the processus coronoideus, and the left ramus mandibulae broken (Figure 3 A`). Collected by E. Torres, J.C. Illera, J.C. Rando, H. Pieper, O. Runze & J.A. Alcover, 20–24.06.2015.

**Type locality.** Furna do Calcinhas, small cave (22.5 m length, 7 m wide, 3.5 m maximum height) situated at 175 m a.s.l. inside the Caldeira volcano, southeastern portion of Ilha da Graciosa, Azores (Figure 1).

**Horizon.** Holocene. The Caldeira volcano is 12,000 years old (França *et al.* 2003), so the materials inside the cave are necessarily younger. The remains of a *Fringilla* obtained in the same sedimentary unit as the material of the new species yielded a $^{14}$C age of 3029±31BP (1400-1190 cal BC; RICH-21754).

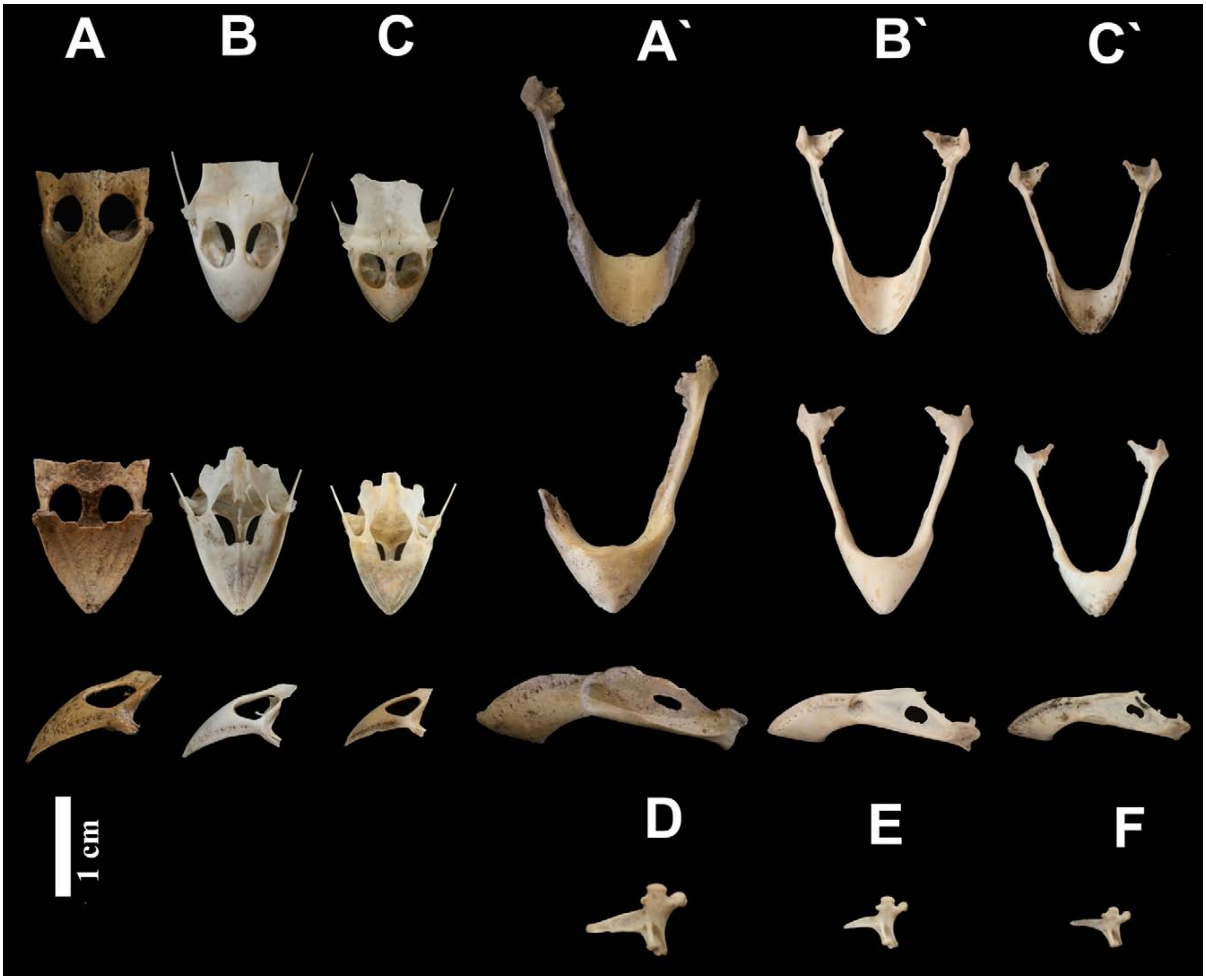

**FIGURE 3.** Premaxilla and mandible of *Pyrrhula crassa* **n.sp.** (A; MCMa 2003.016 holotype, A`; MCMa 2002.016, reversed), *P. murina* (B, B`; SPEA-140) and *P. pyrrhula* (C; LARC- 2328, C`; CIPA-1570). From top to bottom: dorsal, ventral and lateral views. Quadrate of *P. crassa* **n.sp.** (D; MCMa 1998.016), *P. pyrrhula* (E; CIPA-1570), and *Fringilla coelebs* (F; IMEDEA 12518). Lateral view.

**FIGURE 4.** Coracoid, humerus and carpometacarpus of *Pyrrhula crassa* **n.sp.** (A), *P. murina* (B) and *P. pyrrhula* (C). From top to bottom: left coracoid dorsal view, left humerus caudal view and right carpometacarpus ventral view. Right tibiotarsus of *P. crassa* **n.sp.** (A`), *P. murina* (B`) and *P. pyrrhula* (C`), cranial view. From top to bottom (A): MCMa 2010.016, MCMa 1998.016, MCMa 2009.016; (B): SPEA-120; (C): CIPA 2057, CIPA 1570, CIPA 2328. (A`): MCMa 1998.016; (B`): SPEA-120; (C`): LARC 2328.

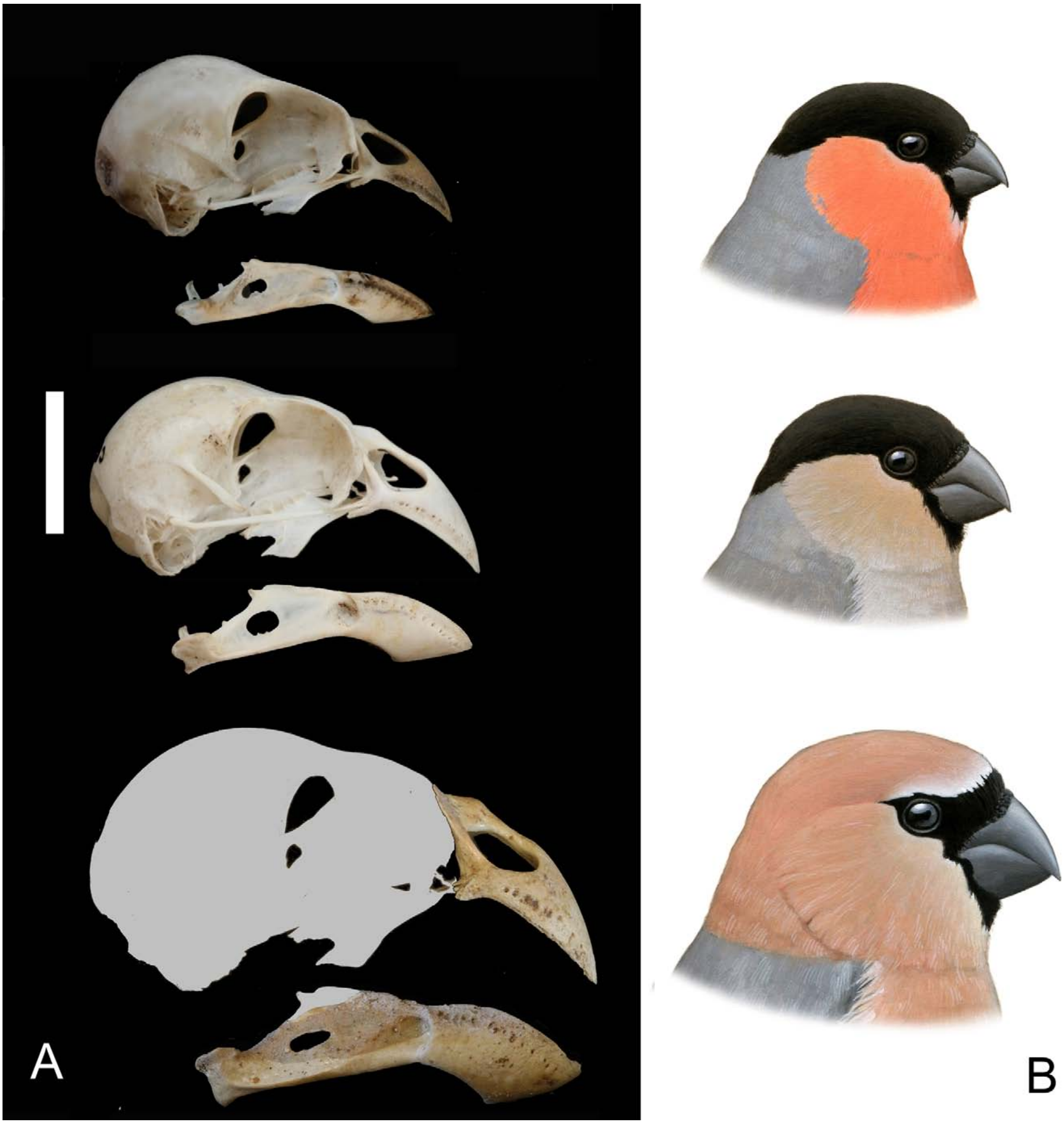

**FIGURE 5.** A: Skull and mandible, lateral view. From top to bottom: *Pyrrhula pyrrhula*, LARC 2328; *P. murina*, SPEA 120; *P. crassa* **n.sp.**, based on premaxilla MCMa 2006.016 and mandible MCMa 2002.016. The missing parts have been added using the equivalent parts of *P. murina*. Scale = 1 cm. B: From top to bottom: aspect of extant *P. pyrrhula*; *P. murina*; and possible aspect in life of *P. crassa* n.sp. (colours are speculative). Art by Pau Oliver.

**Status.** Extinct.

**Etymology.** From Latin, *crassa*, thick, referring to the large size of the species and particularly to its notably heavy bill.

**Vernacular names proposed:** Greater Azores Bullfinch (English) – Priolo maior dos Açores (Portuguese).

**Paratypes: MCMa 1998.016**: an assemblage of bones found together, probably belonging to an associated individual: 2 humeri (left and right), left carpometacarpus; 2 quadrati, right tibiotarsus, left coracoid; **MCMa 1999.016**: fragmentary mandible; **MCMa 2000.016**: fragmentary mandible; **MCMa 2001.016**: fragmentary mandible; **MCMa 2003.016**: fragmentary premaxilla; **MCMa 2004.016**: fragmentary premaxilla; **MCMa 2005.016**: fragmentary premaxilla; **MCMa 2006.016**: fragmentary premaxilla; **MCMa 2007.016**: fragmentary premaxilla; **MCMa 2008.016**: fragmentary premaxilla; **MCMa 2009.016**: associated right humerus and right carpometacarpus; **MCMa 2010.016**: right carpometacarpus. All the bones were collected by E. Torres, J.C. Illera, J.C. Rando, H. Pieper, O. Runze & J.A. Alcover, 20.–24.06.2015, excepting the mandible **MCMa 1999.016**, collected by E. Torres, F. Pereira and J.A. Alcover, 12.09.2014. See supplementary figures S1, S2 and S3.

**TABLE 1.** Cranial measurements (traits 1–16; as in figure 2) of *Pyrrhula crassa* n. sp., *P. murina*, *P. pyrrhula* and *P. erythaca*. Mean length (mm) ± standard error, sample size shown in brackets and range.

| | *P. crassa* **n.sp.** | *P. murina* | *P. pyrrhula* | *P. erythaca* |
|---|---|---|---|---|
| 1:Cranium length | | 28.4 (1) | 26.6±0.8 (10)<br>25.0–28.5 | 26.6±0.2 (4)<br>26.4–27 |
| 2:Premaxilla dorsal length | 17.3 (1) | 15.1 (1) | 12.4±0.5 (11)<br>11.6–13.2 | 11.9±0.3 (11)<br>11.5–12.3 |
| 3:Premaxilla ventral length | 9.4±0.3 (4)<br>9.0–9.9 | 7.7 (1) | 6.5±0.4 (11)<br>5.7–7.3 | 6.7±0.1 (11)<br>6.4–6.9 |
| 4:Nostril length | 5.1±0.2 (6)<br>4.9–5.45 | 4.6 (1) | 4.0±0.3 (11)<br>3.5–4.5 | 3.8±0.2 (11)<br>3.5–4 |
| 5:Nostril width | 4.4±0.2 (6)<br>4–4.7 | 4.0 (1) | 3.4±0.2 (11)<br>3–3.9 | 3.3±0.1 (10)<br>3.2–3.5 |
| 6:Processus dorsonarialis width | 1.60.1 (5)<br>1.6–1.8 | 1.1 (1) | 0.9±0.1(11)<br>0.8–1.1 | 1.0±0.1 (10)<br>0.9–1.1 |
| 7:Premaxilla width | 10.6±0.3 (5)<br>10.2–11.3 | 8.5 (1) | 7.6±0.3 (6)<br>7.1–8.1 | |
| 8:Premaxilla height | 4.9±0.1 (5)<br>4.8–5.3 | 4.2 (1) | 3.4±0.1 (6)<br>3.2–3.5 | |
| 9:Mandible length | 27.7 (1) | 22.5 (1) | 19.9±0.7 (10)<br>18.9–21.2 | 19.6±0.3 (8)<br>19.2–20 |
| 10:Symphysis length | 7.6±0.6 (4)<br>7.2–8.7 | 5.8 (1) | 4.9±0.3 (10)<br>4.3–5.4 | 5.0±0.2 (11)<br>4.7–5.4 |
| 11:Symphysis width | 13.4±0.4 (2)<br>12.9–13.8 | 10 (1) | 9.0±0.4 (9)<br>8.4–9.7 | 9.3±0.3 (9)<br>9–9.7 |
| 12:Minimum height of mandibular ramus | 4.7±0.2 (3)<br>4.5–5 | 3.3 (1) | 2.7±0.2 (11)<br>2.4–3 | 2.7±0.1 (10)<br>2.6–2.9 |
| 13:Maximum mandible height | | 4.6 (1) | 4.1±0.1 (11)<br>3.8–4.3 | 4.0±0.2 (10)<br>3.7–4.2 |
| 14.Minimal mandible height | 3.8 (1) | 2.2 (1) | 1.9±0.1 (11)<br>1.8–2.2 | 1.8±0.1 (10)<br>1.7–2 |
| 15:Length of lateral cotyla | 3.5 (1) | 3 (1) | 2.7±0.1 (6)<br>2.6–2.9 | |
| 16:Maximum mandible width | | 17.7 (1) | 15.8±0.5 (9)<br>15.1–16.2 | 15.8±0.3 (6)<br>15.6–16.3 |

**Diagnosis.** Quadrate larger than in any other known species of *Pyrrhula*. The premaxilla is very robust, while the nostrils are relatively smaller in relation to the bill size than they are in *P. murina* or *P. pyrrhula*, and the processus dorsonarialis is relatively wide (84% and 50% wider than in *P. pyrrhula* and *P. murina* respectively) . The mandible is much larger, higher and more robust than in congeners. The symphyseal part of the mandible is higher than in its congeners (on average, 75.6% higher than in *P. pyrrhula* and 42% than in *P. murina*), while its length is only 57% longer than in *P. pyrrhula* and 32% longer than in *P. murina*. The humerus, carpometacarpus, coracoid, and tibiotarsus are longer and more robust than in the other known species of the genus (Figures 3 and 4).

## Comparative osteometry

All the bones of *P. crassa* are larger and more robust than those of *P. murina* or *P. pyrrhula* (Figures 3, 4, 5, and 6).

Size differences between *P. murina* and *P. crassa* are greater than those between *P. murina* and *P. pyrrhula* (Table 1 and 2).

In relation to *P. pyrrhula*, *P. crassa* has a more robust premaxilla, some 40 to 52% longer (depending on the measurement) and an estimated 40% greater width, with relatively small nostrils (in relation to the premaxilla size) separated by a very robust nasal bar (84% more robust than in *P. pyrrhula*). The mandible is 40% longer than in *P. pyrrhula*. The symphysis is relatively more developed in *P. crassa*, being 57% longer and 48% wider than in *P. pyrrhula*. The ratio of symphysis width to length is 27.5% in *P. crassa* versus 25.6% in *P. murina* and 24.5% in *P. pyrrhula*. The mandible is relatively higher in the new species than in *P. pyrrhula* (symphysis height, 75.6% higher; cotylar height, 100% higher) (Table 1).

Although we have no complete mandible, it has been possible to reconstruct its shape using a mirror image of the single available half mandible (MCMa 2000.016, holotype). This reconstruction suggests a relatively wider and especially higher mandible in comparison to *P. pyrrhula*, *P. erythaca* or *P. murina*. The humeri of the new species are 24% longer than in *P. pyrrhula*, and relatively more robust (29%). The tibiotarsus is longer (30%) than in *P. pyrrhula,* but relatively more robust (40%). The differences in size between *P. crassa* and *P. erythaca* are in general slightly greater than those recorded between the first and *P. pyrrhula* (Tables 1 and 2).

**TABLE 2.** Post-cranial measurements (traits 17–27; as in figure 2) of *Pyrrhula crassa* n. sp., *P. murina*, *P. pyrrhula* and *P. erythaca*. Mean length (mm) ± standard error, sample size shown in brackets and range.

| | *P. crassa* **n.sp.** | *P. murina* | *P. pyrrhula* | *P. erythaca* |
|---|---|---|---|---|
| 17:Humerus length | 22.8±0.1 (2)<br>22.7–22.9 | 19.3 (1) | 18.4±0.9 (13)<br>17.1–20.1 | 18.2±0.3 (11)<br>17.7–18.6 |
| 18:Humerus proximal width | 7.820 (2)<br>7.8–7.9 | 6.2 (1) | 6.2±0.3 (13)<br>5.8–6.5 | 5.9±0.1 (12)<br>5.7–6.1 |
| 19:Humerus shaft width | 2.4±0 (2) | 1.9 (1) | 1.8±0.1 (13)<br>(1.7–1.9) | 1.8±0.1 (8)<br>(1.7–1.9) |
| 20:Humerus distal width | 6.1±0.1 (2)<br>6.0–6.2 | 4.7 (1) | 4.7±0.3 (13)<br>4.2–5.1 | 4.8±0.2 (11)<br>4.6–4.9 |
| 21:Carpometacarpus length | 15.80.5 (3)<br>15.3–16.5 | | 12.9±0.8 (13)<br>11.9–14.3 | 12.3±0.3 (8)<br>11.8–13.0 |
| 22:Carpometacarpus proximal width | 4.2±0.1 (3)<br>4.0–4.3 | | 3.2±0.2 (13)<br>2.9–3.7 | 3.0±0.1 (8)<br>2.9–3.1 |
| 23:Carpometacarpus distal width | 3.80.1 (3)<br>3.75–3.9 | | 3.0±0.2 (13)<br>2.6–3.2 | 2.8±0.1 (9)<br>2.6–2.9 |
| 24:Coracoid length | 21.2 (1) | 17.7 (1) | 17.1±0.5 (7)<br>16.4–18.2 | 15.9±0.3 (11)<br>15.6–16.5 |
| 25:Tibiotarsus length | 34.9 (1) | 32.3(1) | 27.2±1.0 (12)<br>25.3–29.4 | 26.8±0.5 (9)<br>26.2–27.8 |
| 26:Tibiotarsus shaft width | 1.6 (1) | 1.4 (1) | 1.1±0.1 (12)<br>1–1.3 | 1.1±0.1 (11)<br>1–1.3 |
| 27:Tibiotarsus distal width | 3.5 (1) | 2.7 (1) | 2.4±0.1 (13)<br>2.1–2.5 | 2.4±0.1 (9)<br>2.2–2.5 |

We have been able to compare the fossil bones of *P. crassa* with those of a single partial skeleton of *P. murina*. Relative to that species, *P. crassa* also has a more robust premaxilla, about 18% longer and 25% wider, with a very robust nasal bar (50 % more robust than in *P. murina*). The mandible is 23% longer than in *P. murina*. The symphysis is relatively more developed in *P. crassa*, being 32% longer and 35% wider than in *P. murina*. The mandible is relatively higher in the new species than in *P. murina* (symphyseal height, 42.5% higher, cotylar height, 69% higher). The humerus of the new species is 18% longer than in *P. pyrrhula*, and relatively more robust. The tibiotarsus is longer (8%) and relatively wider (13%) than in *P. murina*.

The premaxillae and mandibles of *P. crassa* are larger than the observed range for *P. pyrrhula* or *P. erythaca* in all dimensions, without overlapping. The size differences between *P. murina* and *P. crassa* are larger than those recorded between *P. murina* and *P. pyrrhula*. The magnitude of the size difference recorded between the fossil remains and the bones of both *P. pyrrhula* and *P. murina* are too great to be attributable to an intraspecific variation of one of those two species.

The MANOVA performed with traits 3, 4, 7, 8 and 10 (maxilla ventral length, nostril length, premaxilla width, premaxilla height and symphysis length) identified significant morphological differences between *P. crassa* and *P. pyrrhula* (Wilks' lambda = 0.014, d.f. = 5, 4; p=0.001). The new bird has a longer ($F_{1,10}$ = 96.16; p<0.001), wider ($F_{1,10}$ = 133.22; p<0.001) and higher ($F_{1,10}$ = 220.57; p<0.001) premaxilla (differences are around 32%, 25% and 26% respectively), a greater symphysis length ($F_{1,10}$ = 68.8; p<0.001) (35%) and a longer nostril ($F_{1,10}$ = 42.1; p<0.001) (21%). The mandible is around 28% longer, 40% higher and the processus dorsonarialis is around 43% wider than in *P. pyrrhula*. In addition, the new species has a longer carpometacarpus (U = -2.62; p = 0.009), around 18%, and tibiotarsus (22%) than *P. pyrrhula*.

The quadrate of *P. crassa* was compared with that of *P. pyrrhula* and *F. coelebs*. Its shape fits well with that of *P. pyrrhula*, although it is considerably larger and stouter. In *Pyrrhula*, the tuberculum adductor mandibulae is markedly stronger than in *Fringilla*, indicating a stronger biting power, and in addition the processus orbitalis quadrati is more dorsally oriented (Figure 3).

The PCA performed with premaxilla ventral length, nostril length, and premaxilla width and height (traits 3, 4, 7 and 8) produced two principal components explaining 98.9% of the total variance, 96.9% is explained by PC1, which shows a high positive weighting for all traits. PC2 explained 2% of the variance and shows a small positive weighting for nostril length, and a small negative weighting for the other three traits (Figure 6A). The PCA performed with mandible length, symphysis length and width (traits 9, 10 and 11) produced two principal components explaining 98.4% of the total variance, 95% is explained by PC1, which shows a high positive weighting for the three traits. PC2 explained 3.4% of the variance and shows a moderate positive weighting for symphysis length, and a moderate negative weighting for mandible length and symphysis width (Figure 6B).

**Flight capability.** According to the performed equations, the wing length of *P. crassa* was 100.21±0.3 mm and wing area 51.51±0.3 $cm^2$ (n=2). Using the same methodology, the wing length of the sole specimen of *P. murina* is 88.46 mm, a value within the range of variation (85–93 mm) of living specimens of this species (Ramos 1998), and wing area is 40.78 $cm^2$. For specimens of *P. pyrrhula* from the Iberian Peninsula the wing length is calculated at 82.75±1.3 mm, a value within the range of populations of Western Europe (78–85 mm; Snow & Perrins 1998), and wing area is 35.57±1.2 $cm^2$ (n=5). These data show that wing length of *P. crassa* is around 12% and 17% greater than in *P. murina* or *P. pyrrhula* from the Iberian Peninsula, and wing area is around 20% and 31% larger respectively.

The estimated weights are 19.4±1.3 g (17.4 – 21.02; n =5) for *P. pyrrhula* from the Iberian Peninsula, 36.7 g for *P. murina*, and 46.4 g for *P. crassa*. The estimated mean weight for *P. pyrrhula* is within the range of birds from central Europe (16–26 g) (Snow & Perrins 1998), but the estimated mean weight for *P. murina* is slightly out of the range (26.5–35 g) (Ramos 1998), so this estimate, and very probably that of *P. crassa*, exceeds slightly the real weight of these birds.

We calculated the ratio of body weight to wing area and we obtained a wing loading of 0.27±0.01 g $cm^{-2}$ (n=5) for *P. pyrrhula* from the Iberian Peninsula, a similar figure to that of other continental finches such as *Carduelis chloris* (0.28±0.02 g $cm^{-2}$) (Rando *et al.* 2010). The figure obtained for *P. murina* is 0.45 g $cm^{-2}$. Just as the estimated weight of this bird is greater than the real weight, this wing loading is very probably higher than the real value. Using the mean weight of living birds (30 g; Ramos 1998), instead of the estimated weight, the wing loading of *P. murina* is 0.37 g $cm^{-2}$, a value probably more close to the real wing loading. For *P. crassa*, the wing loading is 0.45 g $cm^{-2}$, a figure that probably is an overestimate due to the same problem (overestimation of the weight), with the real wing loading of this bird being smaller.

Overall, these data seem to indicate that *P. crassa* had a flight capability similar to that of *P. murina*.

## Discussion

The bill height and width are morphological traits directly related to the maximum compression force that the mandibles can apply (Bock 1966), and the size and hardness of seed that might be eaten (Grant & Grant 2007; Díaz 1994). The bill size and shape of *P. crassa* (Figures 3, 5 and 6) could give access to a wider diet than other bullfinches including large to small seeds, berries, fruits and buds. It could have eaten the seeds of the laurel forest plants that have large and hard seeds, such as *Prunus azorica*, *Frangula azorica*, *Viburnum treleasei, Juniperus brevifolia* and others.

The assignment of the fossils described here to the genus *Pyrrhula* is based mainly in the bill morphology. Its closest relative is *Pinicola*, a genus with a more conical bill. Currently, the genus *Pyrrhula* consists of seven living species that have been separated in three groups: Eurasian bullfinches (*P. pyrrhula* and *P. murina*), Himalayan bullfinches (*P. erythrocephala*, *P. erythaca* and *P. aurantica*), and SE Asian bullfinches (*P. nipalensis* and *P. leucogenis*). *P. crassa* should be situated within the Eurasian bullfinch group.

The finding of a second species of *Pyrrhula* in the Azores, raises two possibilities for their history of colonization: (i) *P. murina* and *P. crassa* evolved from a single colonization from the mainland; or (ii) each taxon is the product of separate colonization events occurring at different times.

Because the extant Macaronesian avifauna shows very little diversification within lineages, some genera indicate several independent colonization events from the continent (e.g., *Regulus*, *Erithacus*, *Cyanistes* [*Parus*] or *Fringilla*) with subsequent incipient radiation (Illera *et al.* 2012; 2016). The species of *Pyrrhula* in the Azores could, parallel the situation in the genus *Fringilla* in the Canary Islands where two morphologically different species (*F. teydea* and *F. coelebs*) are the consequence of two colonization events 1.99 and 1.09 My respectively (Rando *et al.* 2010). Similarly, two morphologically different species are present in this same archipelago in the fossil record, where two extinct greenfinches (*Carduelis triasi* and *C. aurelioi*) lived until the human alterations of the pristine forest (Alcover & Florit 1987; Rando *et al.* 2010).

It is important to take into account that *P. pyrrhula* is an unusual species amongst the European finches in terms of movement patterns: some populations (even subspecies, like *P. pyrrhula pileata* from Britain and *P. pyrrhula iberiae* from northern Iberia; Pennington & Meek 2006) are fairly sedentary or only partially migratory, whilst others (as the larger Northern *P. pyrrhula pyrrhula*) are irruptive, with some groups moving up to several thousand kilometres between wintering seasons (Newton 1972). It was established that birds arriving in Denmark in one of these irruptive events (winter of 2004) very probably came from the Komi Republic in Eastern Russia, 2,300 km distant (Fox 2006). A conservative estimate of the 2004 irruptive event postulated that at least 4,000 individuals arrived in Britain (Pennington & Meek 2006), perhaps from Finland (2,800 km distant) or from some other eastern location. Such irruptive behaviour in northern populations makes them more likely candidates for overseas colonization of Azores than the more sedentary southern populations.

Kessler (2013) named 98 new species of passerine birds from postcranial remains from the late Miocene and Pliocene of Hungary. The "diagnoses" consist mainly of minute, non-comparative descriptive details that do not serve to diagnose the new species from others of their genera and comparative measurements were based on very low sample sizes. Of the two species of *Pyrrhula* proposed (Kessler 2013: 81–82), *P. galae* (*nec gali* as the species was named after female Hungarian paleornithologist, Erika Gál) was said only to correspond "in its characters to recent species of the genus" and *P. minor* (*nec Pyrrhula minor* Brehm, 1855) was said only to correspond "in its characteristics to [the] recent genus, but differs in dimensions." Even if these few bones are actually referable to the genus *Pyrrhula*, they obviously have no direct connection to the evolution of a large species of *Pyrrhula* in the Azores.

*Pyrrhula crassa* represents the second endemic bullfinch in the Azores and the first fossil endemic passerine so far described there. Its restricted distribution (only known from one island, Graciosa), so far from that of *P. murina*, only known from São Miguel island, suggests the likelihood that both species may have been widely distributed in the Azores, at least in the eastern and central islands, or that each is the allopatric equivalent inside a radiation across the archipelago. On both cases, new extinct populations of *Pyrrhula*, belonging either to some of the known or to some unknown new species, may be expected to be discovered.

The extinction of *P. crassa*, was very probably related to destruction of pristine habitats in the Azores through burning and the introduction of alien species, as prior to human arrival the Azores were almost entirely covered by laurel forest that has since been reduced to only 3% of its original area (Terzopoulou *et al.* 2015).

The discovery of a recently extinct new species of Fringillidae in the Azores represents the addition of a new endemic to the archipelago. It is the fifth endemic species described in the Azorean fossil record. Until now the paleontological exploration of the Azores revealed the addition of a new scops owl (*Otus frutuosoi*; Rando et al. 2013), and three new species of rails (*Rallus carvaoensis*, *R. montivagorum* and *R. nanus*; Alcover *et al*. 2015, 2016). These new species indicate an original, pre-human, terrestrial avifauna with a high level of endemism. Further discoveries are expected to expand our knowledge of this diversity.

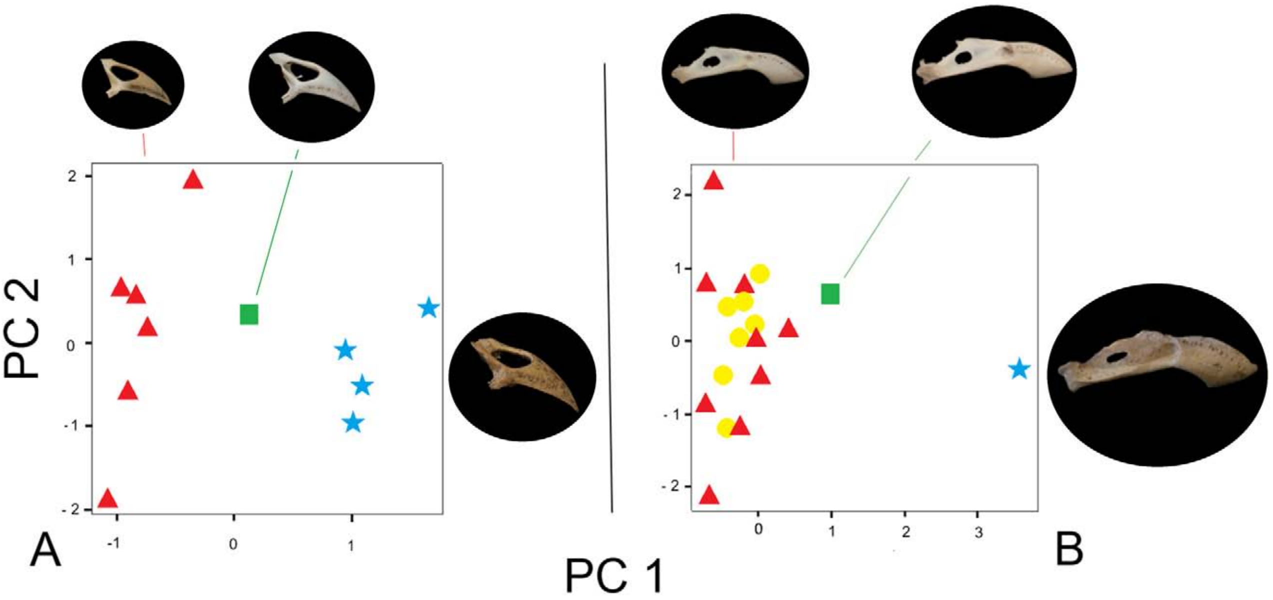

**FIGURE 6.** (A): PCA plot for the two principal components obtained from premaxilla ventral length, nostril length, and premaxilla width and height (traits 3, 4, 7 and 8). (B): PCA plot for the two principal components obtained from mandible length, symphysis length and width (traits 9, 10 and 11). *Pyrrhula pyrrhula* (triangles), *P. erythaca* (circles), *P. murina* (squares), and *P. crassa* **n.sp.** (stars).

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**APPENDIX 1.** Comparative material examined.

***Pyrrhula murina* (Godman, 1866):** 1 partial skeleton, SPEA 140-2011.

***Pyrrhula pyrrhula* (Linnaeus, 1758):** IMEDEA 39024 (complete unsexed skeleton, unknown provenance). IMEDEA 12580 (partial postcranial unsexed skeleton, Iberian Peninsula), IMEDEA 20755 (complete unsexed skeleton, Iberian Peninsula); LARC 2328 (female, Beira Baixa, Portugal), CIPA 1569 (female, ICN, Parque Nacional de Peneda-Geres, Portugal); CIPA 2057 (male, Cañada de los Pájaros, Andalusia, Spain); CIPA 1570 (male, ICN, Parque Nacional de Peneda-Geres, Portugal); CIPA 1566 (female, ICN, Parque Nacional de Peneda-Geres, Portugal). USNM 498832 (male, England). CIPA 57 (male, Poland); USNM 620127 (female, Sweden); USNM 637510 (female, Greece); USNM 637525 (female, Greece); USNM 637523 (male, Greece).

***Pyrrhula erythaca* Blyth, 1862:** USNM 319061 (unsexed, China); USNM 319057 (unsexed, China); USNM 319055 (male, China); USNM 321879 (male, China); USNM 319616 (male, China); USNM 318347 (male, China); USNM 289933 (male, China); USNM 319387 (male, China); USNM 319385 (male, China); USNM 319386 (male, China); USNM 318348 (male, China); USNM 319388 (female, China).

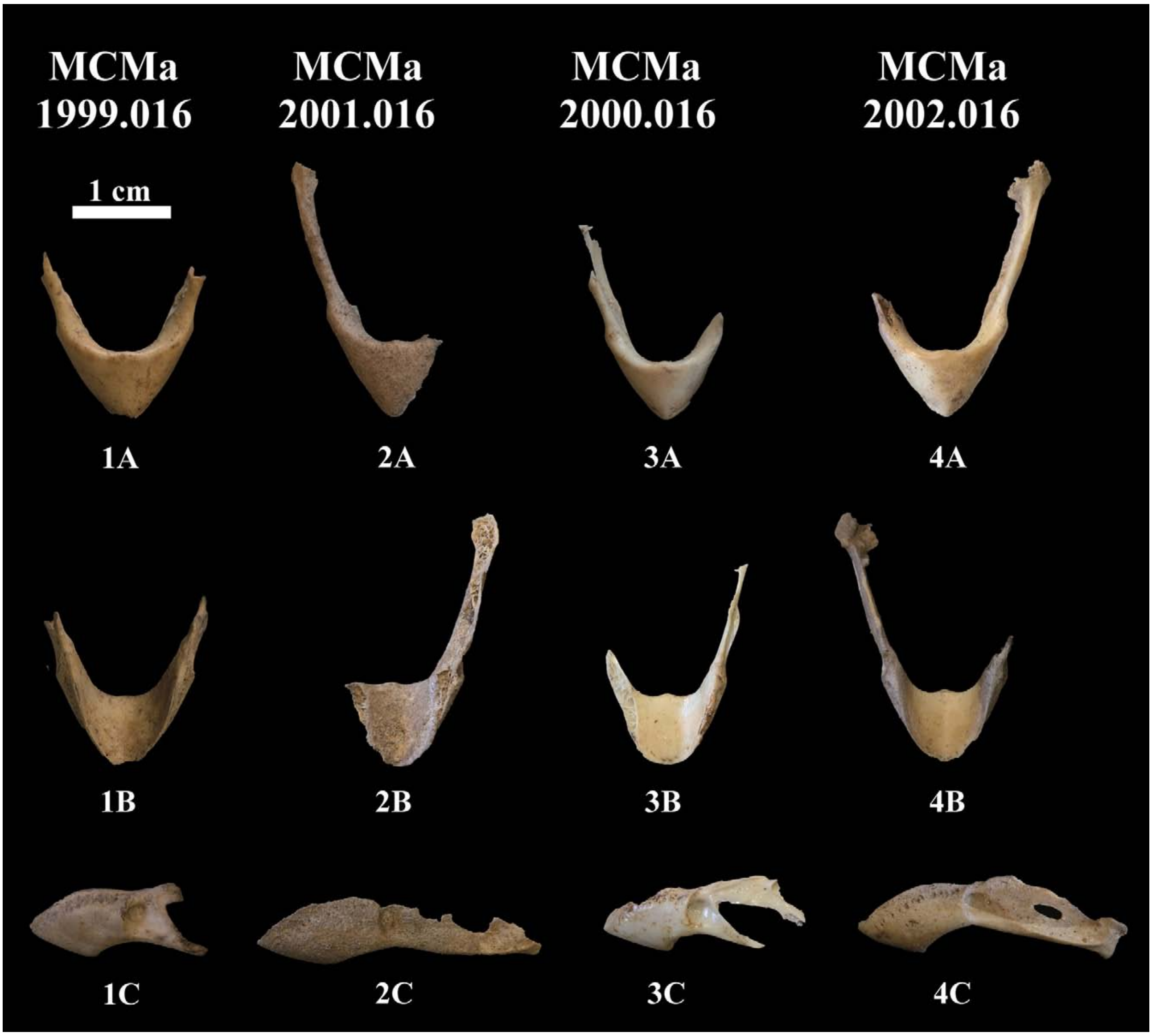
***Pinicola enucleator* Linnaeus, 1758:** IMEDEA 12025 (unsexed, Lapland, Sweden); IMEDEA 20618 (female, Västerbotten, Sweden); IMEDEA 12025 (male, Varmland, Sweden).

***Coccothraustes coccothraustes* (Linnaeus, 1758):** IMEDEA 12472 (unsexed, Aldeávila, Salamanca, Spain); IMEDEA 12473 (unsexed, Mallorca); IMEDEA 20745 (male, Spain); IMEDEA 104077 (unsexed, Mallorca).

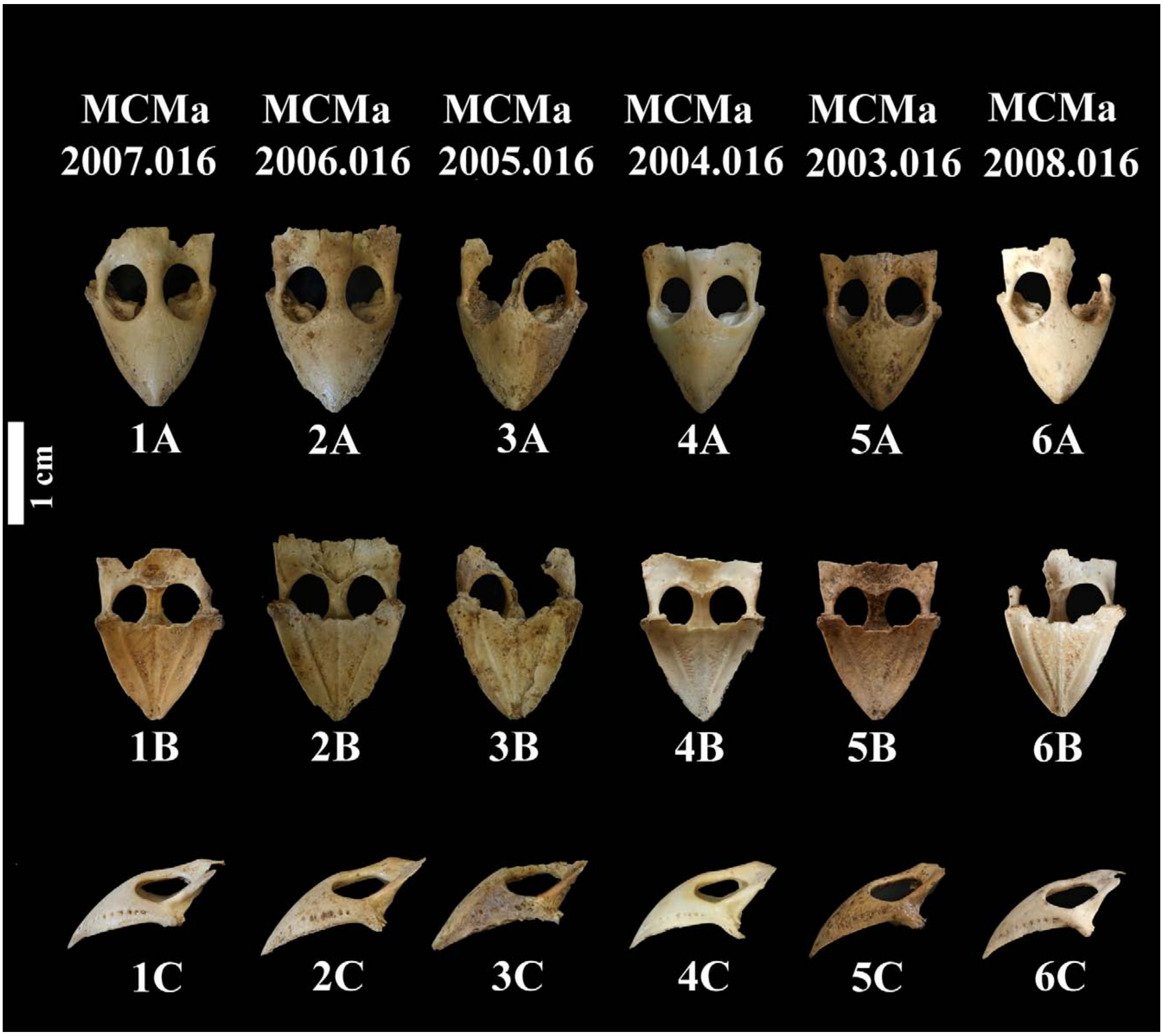
***Loxia pytyopsitacus* Borkhausen 1793:** IMEDEA 12483 (unsexed, Herrestad, Uddevalla, Bohuslän, Sweden).

***Loxia curvirostra* Linnaeus, 1758:** IMEDEA 9951 (male, Hoz del Beteta, Cuenca, Spain), IMEDEA 12582 (unsexed, Artà, Mallorca), IMEDEA 20826 (unsexed, Valldemossa, Mallorca), IMEDEA 21741 (female, Mallorca), IMEDEA 45001 (unsexed, La Vileta, Palma, Mallorca), IMEDEA 94308 (unsexed, Mallorca).

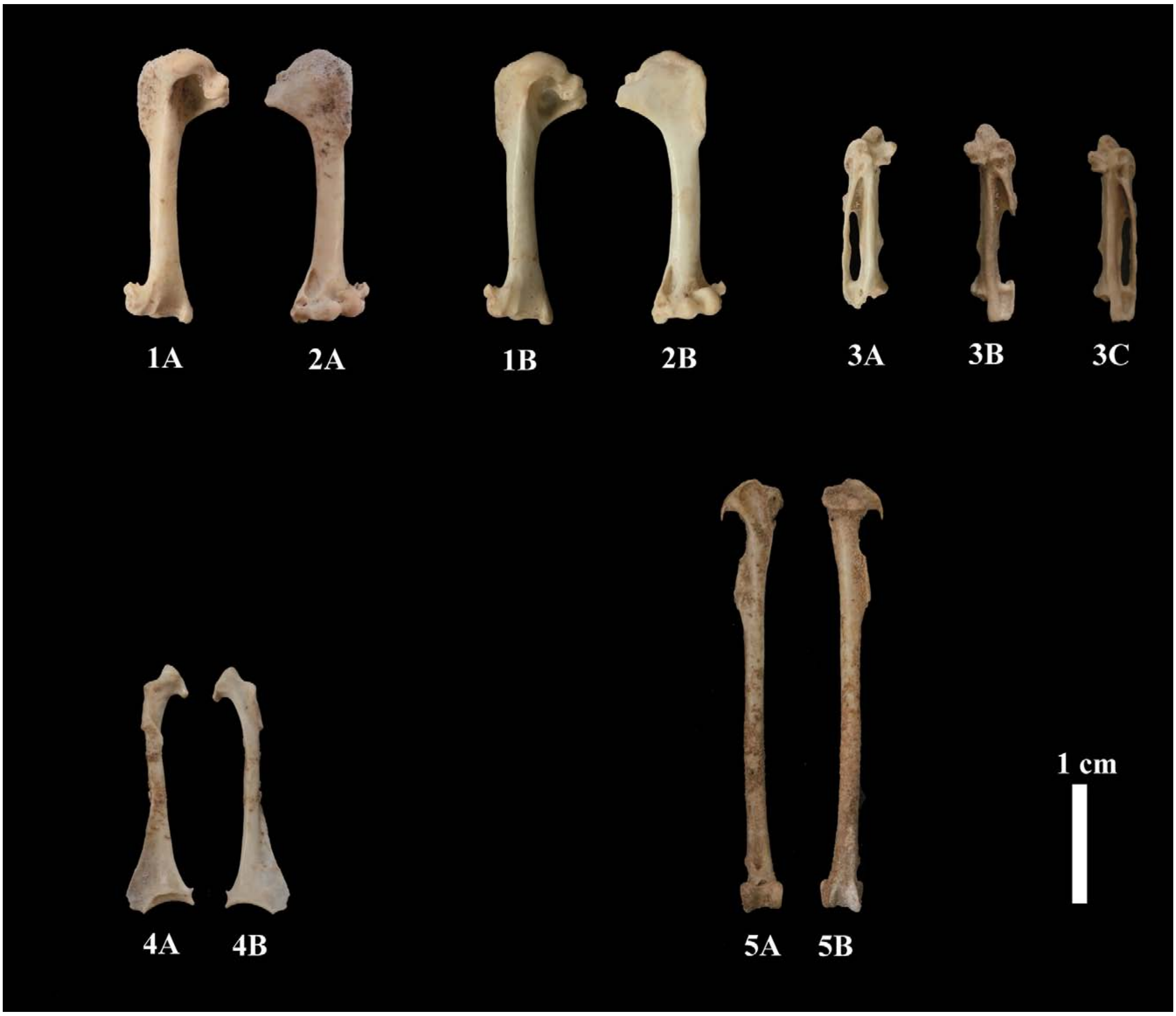
**APPENDIX 2.** Supplementary figures



**SUPPLEMENTARY FIGURE S1.** Known mandibles of *Pyrrhula crassa* **n. sp.** A: ventral view. B: dorsal view. C: lateral view. **1.** MCMa 1999.016. **2.** MCMa 2001.016. **3.** MCMa 2000.016. **4.** MCMa 2002.016 holotype.



**SUPPLEMENTARY FIGURE S2.** Known premaxilla of *P. crassa* n.sp. A: dorsal view. B: ventral view. C: lateral view. **1.** MCMa 2007.016. **2.** MCMa 2006.016. **3.** MCMa 2005.016. **4.** MCMa 2004.016. **5.** MCMa 2003.016. **6.** MCMa 2008.016.



**SUPPLEMENTARY FIGURE S3.** Known long bones of *P. crassa* **n.sp.** **1.** Humerus, caudal view. **2.** Humerus, cranial view. **3.** Carpometacarpus, ventral view. **4.** Coracoid, dorsal view. **5.** Tibiotarsus, cranial and caudal views. **1A**, **2A**: MCMa 1998.016. **1B**, **2B**: MCMa 2009.016. **3A**: MCMa 1998.016; **3B**: MCMa 2009.016; **3C**: MCMa 2010.016. **4A**, **4B**: MCMa 1998.016. **5A**, **5B**: MCMa 1998.016.