Article

Five new extinct species of rails (Aves: Gruiformes: Rallidae) from the Macaronesian Islands (North Atlantic Ocean)

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Summary

Five new species of recently extinct rails from two Macaronesian archipelagoes (Madeira and Azores) are described. All the species are smaller in size than their presumed ancestor, the European rail *Rallus aquaticus*. Two species inhabited the Madeira archipelago: (1) *Rallus lowei* **n. sp.**, the stouter of the species described herein, was a flightless rail with a robust tarsometatarsus and reduced wings that lived on Madeira Island; (2) *Rallus adolfocaesaris* **n. sp.**, a flightless and more gracile species than its Madeiran counterpart, inhabited Porto Santo. So far, six Azorean islands have been paleontologically explored, and the remains of fossil rails have been found on all of them. Here we formally describe the best-preserved remains from three islands (Pico, São Miguel and São Jorge): (1) *Rallus montivagorum* **n. sp.**, a rail smaller than *R. aquaticus* with a somewhat reduced flying capability, inhabited Pico; (2) *Rallus carvaoensis* **n. sp.**, a small flightless rail with short and stout legs and a bill apparently more curved than in *R. aquaticus*, was restricted to São Miguel; (3) *Rallus minutus* **n. sp.**, a very small (approaching *Atlantisia rogersi* in size) flightless rail with a shortened robust tarsometatarsus, lived in São Jorge. We note also the presence of rail fossils on three other Azorean islands (Terceira, Graciosa and Santa Maria). In addition, we describe an extraordinarily complete fossil of an unnamed *Rallus* preserved in silica from the locality of Algar do Carvão on Terceira.

Key words: Extinction, Macaronesia, Quaternary, *Rallus lowei* **n. sp.**, *R. adolfocaesaris* **n. sp.**, *R. carvaoensis* **n. sp.**, *R. montivagorum* **n. sp.**, *R. minutus* **n. sp.**

Resumo

São descritas como novas para a ciência cinco espécies de Frangos-de-água recentemente extintas da Macaronésia. Todas estas espécies são mais pequenas do que o seu presumível antepassado o Frango-de-água Europeu *Rallus aquaticus.* Duas destas espécies novas ocorrem no arquipélago da Madeira. *Rallus lowei* **n. sp.**, viveu na Ilha da Madeira sendo de todas as cinco espécies aqui descritas a mais robusta, tratando-se de uma espécie sem capacidade de voo com tarsometatarso curto e robusto e asas reduzidas. *Rallus adolfocaesaris* **n. sp.**, viveu em Porto Santo, também sem capacidadede voo é uma espécie mais pequena do que a espécie da Madeira. Seis ilhas dos Açores foram até agora investigadas em termos paleontológicos e em todas elas encontrámos fósseis de Frangos-de-água. Em três das ilhas encontrámos material suficiente para uma descrição adequada das suas espécies de Frango-de-água actualmente extinctos. *Rallus montivagorum* **n. sp.**, com reduzida capacidade de voo, mais pequeno que *Rallus aquaticus,* viveu na ilha do Pico. *Rallus carvaoensis* **n. sp.**, foi uma espécie pequena sem capacidade de voo com pernas curtas e grossas e um bico aparentemente mais curto do que em *Rallus aquaticus,* viveu em São Miguel. *Rallus minutus* **n. sp.**, uma espécie muito pequena (tamanho parecido com *Atlantisia rogersi*) também sem capacidade de voo e com tarsometatarso curto e robusto, viveu em São Jorge. O material encontrado nas ilhas Terceira, Graciosa e Santa Maria foi insuficiente para a descrição das suas espécies. Em adição, descrevomos um fossil notável de um *Rallus* encontrado no Algar do Carvão na ilha Terceira.

Introduction

Rails (Gruiformes: Rallidae) are among the species of birds most prone to colonize and evolve on islands (e.g., Olson 1977; Steadman 2006). They usually become extinct soon after the arrival of humans and their introduced companions (rats, cats, and mice). Endemic rails are still present on a few remote islands of the world (*e.g.*, Galápagos, Guam, Okinawa, Inaccessible, New Zealand, Henderson, Lord Howe), but these are merely the survivors of a much higher past diversity. It has been estimated that 2,000 species of insular rails may have become extinct as a result of human colonization (Steadman 1995), although this may be an overestimate (Livezey 2003). Rails that evolved on islands devoid of terrestrial mammals almost always lost or reduced their flying capabilities and acquired a more terrestrial mode of life.

The great number of isolated islands in the Pacific produced a huge diversity of flightless rails, which has been only partially described by palaeornithologists (*e.g.*, Olson & James 1991; Steadman 1991, 1995, 1997, 2006; Worthy 2004; Kirchman & Steadman, 2005, 2006a, 2006b, 2007). The Atlantic Ocean has far fewer islands than the Pacific and the only ones with historically known species of endemic rails are Inaccessible Island (*Atlantisia rogersi*), Tristan da Cunha and Gough Islands (*Gallinula nesiotis* and *G. comeri*) and Cuba (*Cyanolimnas cerverai*). Relatively recently extinct species lived in St. Helena (*Aphanocrex podarces, Porzana astrictocarpus*), Ascension (*Mundia elpenor*), the West Indies (three species of the genus *Nesotrochis*, on Puerto Rico –transported prehistorically to Mona Island and the Virgin Islands–Cuba and Hispaniola). Extinct species of rails have also been described from Bermuda (*Rallus ibycus*, *R. recessus*, *Porzana piercei*; Olson & Wingate 2000, 2001) and Abaco in the Bahamas (*Rallus cyanocavi,* Steadman *et al*. 2013).

The volcanic Macaronesian archipelagos (Azores, Madeira, Selvagens, Canary Islands and Cape Verde) are located in the North Atlantic Ocean (15ºN–39ºN and 10ºW–30ºW), and between ~100 km (Canary Islands) and ~1350 km (Azores) from the mainland (Africa and Europe, respectively).

The two northernmost archipelagos are the Azores and Madeira (Figure 1). The Azores is the most isolated archipelago of Macaronesia, and extends over c. 600 km. It consists of nine main islands, ranging northwest to southeast roughly between 37º to 40º N and 25º to 31º W, that may be divided into a western (Corvo and Flores), a central (Graciosa, Faial, São Jorge, Pico and Terceira) and an eastern group (São Miguel and Santa Maria) (Figure 1). The age of the islands ranges from 8.12 My (Santa Maria) to 0.25 My (Pico) (França *et al*. 2003). The Madeira archipelago is located more than 600 km from northwest Africa and more than 700 km from the Azores. It includes the islands of Madeira, Porto Santo, and the Desertas (Deserta Grande, Bugio and Ilhéu Chão). Their maximum geological ages are 4.63, 14.3 and 3.62 My respectively (Geldmacher *et al*. 2001).

Hitherto no fossil endemic rails have yet been described from the Macaronesian archipelagos. Pieper (1985) reported the presence of fossil rails in both Madeira and Porto Santo, which have remained undescribed until now. Despite a fairly substantial fossil record, none have been reported from the Canary Islands. Recent (2011–2014) fieldwork in the Azorean Islands allowed us to obtain bones of rails from the six islands so far explored palaeontologically: Santa Maria, São Miguel, Terceira, Pico, São Jorge and Graciosa.

The goal of the present paper is to formally describe and name the species of extinct rails from the Macaronesian archipelagos of Madeira and Azores, and to discuss the chronology and possible causes of their extinction. We also speculate on the apparent absence of endemic rails in the Canary Islands.

Material and methods

The bones examined are listed under the description of each species. Skeletons used for comparisons come from The Natural History Museum (NHMUK, London) and the Institut Mediterrani d'Estudis Avançats (IMEDEA, Mallorca). The following modern specimens of *Rallus aquaticus* have been used as comparative material: NHMUK S-1984-100-4, NHMUK S-1992-45-1, NHMUK S-1985-95-2, NHMUK S-1986-3-4, NHMUK S-1993-26-1, NHMUK S 1953-11-1, NHMUK S-1983-106-1, NHMUK S-1984-33-1, NHMUK S-1986-36-4, NHMUK S-1986-21-1, NHMUK S-1989-9-1, NHMUK S-1985-73-5, NHMUK S-1982-41-6, NHMUK S-1986-3-5, NHMUK sn, NHMUK S-1985-21-1, NHMUK S-1982-51-1, NHMUK S-1981-72-6, NHMUK S-1973-32-1, NHMUK S-1930-24-54, NHMUK 1859-4-7-1, NHMUK 1909-12-29-1, NHMUK 1930-3-24-52, NHMUK 1930-3-24-49, NHMUK 1922-3-27-1, NHMUK 1849-11-13-57, IMEDEA 21867, IMEDEA 20706, IMEDEA 12569, IMEDEA

sn, IMEDEA 12474, IMEDEA 21914, IMEDEA 9946, IMEDEA 9948, IMEDEA 11945, IMEDEA 9964, IMEDEA 12579. We also used the descriptions and measurements of *Rallus longirostris* and *R. elegans* presented by Olson and Wingate (2000, 2001).

We examined the fossil specimens of *Rallus* rails curated at the IMEDEA, including all the material of the extinct Eivissan rail *Rallus eivissensis* (Upper Pleistocene-Holocene; McMinn *et al.* 2005). We have also used descriptions and measurements of the extinct Bermudan species *Rallus recessus* (Upper Pleistocene; Olson & Wingate 2001) and *Rallus ibycus* (Middle Pleistocene; Olson & Wingate 2000) based on material held at USNM and Florida Museum of Natural History, Gainesville, and of the extinct Bahamian *Rallus cyanocavi*, from Abaco (Upper Pleistocene; Steadman *et al.*, 2013).

The fossil specimens described herein are deposited in the following collections: (1) Museu Municipal do Funchal (MMF), Funchal, Madeira; (2) Museu Carlos Machado (MCMa), São Miguel, Açores; (3) Departamento de Geologia da Universidade dos Açores (DBUAF), São Miguel, Açores; (4) Museu dos Montanheiros, Angra do Heroísmo, Terceira, Açores (no collection acronym); (5) Departamento de Zoología de la Universidad de La Laguna (DZUL), Tenerife, Canary Islands; and (6) Institut Mediterrani d'Estudis Avançats (IMEDEA), Mallorca, Balearic Islands.

Measurements of long bones do not include broken or juvenile specimens. Some broken bones have been used in the discussion, as they allowed us to establish minimal sizes or to discern diagnostic characters.

Measurements were taken with electronic digital calipers to 0.01 mm, and rounded to the nearest 0.1 mm. We followed the criteria of McMinn *et al.* (2005) in taking measurements of long bones, except for tibiotarsus length, which was measured both including the cnemial crest (total length) and excluding it (medial length). Bone measurements not considered by the former authors (radius, scapula, synsacrum, skull, mandible) were determined following the criteria of von den Driesch (1976). Photographs were taken with a Canon EOS 500D digital camera. Osteological terminology mainly follows Livezey and Zusi (2006).

Mensural differences among *Rallus* were evaluated using a multivariate analysis of variance (MANOVA) on the lengths of tarsometatarsus (total length and distal width; traits 26 and 29). Differences in femur length (trait 17) between bones from São Miguel, Pico Islands and *R. aquaticus*, and in tibiotarsus distal width (trait 25) between *Rallus* from Porto Santo, Pico and *R. aquaticus* were explored through an analysis of variance (ANOVA). Additional ANOVAs were performed to compare length pairs. When it was necessary, variables were $\log_{10}$ transformed in order to meet normality and homogeneity of variances. Those variables that did not meet parametric assumptions and elements known only from three specimens were compared with nonparametric tests (Mann–Whitney U tests).

The relative proportions of femur and tarsometatarsus with respect to the total length of leg bones (femur+tibiotarsus+tarsometatarsus) in extinct and extant rail species were used as a discriminating criterion among them. We performed a Principal Component Analysis (PCA) to summarize segregation and to explore morphological patterns in relation to wing and leg bone proportions.

When possible, we attempted to assess flight capability using two sets of criteria. When the sternum was available, a slightly decreased depth of the carina sterni was considered to be indicative of a reduced capability, while a markedly decreased carina sterni pointed to a flightless condition. When the sternum was not available, we considered flightless species to be characterized by (1) a humerus/femur ratio less than 0.9 (Livezey 2003, p. 189 and Figure 44), or, when all the pertinent measures were available, (2) using the ratios of combined humerus+ulna+carpometacarpus length to femur length (Millener 1989; Millener & Worthy 1991; Rando *et al.* 1999, 2010) or to the combined femur+tibiotarsus+tarsometarsus length (Steadman *et al.* 2013). When these bones were available, indexes such as carpometacarpus length vs humerus length (a low value indicating an extremely weak development of primary flight feathers; see Steadman *et al.* 2013) or tarsometatarsus length vs femur length (a relatively short and stout tarsometatarsus indicating the animal could only be able of slow running; see Steadman *et al.* 2013) were also used to characterize the different island species. The relative width of synsacrum has been used as an estimate of body robustness.

All statistical analyses have been performed with SPSS 18.0 (PASW Statistic 18 2011).

The holotypes of the new species from Pico, São Miguel and São Jorge were selected on the basis that they were the most complete associated skeleton. When associated skeletons were not available (Madeira, Porto Santo), the most complete tarsometatarsus (as the most characteristic bone) that was closest to the mean size of the available series was selected as the holotype.

FIGURE 1. Map of the Macaronesian Islands. Asterisks indicate the islands where bones of *Rallus* have been found.

None of the Macaronesian rails are likely to be conspecific with flightless species occurring elsewhere. Therefore, in order to establish comparisons our analyses concentrated on Macaronesian rails and their most likely ancestor, *R. aquaticus*.

List of abbreviations used in the lists of material

Element. hum: humerus; uln: ulna; rad: radius; cmc: carpometacarpus; cor: coracoid: ste: sternum; sca: scapula; syn: synsacrum; pel: pelvis; fem: femur; tmt: tarsometatarsus; tbt: tibiotarsus; ver: vertebrae; sku: skull; qua: quadratum; man: mandible; pmx: premaxilla; ped pha: pedal phalanx; frag: fragment/fragmented; prox: proximal; dis: distal; sha: shaft; L: left; R: right; LR: left and right; juv: juvenile.

Collectors of material. DS: David Silva; EB: Elisa Blanco; ET: Enric Torres; FP: Fernando Pereira; HP: Harald Pieper; IA: Isabel Amorim; JAA: Josep Antoni Alcover; JCI: Juan Carlos Illera; JCR: Juan Carlos Rando; KG: Klaus Groh; MT: Miquel Trias; OR: Ortrud Runze; OT: Odília Teixeira; SA: Sergio Ávila.

Results

SYSTEMATIC PALEONTOLOGY

Order Gruiformes

Family Rallidae Vigors, 1825

Genus *Rallus* Linnaeus, 1758

We are able to document the existence of at least five new endemic species, two species in Madeira (one on Madeira and one on Porto Santo), and three Azorean species, each confined to a single island. The bill of all of the new species described herein differs from the short and relatively broad bills of *Porzana* or *Gallinula*. The very long and slender bill (premaxillae and mandible) displayed by the new species clearly places them in *Rallus* (Olson 1973a; Olson and Wingate 2000, 2001). These new rails are presumably derived from *Rallus aquaticus*, although a derivation from some other *Rallus* species of North American origin cannot be excluded. Additionally, the material of *Rallus* obtained at three Azorean Islands (Santa Maria, Terceira and Graciosa) is presented, but is left unassigned to a species pending the discovery of more complete additional material.

PART 1. RAILS FROM THE ARCHIPELAGO OF MADEIRA

Rallus lowei new species
Madeira rail
[Figures 2, 8G, 11A, 12A, 14A, 15A, 16A, 17A]
Artistic reconstruction: Figure 23

Holotype: **MMF 43411**, L tmt.
   **Type locality: "**Ribeira Groh", Ponta de São Lourenço, Madeira, 6 Apr 1984.
    Collectors: All the paratypes were collected by HP and OR, except those that are specifically attributed to other collectors.
    Measurements of the holotype: total length, 35.7 mm; proximal width, 6.6 mm; minimum shaft width, 3.7 mm; distal width, 7.25 mm.
    Paratypes: "Ribeira Groh": **MMF 43412**, L tmt, 8 Apr 1984; **MMF 43413**, R tmt, 9 Apr 1984; **MMF 43416**, L uln, 10/11 Sept 1988; **MMF 43419**, R tmt, 15/16/20 Nov 1990; Ponta de São Lourenço: **MMF 43414**, dis L hum, 1994, coll. G.E. Maul. "Main Sand Place": **MMF 43415**, R uln, 1985; **MMF 43417**, R fem, 11/12 Nov 1985; **MMF 43418**, L uln, 11/12 Nov 1985; **MMF 43420**, L fem, 15/16 Sept 1990; **MMF 43421**, pmx, 9/10/16 May 1992; **MMF, 43422**, man, 17/18 Nov 1994; **MMF 43423**, R fem, 17/18 Sept 1994; **MMF 43424**, L tmt, 17/18 Sept 1994; **MMF 43425**, R tmt, 17/18 Sept 1994; **MMF 43426/43427**, R tbt, 17/18 Sept 1994; **MMF 43428**, pel, 17/18 Sept 1994.
    Measurements of paratypes (following the order of the specimens listed above): Tarsometatarsus: length 36.4, 33.2, 33.9, 33.3, 32.4 mm; proximal width 6.9, 6.1, 6.4, 6.3, 6.4 mm; minimum shaft width 3.8, 3.4, 3.4, 3.0, 3.2 mm; distal width 7.3, 6.8, 6.6, 6.6, 6.6 mm. Tibiotarsus: length 54.0 mm; medial length 53.2 mm, proximal width 6.7 mm; minimum shaft width 2.9 mm; distal width 5.5 mm. Femur: length -, 37.8, 38.3 mm; proximal width

-, 6.65, 6.7 mm; diaphysis width 2.9, 2.8, 2.9 mm; distal width 7.0, 7.1, 6.8 mm. <u>Humerus</u>: length -, minimum shaft width 2.0 mm. <u>Ulna</u>: length 22.6, 23.3, - mm; proximal width 3.3, 3.1, - mm; proximal diameter 2.86, -, -; minimum shaft width 1.4, 1.6, 1.6 mm; distal width 2.9, 2.8, 2.6 mm. <u>Synsacrum</u>: length c.36.3; vertebral length 30.3; antitrochanterian width c.17.7 mm.
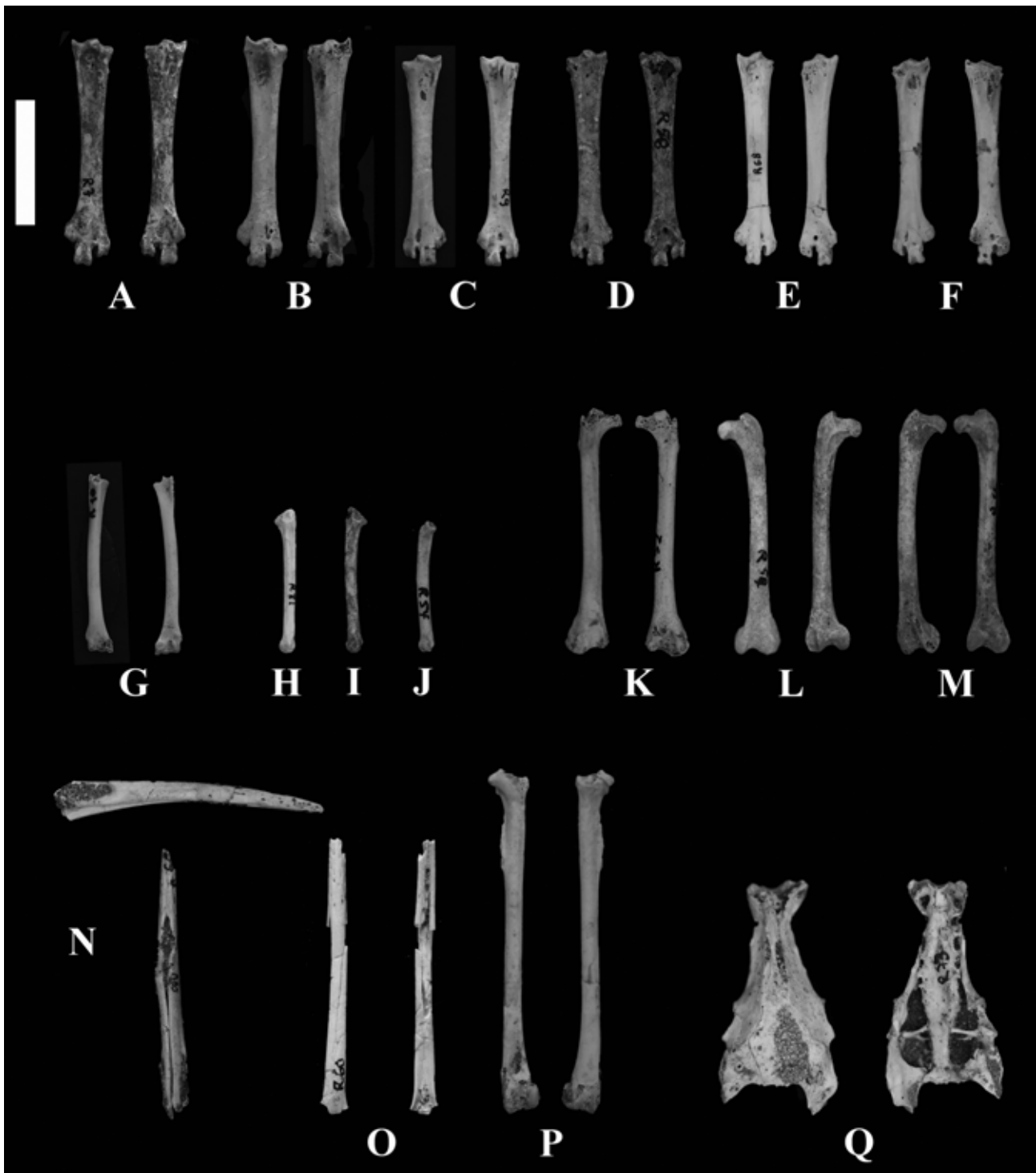
FIGURE 2. Type series of *Rallus lowei*. **A,** Holotype, **MMF 43411,** L tarsometatarsus (L, dorsal, and R, plantar view in bones A–F). B–Q, Paratypes. **B, MMF 43412,** LL tarsometatarsus. **C, MMF 43413,** R tarsometatarsus. **D, MMF 43419,** R tarsometatarsus. **E, MMF 43424,** L tarsometatarsus. **F, MMF 43425,** R tarsometatarsus. **G, MMF 43414,** L humerus (L, caudal, and R, cranial view). **H, MMF 43415,** R ulna (ventral view in bones H–J). **I, MMF 43416,** L ulna. **J, MMF 43418,** L ulna. **K, MMF 43417,** R femur (L, cranial, and R, caudal view in K, M, and P). **L, MMF 43420,** L femur. **M, MMF 43423,** R femur. **N, MMF 43422,** mandible (lateral and ventral views). **O, MMF 43421,** premaxilla (dorsal and ventral views). **P, MMF 43426/43427,** R tibiotarsus. **Q, MMF 43428,** synsacrum and pelvis (L, dorsal, and R, ventral view). Scale bar: 2 cm.

Age: Undetermined Late Quaternary (Late Pleistocene to Late Holocene) age. Material of an undescribed species of quail (*Coturnix*) from "Ribeira Groh" (KIA-47430) rendered a ^{14}C age of 2755±55 BP (1021-806 cal BC) (Rando *et al*. 2014).

Diagnosis. A species of *Rallus* that is overall smaller and stouter than *R. aquaticus*, and notably larger than *R. carvaoensis* **n. sp.** from São Miguel and *R. minutus* **n. sp.** from São Jorge. This species combines relatively smaller wing bones (humerus and ulna) with massive leg bones (mainly tarsometatarsus) and a wider synsacrum than *R. aquaticus* and *R. montivagorum* **n. sp.** The available wing bones are smaller than in *R. montivagorum* **n. sp.** and *R. adolfocaesaris* **n. sp.**, and larger than in *R. carvaoensis* **n. sp.** and *R. minutus* **n. sp.** The femur and tibiotarsus are only slightly shorter than those of *R. aquaticus*, the tarsometatarsus being the most reduced leg bone. The distal leg bones (tibiotarsus and tarsometatarsus) are more robust than their counterparts in the other species of *Rallus* described herein (especially compared with the neighbouring Porto Santo rail), except for *R. minutus* **n. sp.** from São Jorge. [Figures 2, 15A, 16A, 17A; Table 1]

Etymology. The specific name honours Richard Thomas Lowe, who during his time in Madeira was an assiduous student of the flora and fauna (mainly fishes and molluscs) of the archipelago and who published many important books and articles (da Silva and de Meneses 1984). He was born 4 Dec 1802 in Findern, Derbyshire (England). After finishing school and theological studies, he visited Madeira for the first in 1828 and became an Anglican chaplain on the island in 1832. Later on, he returned to England and lived in Lea, Lincolnshire. He returned to Madeira several times, the last one in April 1874 from Liverpool, but he was shipwrecked soon after setting out and drowned, together with his wife, southwest of the Scilly Islands. In one of his publications (Lowe 1853) he mentioned for the first time the discovery of (sub)fossil lizard and bird bones. Richard Owen, who studied the material, could not identify the bones of the three species found, but could only give their size as similar to that of "gull or crow," " thrush" and "sparrow".

Rallus adolfocaesaris, new species
Porto Santo rail
[Figures 3, 8H, 11B, 15B, 16B, 17B]
Artistic reconstruction: Figure 23

Holotype: MMF 43444, R tmt.

Type locality: Porto dos Frades, Porto Santo, 1985.

Collectors: All the paratypes were collected by HP and OR, except those that are specifically attributed to a different collector.

Measurements of holotype: total length, 33.4 mm; proximal width, 5.7 mm; diaphysis width, 2.8 mm; distal width, 5.8 mm.

Paratypes: Fonte da Areia: **MMF 43445**, R tmt, 1981; **MMF 43453**, R fem, 1984. Porto dos Frades: **MMF 43446**, L tmt, 22 June1983, coll. KG; **MMF 43447**, L tbt, 1994; **MMF 43448**, R tbt, 12 Aug 1984, coll. KG; **MMF 43449**, R tbt, 1985; **MMF 43450**, pmx frag, 1985; **MMF 43451**, R hum frag, 1985.

Measurements of paratypes (following the order of the specimens listed above): Tarsometatarsus—total length, 33.4, 31.4, 33.4 mm; proximal width, 4.8, 5.1, 5.7 mm; diaphysis width, 2.6, 2.6, 2.8 mm; distal width, 5.5, 5.3, 5.8 mm. Tibiotarsus—total length, 52.0, -, - mm; medial length: 50.2, 50.8, 52.3; proximal width, 6.9, -, - mm; diaphysis width, 2.3, 2.6, 2.6 mm; distal width, 5.0, 5.2, 5.0 mm. Femur—total length, 38.6 mm; proximal width, 7.3 mm; diaphysis width, 3.0 mm. Humerus—total length, - mm (c. 33 mm); diaphysis width, 2.2 mm; distal width, 5.1 mm.

Age: Undetermined Late Quaternary age (from Late Pleistocene to Late Holocene).

Diagnosis. *R. adolfocaesaris* **n. sp.** is a species of *Rallus* that is overall smaller than *Rallus aquaticus*, and has relatively gracile legs. The humerus is larger than that of *R. lowei* **n. sp.**, but smaller than that of *R. aquaticus*. The femur is c. 7% shorter than in *Rallus aquaticus*, while the tibiotarsus is 19% shorter, the tarsometatarsus being proportionately the shortest leg bone (20%). The femur is slightly larger than in *R. montivagorum* **n. sp.** The tibiotarsus and particularly the tarsometatarsus are considerably more slender than in *R. lowei* **n. sp.** (Figures 16B, 17B). The tarsometatarsus is more gracile than that of *R. lowei* **n. sp.** and longer and more gracile than those of *R. carvaoensis* **n. sp.** and *R. minutus* **n. sp.** (Figure 17B; Table 1).

TABLE 1. Measurements (1-29) of *Rallus lowei* n. sp., *R. adolfocaesaris* n. sp., *R. carvaoensis* n. sp., *R. montivagorum* n. sp., *R. minutus* n.sp., *Rallus* sp. A, *Rallus* sp. B, *Rallus* sp. C and *R. aquaticus*: sample size, mean length ± standard error (mm), and range. Measurements as in McMinn et al (2005) and von den Driesch (1976) [see text].

	R. lowei Madeira	*R. adolfocaesaris* Porto Santo	*R. carvaoensis* São Miguel	*R. montivagorum* Pico	*R. minutus* São Jorge	*Rallus* sp. A Graciosa	*Rallus* sp. B Terceira	*Rallus* sp. C Santa Maria	*R. aquaticus* Europe
Coracoid									
[1]Length	-	-	(3) 15.5±0.7 [15.1-16.5]	(17) 17.6±0.1 [16-20]	(2) 13.1±0.4 [12.7 – 13.5]	(3) 19 [18.6 – 19.2]	(5) 17.1±0.5 [16.5-17.8]		(33) 20.9±0.9 [18.8-22.5]
Scapula									
[2]Length	-	-	(1) 25.6	(3) 29.4±0.6 [29-30.2]					(31) 35.5±2.1 [30.6-39.2]
[3]Proximal width	-	-	(2) 3.5 [3.5-3.6]	(14) 4.6±0.2 [4-4.9]	(1) 3.6		(3) 4.1±0.2 [3.8-4.3]		(32) 5.0±0.3 [4.5-5.6]
Humerus									
[4]Length	-	-	(3) 27.4±0.7 [26.7-28.6]	(18) 33.8±1.3 [31.2-36.1]	(2) 25.1±0.6 [24.5 – 25.6]	(1) 32.4	(1) 32.9		(35) 38.9±1.7 [35-42.1]
[5]Proximal width	-	-	(6) 5.7±0.5 [5.1-6.3]	(17) 6.7±0.2 [6.3-7.2]	(3) 5.2±0.4 [4.7 – 5.6]	(3) 7.0 [6.9 – 7.1]	(4) 6.8±0.3 [6.5-7.1]		(35) 8.0±0.4 [7.3-8.7]
[6]Shaft width	(2) 1.9±0.1 [1.8-2]	(2) 2.3±0.1 [2.2-2.4]	(6) 1.6±0.2 [1.3-1.9]	(23) 2.1±0.1 [1.9-2.3]	(2) 1.5±0.1 [1.4 – 1.5]	(3) 2.2 [2.1 – 2.4]	(3) 2.2±0.1 [2.1-2.4]	(3) 2.4 [2.4 – 2.5]	(35) 2.4±0.2 [2.1-2.8]
[7]Distal width	-	(1) 5.1	(4) 3.9±0.2 [3.6-4.1]	(25) 4.8±0.2 [4.2-5.2]	(2) 3.8±0.3 [3.4 – 4.1]	(1) 4.8	(3) 4.7±0.3 [4.3-5]	(3) 5.3±0.2 [5.1 – 5.4]	(35) 5.3±0.2 [4.9-5.7]
Ulna									
[8]Length	(2) 22.9±0.4 [22.6-23.3]	-	-	(14) 26.6±1.7 [23.7-30.3]	(3) 16.6±0.7 [16.1 – 17.6]		(3) 25.6±0.5 [24.9-26.2]		(34) 31.4±1.4 [28-33.9]
[9]Proximal width	(2) 3.2±0.1 [3.1-3.3]	-	(2) 2.5±0.1 [2.4-2.6]	(18) 3.2±0.2 [2.9-3.6]	(3) 2.4±0.1 [2.3 – 2.5]		(3) 3.4±0.2 [3.1-3.6]		(34) 4.6±0.2 [4.2-5]
[10]Proximal diameter	(1) 2.9	-	(2) 2.4±0.2 [2.2-2.5]	(16) 3±0.3 [2.4-3.6]	(3) 2.2±0.3 [1.7 – 2.4]		(2) 3.2±0.1 [3.1-3.4]		(34) 3.5±0.2 [3.1-3.9]
[11]Shaft width	(3) 1.5±0.1 [1.4-1.6]	-	(2) 1.2 [1.2-1.3]	(16) 2±0.1 [1.8-2.2]	[3] 1.2±0.1 [1.1 – 1.3]		(5) 2±0.1 [1.9-2.2]		(34) 1.7±0.1 [1.5-2]
[12]Distal width	(3) 2.8±0.1 [2.6-2.9]	-	(1) 2.4	(12) 3±0.2 [2.7-3.3]	(2) 2.3±0.2 [2.1 – 2.4]		(4) 2.9±0.2 [2.7-3.1]		(34) 3.4±0.2 [3.2-3.8]
Radius									
[13]Length	-	-	-	-			(2) 23.1±0.4 [22.8-23.5]		(34) 28.8±1.4 [25.6-31.2]

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TABLE 1. (Continued)

	R. lowei Madeira	*R. adolfocaesaris* Porto Santo	*R. carvaoensis* São Miguel	*R. montivagorum* Pico	*R. minutus* São Jorge	*Rallus* sp. A Graciosa	*Rallus* sp. B Terceira	*Rallus* sp. C Santa Maria	*R. aquaticus* Europe
Carpometacarpus									
[14]Length	-	-	(1) 14.9	(14) 18.9±1.5 [16.7-21.5]	(1) 11.0	(1) 17.3	(2) 17.5±0.2 [17.3-17.7]		(33) 21.5±1 [19.4-23.3]
[15]Proximal width	-	-	(1) 3.7	(15) 4.8±0.5 [4.2-5.8]	(1) 3.4		(1) 4.5		(33) 4.7±0.2 [4.2-5.1]
[16]Distal width	-	-	(1) 2.1	(14) 2.8±0.3 [2.3-3.4]		(1) 2.4	(2) 2.8 [2.8-2.9]		(33) 2.7±0.2 [2.2-3.1]
Femur									
[17]Length	(2) 38.1±0.3 [37.8-38.4]	(1) 38.6	(5) 36.3±2 [33.1-39.1]	(27) 35.8±1.4 [33.2-38.8]	(1) 29.8	(2) 35.44±0.2 [35.2 − 35.6]	(1) 34.9	(1) 38.6	(35) 41.3±2 [37.6-44.8]
[18]Proximal width	(2) 6.7 [6.7-6.7]	(1) 7.3	(4) 5.6±0.2 [5.5-6]	(30) 5.9±0.4 [5.1-6.4]	(4) 5.2±0.4 [4.9 − 5.9]	(3) 5.9±0.3 [5.6 − 6.3]	(3) 5.9±0.4 [5.4-6.3]	(1) 7.1	(35) 6.6±0.4 [5.7-7.6]
[19]Shaft width	(4) 2.9 [2.8-2.9]	(4) 2.8±0.2 [2.5-3]	(8) 2.4±0.2 [2.2-2.7]	(39) 2.6±0.1 [2.4-2.9]	(5) 2.2±0.1 [2.1-2.4]	(2) 2.7 [2.6-2.7]	(2) 2.6±0.1 [2.5-2.8]	(1) 3.1	(35) 2.7±0.2 [2.4-3.1]
[20]Distal width	(4) 7±0.1 [6.8-7.1]	-	(5) 5.8±0.2 [5.6-6]	(32) 5.7±0.3 [5.1-6.1]	(3) 5.3±0.3 [5.0 − 5.7]	(2) 5.7±0.1 [5.6 − 5.8]	(2) 5.3±0.3 [5-5.6]	(1) 6.2	(35) 6.1±0.4 [5.4-6.9]
Tibiotarsus									
[21]Length	(1) 54.1	(1) 52	(1) 53.4	(18) 54.3±2.3 [50.3-58.7]	(1) 46.7		(1) 53.7	(1) 56.3	(33) 64.5±3.1 [57.6-68.5]
[22]Medial length	(1) 53.2	(3) 51.1±0.9 [50.2-52.3]	(2) 53.5±1.7 [51.8-55.2]	(20) 52.4±2.2 [48.8-56.7]	(3) 43.8±1.2 [42.2-45.2]		(1) 52.5	(1) 54.3	(33) 62.5±3.2 [55.5-69.3]
[23]Proximal width	(1) 6.7	(1) 6.9	(1) 5.1	(19) 6.3±0.4 [5.6-7]	(3) 5.4±0.3 [5.2 − 5.8]		(2) 5.7±0.3 [5.4-6.1]	(1) 6.4	(33) 7.9±0.5 [7-8.7]
[24]Shaft width	(9) 2.9±0.1 [2.8-3]	(13) 2.4±0.2 [2.1-2.7]	(7) 2.2±0.2 [2-2.5]	(27) 2.5±0.1 [2.3-2.9]	[8] 2.1±0.2 [1.8 − 2.3]	(1) 2.3	(5) 2.4±0.1 [2.3-2.6]	(2) 2.4 2.4-2.4	(33) 2.4±0.2 [2.1-2.8]
[25]Distal width	(2) 6±0.5 [5.5-6.5]	(8) 5±0.3 [4.5-5.6]	(14) 4.6±0.3 [3.8-5.1]	(22) 4.9±0.2 [4.5-5.3]	(7) 4.5±0.3 [4.1 − 5.0]	(1) 4.6	(7) 4.8±0.2 [4.5-5.1]	(2) 5.2±0.1 [5.1-5.3]	(33) 5.1±0.3 [4.5-5.6]
Tarsometatarsus									
[26]Length	(7) 34±1.3 [32.4-36.4]	(3) 33.1±1.3 [31.4-34.5]	(8) 30.4±1.7 [27.5-32.4]	(15) 34.1±2.4 [29.8-38.7]	(5) 26.4±1.4 [24.8 − 28.6]	(1) 37.4	(5) 35.9±1.1 [34.1-37.3]		(34) 41.3±2.3 [37-45.3]
[27]Proximal width	(7) 6.5±0.2 [6.1-6.9]	(4) 5.2±0.3 [4.8-5.7]	(9) 5.1±0.2 [4.7-5.3]	(16) 5.2±0.4 [4.5-5.8]	(6) 4.8±0.3 [4.5 − 5.4]	(1) 5.8	(5) 5.2±0.1 [5-5.4]		(34) 5.3±0.3 [4.8-5.8]
[28]Shaft width	(9) 3.6±0.3 [3-3.9]	(4) 2.6±0.1 [2.6-2.8]	(13) 2.4±0.1 [2.2-2.7]	(19) 2.4±0.1 [2.2-2.8]	(9) 2.5±0.2 [2.2 − 2.8]	(1) 2.8	(6) 2.5±0.1 [2.4-2.6]	(1) 2.6	(33) 2.5±0.2 [2.2-2.8]
[29]Distal width	(8) 6.8±0.3 [6.4-7.3]	(3) 5.5±0.2 [5.3-5.8]	(7) 5.2±0.2 [4.7-5.5]	(15) 5.2±0.4 [4.6-5.9]	(6) 5.3±0.3 [5 − 5.8]	(1) 5.8	(6) 5.5±0.3 [5-5.9]	(1) 5.4	(34) 5.7±0.3 [5.2-6.2]
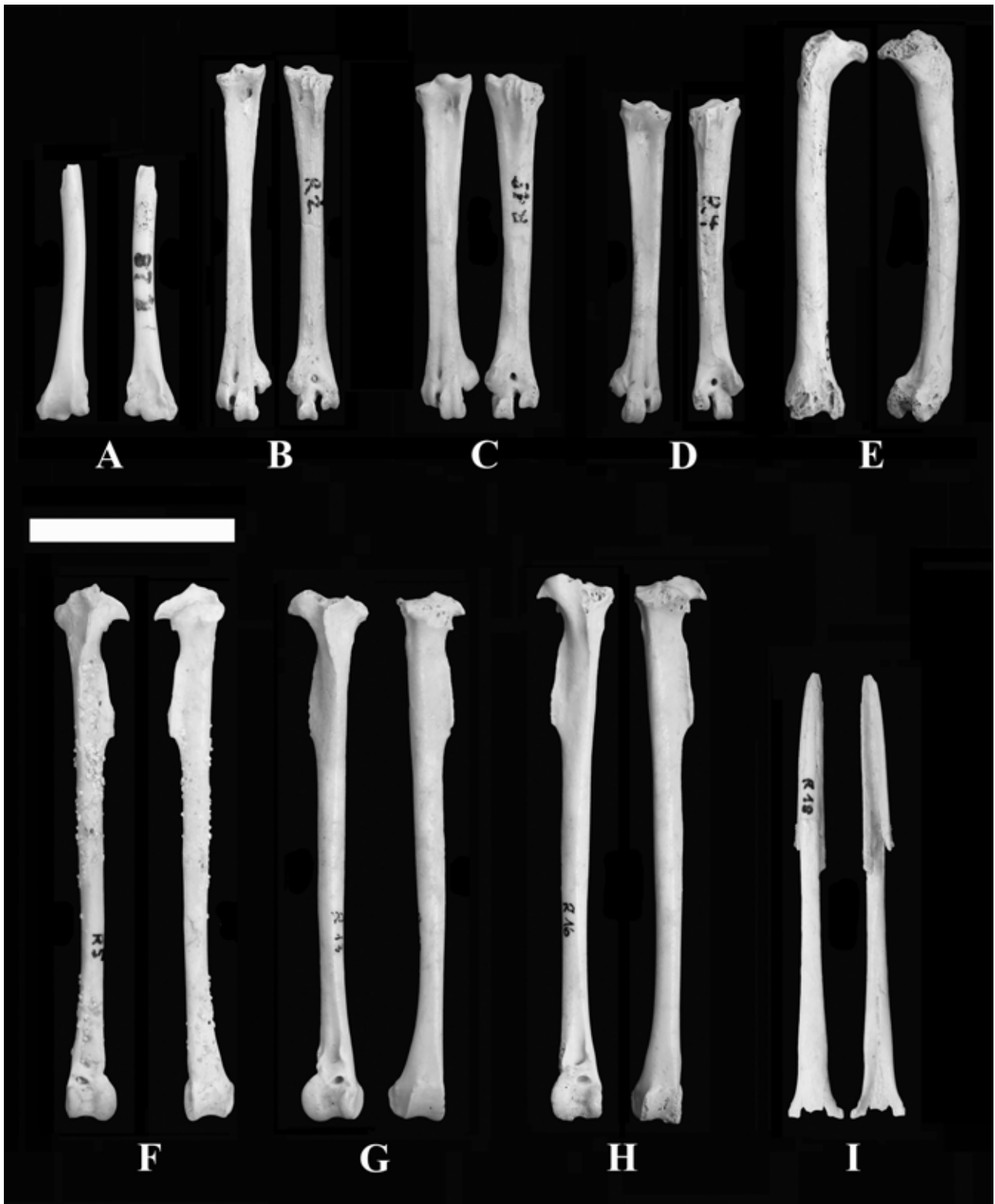
FIGURE 3. Type series of *Rallus adolfocaesaris* **n. sp. C,** Holotype, **MMF 43444**, R tarsometatarsus (left, dorsal, and right, plantar view in bones B–D). A–B, D–I, Paratypes. **A, MMF 43451**, R humerus (left, caudal, and right, cranial view). **B, MMF 43445**, R tarsometatarsus. **D, MMF 43446**, L tarsometatarsus; **E, MMF 43453**, R femur. **F, MMF 43447**, L tibiotarsus (left, cranial, and right, caudal view in bones F–H, and E). **G, MMF 43448**, R tibiotarsus. **MMF 43449, H,** R tibiotarsus. **I, MMF 43450**, premaxilla (dorsal and ventral views). Scale bar: 2 cm.

Etymology. Dedicated to Adolfo César de Noronha for his contributions to the biology and paleontology of Madeira (Clode 1984, da Silva and de Meneses 1984). He was born 9 Sept 1873 in Funchal /Madeira and died there 6 Apr 1963. After his education in Madeira and on the Portuguese mainland he was librarian at the Biblioteca

Municipal do Funchal and after 1928 its director. Later he also became the first director of the Museu de Historia Natural (as it is now termed) which was established in 1929. During his long life he published together with A.A. Sarmento "Vertebrados da Madeira" in 1948, and numerous other papers, mainly on the marine fishes of the Madeiran Archipelago, but also on crustaceans and birds. He also collected plants and fossils, including fossil bird bones in São Lourenço in the early years of last century, and these are still conserved in the MHNF.

Rallus sp.
[Figure 4]

Three further bones from the Madeiran archipelago do not match the taxa previously discussed, because of their absolute size, proportions and morphology. A femur and a tibiotarsus from Madeira and a tarsometatarsus from Porto Santo are larger than the remaining material from the islands and fall within the size range of *R. aquaticus*, *R. limicola* and *R. longirostris*. We are unsure about their species attribution, and consequently refer them to *Rallus* sp.

   Material: MMF 43478, R tbt, "Ribeira Groh", Madeira, 17/18 Sept 1994, coll. HP; **MMF 43479,** R fem, "Main Sand Place", Madeira, 1985, coll. HP. **MMF 43480**, L tmt, Fonte da Areia, Porto Santo, 1982, coll. HP.

FIGURE 4. Bones of *Rallus* sp. from Madeira and Porto Santo. **A, MMF 43479**, R femur (1, cranial view; 2, caudolateral view). **B, MMF 43478**, R tibiotarsus (1, cranial view; 2, caudal view). **C, MMF 43480**, L tarsometatarsus. (1, dorsal view; 2, plantar view). Scale bar: 2 cm.

Rallus carvaoensis, new species

São Miguel rail
[Figures 5, 8B–E, 9A, 10C, 11C, 12B, 13A, 15C, 16C, 17C]
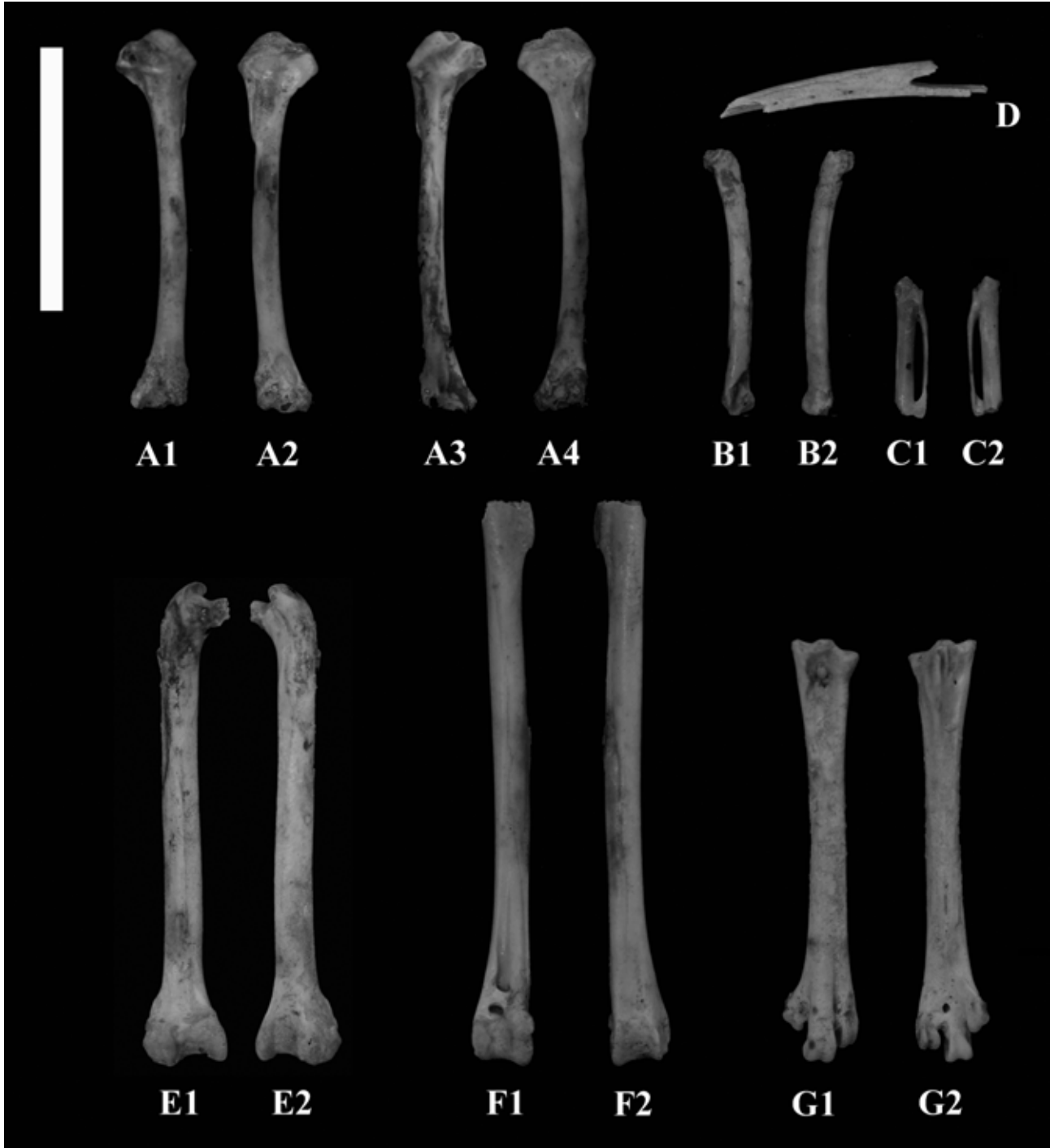Artistic reconstruction: Figure 23

FIGURE 5. Bones of the associated skeleton of the holotype of *Rallus carvaoensis* **n. sp. MCMa 1801.013**. **A,** humeri (1, R, caudal view; 2, R, cranial view; 3, L, caudal view; 4, L, cranial view). **B,** R ulna (1, dorsolateral view, 2, ventral view). **C,** R carpometacarpus (1, ventral view; 2, dorsal view). **D,** premaxilla (lateral view), **E** L femur (1, caudal view; 2, cranial view), **F,** L tibiotarsus (1, cranial view; 2, caudal view). **G** L tarsometatarsus (1, dorsal view; 2, plantar view). Scale bar: 2 cm.

Holotype: MCMa 1801.013, partial skeleton: man, pmx frag, L scap frag, R scap, LR hum, L uln prox, R uln, R cmc frag, pel frag, L fem, R dis fem , LR tbt, LR tmt, quad, 20 vers 7 ped pha.

Measurements of the holotype (right, left, in mm): <u>Humerus</u>—length: 28.5, 28.6; proximal width: 6.2, 6.3; minimum shaft width: 1.9, 1.9; distal width: 4.1, 4.1. <u>Ulna</u>—minimum shaft width: 1.2, 1.3; distal width: 2.4, -. <u>Femur</u>—length: -, 36.0; minimum shaft width: ~2.0, ~2.0; distal width: ~5.0, ~7.0 . <u>Tibiotarsus</u>—minimum shaft width: 2.5, 2.5; distal width: 4.6, 4.6. <u>Tarsometatarsus</u>—length: -, 31.7; minimum shaft width: 2.6, 2.5; distal width: -, 5.5. <u>Scapula</u>—length: 25.6, -; proximal width: 3.6, -.

Type locality and collection information: Gruta do Carvão, São Miguel; all the material of *R. carvaoensis* **n. sp.** was collected in this cave in August 2011 by JCR, MT, and JAA.

Paratypes: **IMEDEA 104068**, partial skeleton (sku frag, man frags, cor frag, pel frag, fem frag, L tbt and dis R tbt, R tmt and dis L tmt, 12 verts, 5 ped phas); **MCMa 1802.013**, partial skeleton (sku frag, pmx frags, R tbt frags, LR tmt frags, verts, ped phas); **MCMa 1803.013**, partial skeleton (man frags, pmx frags, LR tbt frags, tmt frags, 9 ped phas); **DZUL 3183**, partial skeleton (sku frags, pel frags, R fem and prox L fem, R tbt and prox L tbt, tmt and dis tmt); **DZUL 3184**, partial skeleton (man frags, pmx frags, cor, L hum, pel frag, LR fem frags, LR tbt frags, LR tmt frags, 18 vers, pha); **MCMa 1804.013**, partial skeleton (sku frags, man frags, pmx frags, R fem frag, R tbt frag, R tmt and dis L tmt, 6 ped phas); **MCMa 1805.013**, partial skeleton (sku frags, man frag, ste frag, R cor and L cor frag, hum frag, uln frag, rad frag, LR cmc, R fem and L fem frag, LR tbt, pel frag, 10 vers); **IMEDEA 104069**, partial skeleton (pmx frags, R hum, vers); **MCMa 1806.013**, partial skeleton (tbt frags, tmt frag, 5 vers); **MCMa 1807.013**, partial skeleton (man frags, pmx frags, L tmt and R tmt frag, 1 ped pha); **MCMa 1808.013**, partial skeleton (man frag, pmx frag, L cor, L hum and dis R hum, R uln frag, LR tbt, 1 ped pha); **MCMa 1809.013**, partial skeleton (sku frag, man frags, R fem and L sha fem, tbt frag, tmt frag, 6 vers); **MCMa 1810.013**, partial skeleton (LR cor frags, sca frag, L hum frag, femur frag, tbt frag, 10 vers); **MCMa 1811.013**, partial skeleton (fem frag, tbt frags, pel frags, 2 vers); **MCMa 1812.013**, partial skeleton (man frags, pmx frags, L hum and R hum frag, L fem, tbt frags, L tmt, 3 vers); **MCMa 1813.013**, partial skeleton (man frags, uln frag, R tbt frag, L tmt, 3 ped phas); **MCMa 1814.013**, partial skeleton (LR tbt frag); **MCMa 1815.013**, partial skeleton (L tbt fra, LR tmt frags).

Measurements of paratypes: See Table 1.

Age: Probably Holocene-Recent.

Diagnosis. A species of *Rallus* of small body size and with very reduced wing bones (Figures 11-13). The humerus has a reduced fossa pneumotricipitalis, a crista bicipitalis less expanded than in *R. aquaticus*, and a reduced and relatively flattened caput. The tibiotarsus, and especially the tarsometatarsus are very shortened compared to those of *R. aquaticus*, but relatively robust (Figures 16 and 17). The corpus ossi premaxillaris is slightly more curved than in *R. aquaticus* (Figure 8). All the bones are smaller than in *R. aquaticus* and larger than in *R. minutus* **n. sp.** The wing bones and the tarsometatarsus are smaller than those of *R. lowei* **n. sp.**, *R. adolfocaesaris* **n. sp.** and R*. montivagorum* **n. sp.**

Etymology. From the type locality and only known site of this rail.

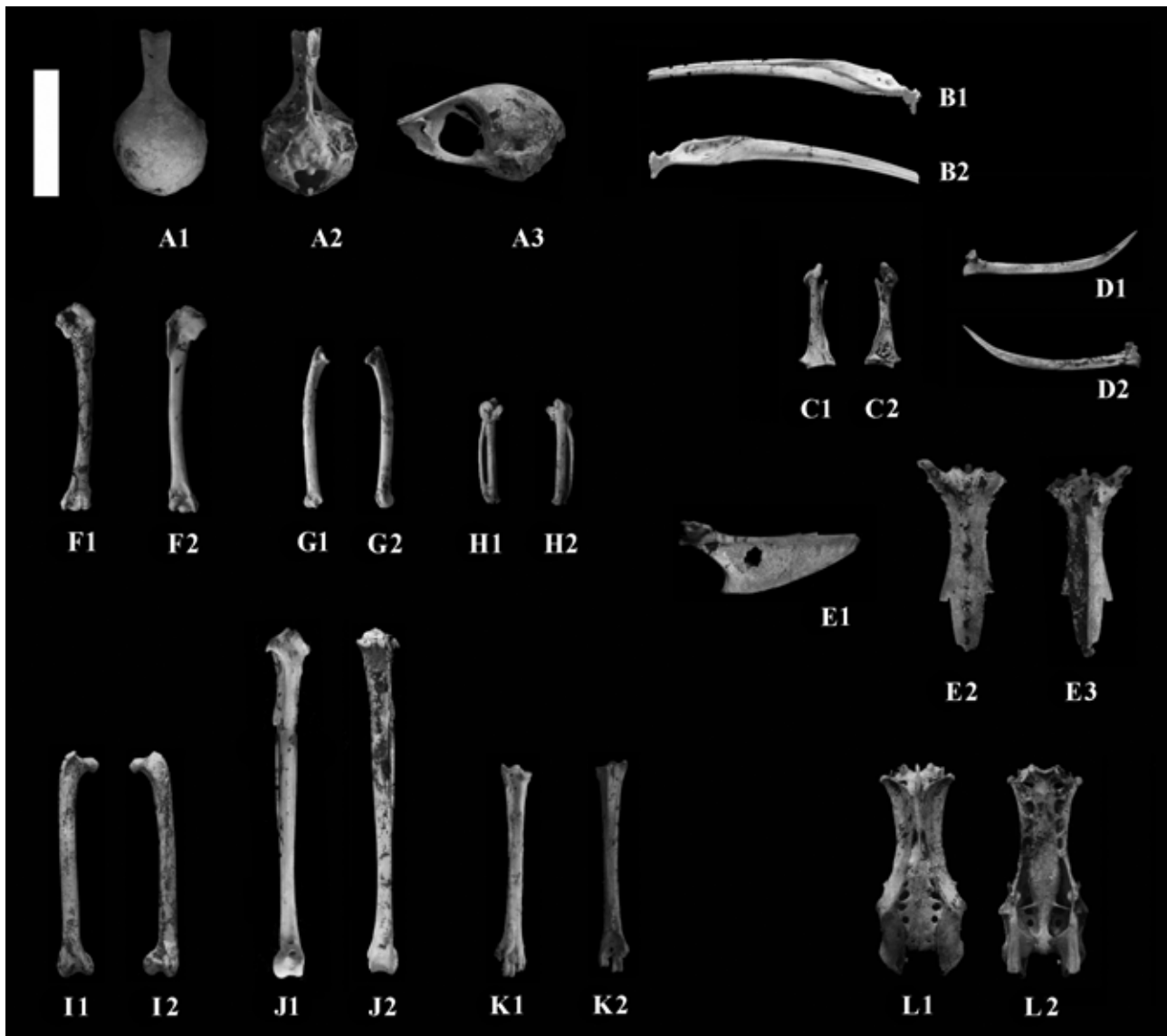*Rallus montivagorum*, **new species**
Pico rail
[Figures 6, 8F, 9B, 10B, 11D, 12C, 13B, 14B, 15D, 16D, 17D]
Artistic reconstruction: Figure 23

Holotype: **McMa 1831.014,** associated skeleton: sku frag, man frags, ster frag, LR scap, R cor, R hum and L hum frags, L uln, L cmc, syn, LR fem, LR tbt, L tmt.

Measurements of holotype (in mm): <u>Humerus</u>—length 32.9, proximal width 6.7, minimum shaft width 2.2, distal width 4.7. <u>Ulna</u>—length: 25.8; proximal width: 3.1; proximal diameter: 2.9; minimum shaft width—2.0; distal width: 3.0. <u>Carpometacarpus</u>—length: 16.8; proximal width: 4.2; distal width: 2.4. <u>Femur</u>—length: 35.8; proximal width: 5.7; minimum shaft width: 2.5; distal width: 5.6. <u>Tibiotarsus</u>—total length: 55.0; medial length: 53.1; proximal width: 5.7; minimum shaft width: 2.4; distal width: 4.9. <u>Tarsometatarsus</u>—length: 33.3; proximal width: 5.1; minimum shaft width: 2.4; distal width: 5.0. <u>Scapula</u>—length: 29.0; proximal width: 4.5. <u>Coracoid</u>: length: 16.8. Cranial length (without the bill)—26.8; cranial width: 14.9; interorbitarium witdth: 3.7; cranial height:

15.3. <u>Sternum</u>—length of the manubrium: 29.8; smallest width: 5.6. <u>Synsacrum</u>—total length: 31.8; vertebral length: 28.9; cranial width: 11.7; smallest beadth: 7.1; antitrochantherian width: 14.1.

FIGURE 6. Bones of the associated skeleton of the holotype of *Rallus montivagorum* **n. sp. McMa 1831.014. A,** skull (1, dorsal view, 2, ventral view, 3, lateral view). **B,** mandible. **C,** R coracoid (1, ventral view; 2, dorsal view). **D,** R scapula (1, lateral view; 2, internal view). **E,** sternum (1, lateral view; 2, dorsal view; 3, ventral view). **F,** R humerus (1, caudal view; 2, cranial view). **G,** L ulna (1, ventral view; 2, dorsal view). **H,** L carpometacarpus (1, ventral view; 2, dorsal view). **I,** R femur (1, cranial view; 2, caudal view). **J,** R tibiotarsus (1, cranial view; 2, caudal view). **K,** L tarsometatarsus (1, dorsal view; 2, plantar view). **L,** synsacrum (1, dorsal view; 2, ventral view). Scale bar: 2 cm.

Type locality: Furna das Torres, Pico, collected 18 July 2013.
Known distribution: Pico, Central Azores.
Collectors: all the material obtained at Pico was collected in July 2013 by JCR, FP, JCI, EB and JAA.
Paratypes: **Furna das Cabras, 17–19 July 2013: MCMa 1832.014,** associated skeleton (sku frags, man frags, pmx frags, LR cor, R scap frag, LR hum, L uln, R cmc, pel frag, LR fem, LR tbt); **MCMa 1833.014,** associated skeleton (LR fem, L tbt frag, L tmt frag); **MCMa 1834.014,** associated skeleton (L cor, cmc frag, syn, LR fem, L tbt frags, tmt, ped phas); **MCMa 1835.014,** associated skeleton (man frag, ste frag, L scap frag, R hum and L hum frags, R uln and L uln frags, syn frags, L fem, tbt and tbt frags, ped phas); **IMEDEA 104089,** associated skeleton (ste frag, R cor, L hum and R hum frag, LR uln, syn frags, LR fem frags, LR tbt frags, LR tmt frags); **MCMa 1836.014,** associated skeleton (sku frags, man frags, LR fem, syn frag, tbt frag); **MCMa 1837.014,** associated skeleton (sku frag, syn frag, LR fem, R tbt frags, tmt frags); **DZUL 3185,** associated skeleton (sku, man

frags, R scap, R cor, ste frag, LR hum frags, R uln frag, L cmc, syns frag, L fem, L tbt frag, L tmt and R dis tmt frag); **MCMa 1838.014,** associated bones (R fem and dis tbt); **MCMa 1839.014,** associated bones (pmx frag, L hum and R hum frag, L uln, LR cmc, 2 R fem, L fem and a R fem frag, R tbt frag, tmt frag); **MCMa 1840.014,** associated skeleton (man frags, pmx frag, L tbt); **MCMa 1841.014,** associated skeleton (man frags, pmx frag, R hum frag, L fem, LR tbt, LR tmt frags, ped pha); **MCMa 1842.014,** associated skeleton (sku frag, L cor, hum frag, L fem, tmt); **MCMa 1843.014,** associated skeleton (sku frag, L fem and sha R fem); **MCMa 1844.014,** associated skeleton (pmx frag, man frags, qua, ste frag, LR cor, R sca, R hum, syn frag, R fem and dis L fem, tbt frag); **MCMa 1845.014,** associated bones (sku frag, man frag, syn frag, 2 R fem, L tbt and R tbt frag, tmt); **MCMa 1849.014,** associated bones (sku frags, man frags, pmx frags, ste frags, 2 R hum, L hum, R cmc, LR fem and LR fem frag, 8 LR tbt, 5 LR tmt); **MCMa 1940.014,** associated bones (man frag, L cor, L hum frag, syn frag, LR fem and L fem frag, LR tbt frags, tmt, vers,); **IMEDEA 104090,** L cmc; **MCMa 1850.014,** L cmc; **MCMa 1851.014,** L cmc; **MCMa 1852.014,** L cmc; **MCMa 1853.014,** L cmc; **MCMa 1854.014,** L cmc; **IMEDEA 104091,** R cmc; **MCMa 1941.014,** R cmc; **MCMa 1855.014,** R cmc; **MCMa 1856.014,** R cmc; **MCMa 1857.014,** R cmc; **MCMa 1858.014,** R cmc; **MCMa 1859.014,** L hum; **IMEDEA 104092,** L hum; **MCMa 1860.014,** L hum; **DZUL 3186,** L hum; **MCMa 1861.014,** L hum; **MCMa 1942.014,** R hum; **MCMa 1862.014,** R hum; **MCMa 1943.014,** R hum; **MCMa 1947.014,** R hum frag; **MCMa 1863.014,** R hum; **DZUL 3187,** R hum; **MCMa 1864.014,** R hum; **MCMa 1865.014,** R hum; **MCMa 1866.014,** L uln; **MCMa 1867.014,** L uln; **IMEDEA 104093,** L uln; **MCMa 1868.014,** L uln; **MCMa 1869.014,** R uln; **DZUL 3188,** R uln; **DZUL 3189,** R uln; **MCMa 1870.014,** R uln; **MCMa 1944.014,** R uln; **MCMa 1945.014,** R uln; **MCMa 1871.014,** L fem; **MCMa 1872.014,** L fem; **IMEDEA 104094,** L fem; **IMEDEA 104095,** L fem; **MCMa 1873.014,** L fem; **DZUL 3190,** L fem; **MCMa 1946.014,** L fem; **MCMa 1874.014,** L fem; **MCMa 1875.014,** L fem; **MCMa 1876.014,** L fem; **MCMa 1877.014,** L fem; **MCMa 1878.014,** L fem; **MCMa 1879.014,** R fem; **MCMa 1880.014,** R fem; **MCMa 1881.014,** R fem; **MCMa 1882.014,** R fem; **MCMa 1883.014,** R fem; **MCMa 1884.014,** R fem; **MCMa 1885.014,** R fem; **MCMa 1886.014,** R fem; **MCMa 1887.014,** R fem; **MCMa 1888.014,** R fem; **MCMa 1889.014,** R fem; **MCMa 1960.014,** R fem frag; **MCMa 1890.014,** R fem; **MCMa 1891.014,** L tbt; **MCMa 1892.014,** L tbt; **MCMa 1893.014,** L tbt; **MCMa 1894.014,** L tbt; **MCMa 1895.014,** L tbt; **MCMa 1896.014,** L tbt; **IMEDEA 104096,** R tbt; **MCMa 1897.014,** R tbt; **IMEDEA 104097,** R tbt; **MCMa 1898.014,** R tbt; **DZUL 3191,** R tbt; **MCMa 1899.014,** R tbt; **MCMa 1900.014,** R tbt; **DZUL 3192,** R tbt; **MCMa 1901.014,** R tbt; **MCMa 1948.014,** R tbt; **MCMa 1983.014**, R tbt; **MCMa 1985.014**, R tbt; **MCMa 1902.014,** R sca; **MCMa 1903.014,** cranial part of R sca; **MCMa 1904.014,** cranial part of R sca; **MCMa 1905.014,** cranial part of R sca; **MCMa 1906.014,** cranial part of L sca; **MCMa 1907.014,** cranial part of L sca; **MCMa 1908.014,** cranial part of L sca; **MCMa 1909.014,** cranial part of L sca; **MCMa 1910.014,** L cor; **MCMa 1911.014,** L cor; **MCMa 1912.014,** L cor; **MCMa 1913.014,** L cor; **MCMa 1914.014,** L cor; **MCMa 1915.014,** L cor; **MCMa 1916.014,** L cor; **MCMa 1917.014,** cranial end of L cor; **MCMa 1918.014,** R cor; **MCMa 1919.014,** R cor; **MCMa 1920.014,** R cor; **MCMa 1921.014,** R cor; **DZUL 3193,** R tmt; **MCMa 1949.014,** R tmt; **IMEDEA 104098,** R tmt; **IMEDEA 104099,** R tmt; **MCMa 1922.014,** L tmt; **MCMa 1923.014,** L tmt; **MCMa 1924.014,** L tmt; **MCMa 1925.014,** tmt; **MCMa 1926.014,** tmt; **MCMa 1927.014,** tmt; **MCMa 1928.014,** tmt; **MCMa 1929.014,** tmt; **MCMa 1930.014,** tmt; **MCMa 1931.014,** tmt; **MCMa 1932.014,** sku; **MCMa 1933.014,** sku; **MCMa 1934.014,** sku; **MCMa 1935.014,** sku; **MCMa 1984.014,** sku frag; **MCMa 1994.014,** sku frag; **MCMa 1995.014,** sku frag; **MCMa 1996.014,** sku frag; **MCMa 1936.014,** ste; **MCMa 1991.014,** ste frag; **MCMa 1992.014,** ste frag; **MCMa 1993.014,** ste frag; **MCMa 1937.014,** syn; **MCMa 1938.014,** syn; **MCMa 1939.014,** syn; **MCMa 1986.014,** pmx frag; **MCMa 1987.014,** pmx frag; **MCMa 1988.014,** man frag; **MCMa 1989.014,** man frag; **MCMa 1990.014,** man frag.

Furna da Galinha, 21 July 2013: MCMa 1846.014, associated skeleton (man frag, tbt frag, tmt frag).

Furna do Frei Matias, 19 July 2013: MCMa 1847.014, associated bones (fem and dis fem);

Furna das Torres, Pico, 18 July 2013: MCMa 1848.014, associated skeleton (sku frags, man frags, qua, cor, sca, LR hum, LR uln, LR cmc, syn, LR fem, LR tbt, LR tmt, ped pha).

Age: Holocene-Recent. We obtained two AMS ^{14}C dates at the Royal Institute for Cultural Heritage (Brussels) on bones of *R. montivagorum* **n. sp.**: RICH 21401 (Furna das Cabras sample, 1.10g of fragmented bones of an associated rail skeleton): 1487± 30 BP, 437–645 cal AD; and RICH 21396 (Furna das Torres sample, 2g of fragmented bones of an associated rail skeleton): 489±29 BP, 1405–1450 cal AD. The last date overlaps the timing of the Portuguese colonization, and shows the species overlapped with humans. It is probably very close to the time of the extinction of the species.

Diagnosis. A species of *Rallus* slightly smaller than *R. aquaticus* in overall size and with a reduced sternum (Figure 10). The femur and tibiotarsus are only slightly smaller than those of *R. aquaticus* (Figures 15 and 16), whereas the tarsometatarsus is about 36% shorter (see Figure 17). *Rallus montivagorum* has a longer coracoid, humerus, carpometacarpus (Figures 9 to 11) and tarsometatarsus than *R. carvaoensis* **n. sp.** The ulna is longer than in *R. lowei* **n. sp.** (Figure 12). The tarsometatarsi of both species are of similar length, but *R. lowei* is much stouter. *Rallus montivagorum* has a smaller and less robust humerus than *R. adolfocaesaris* **n. sp.**, and while the tarsometatarsus of both species are similar in length, that of *R. montivagorum* sp. nov. is more gracile.

Etymology. The specific name is a latinization of the name of the Azorean society *Os Montanheiros*, who we honor here for their long-standing assistance in the palaeontological exploration of the caves of the central Azores.
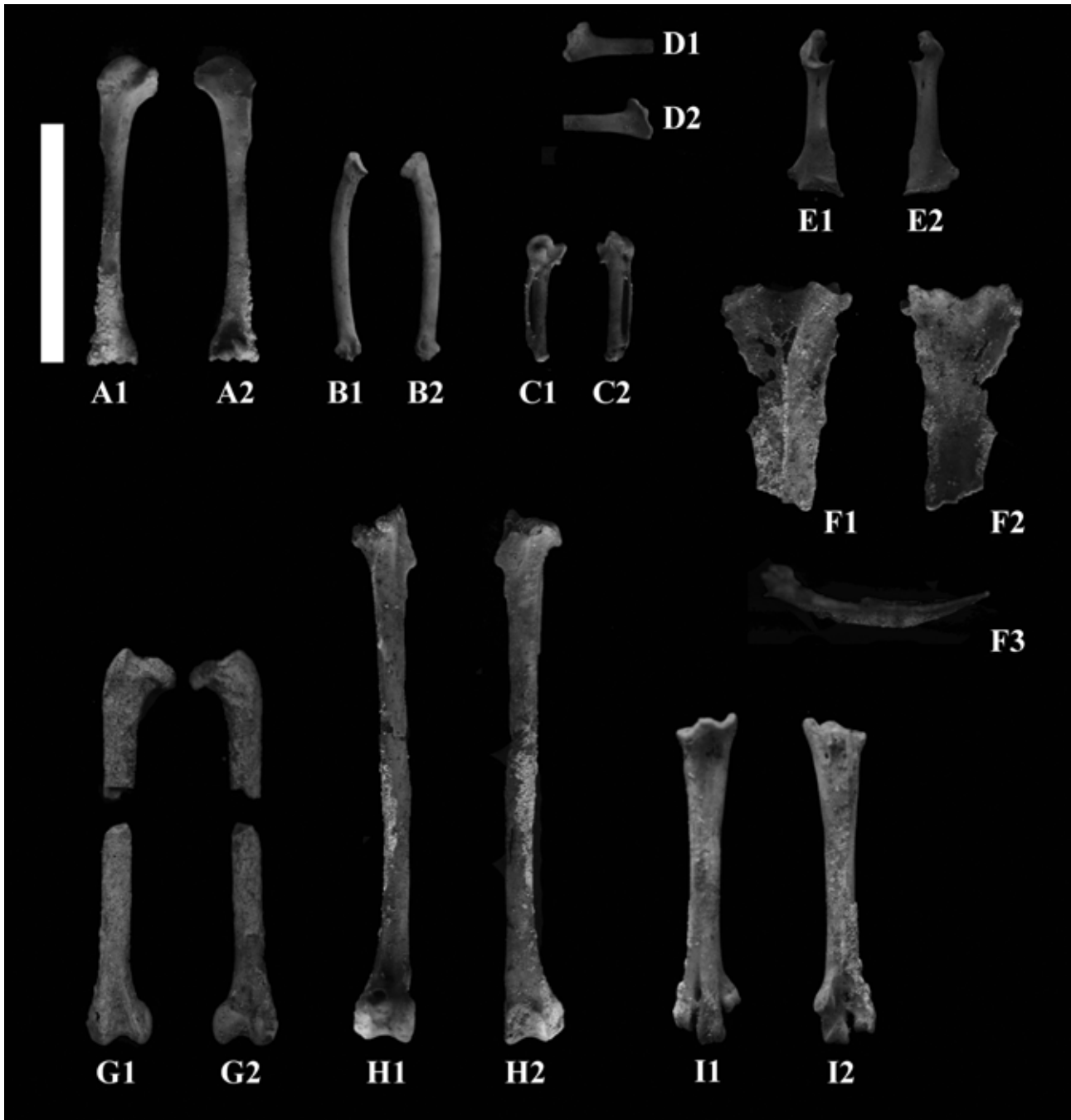

FIGURE 7. Bones of the associated skeleton of the holotype of *Rallus minutus* **n. sp. MCMa 1950.014**. **A,** L humerus (1, caudal view; 2, ventral view). **B,** L ulna (1, ventral view; 2, dorsal view). **C,** L carpometacarpus (1, ventral view; 2, dorsal view). **D,** R scapula (1, lateral view; 2 internal view). **E,** L coracoid (1, dorsal view; 2, ventral view). **F,** sternum fragment (1, ventral view; 2, dorsal view; 3, lateral view). **G,** R femur (1, cranial view; 2, caudal view), **H,** R tibiotarsus (1, cranial view; 2, caudal view). **I,** R tarsometatarsus (1, dorsal view; 2, plantar view). Scale bar: 2 cm.
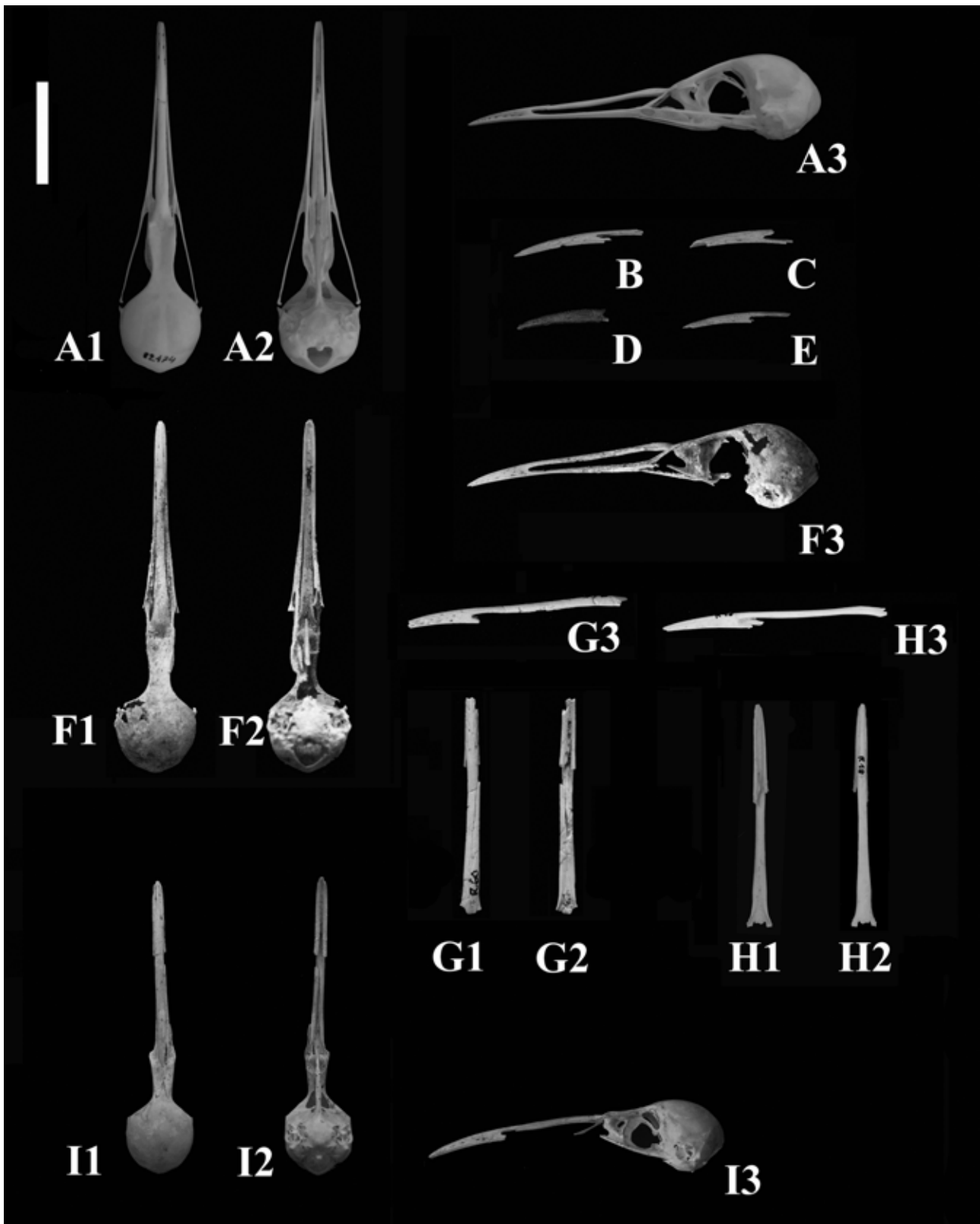
FIGURE 8. Skulls and premaxillae of *Rallus* spp. **A,** *Rallus aquaticus* **IMEDEA 12474**. **B,** *Rallus carvaoensis* **n. sp. IMEDEA 104069**. **C,** *Rallus carvaoensis* **n. sp. MCMa 1801.013**. **D,** *Rallus carvaoensis* **n. sp. MCMa 1804.013**. **E,** *Rallus carvaoensis* **n. sp. MCMa 1812.013**. **F,** *Rallus montivagorum* **n. sp.**, **DZUL 3185,** (paratype). **G,** *Rallus lowei* **n. sp.**, **MMF 43421,** (paratype). **H,** *Rallus adolfocaesaris* **n. sp.**, **MMF 43450,** Porto (paratype). **I,** *Rallus minutus* **n. sp.**, **MCMa 1950.014**. 1, dorsal view. 2, ventral view. 3, lateral view. Scale bar: 2 cm.
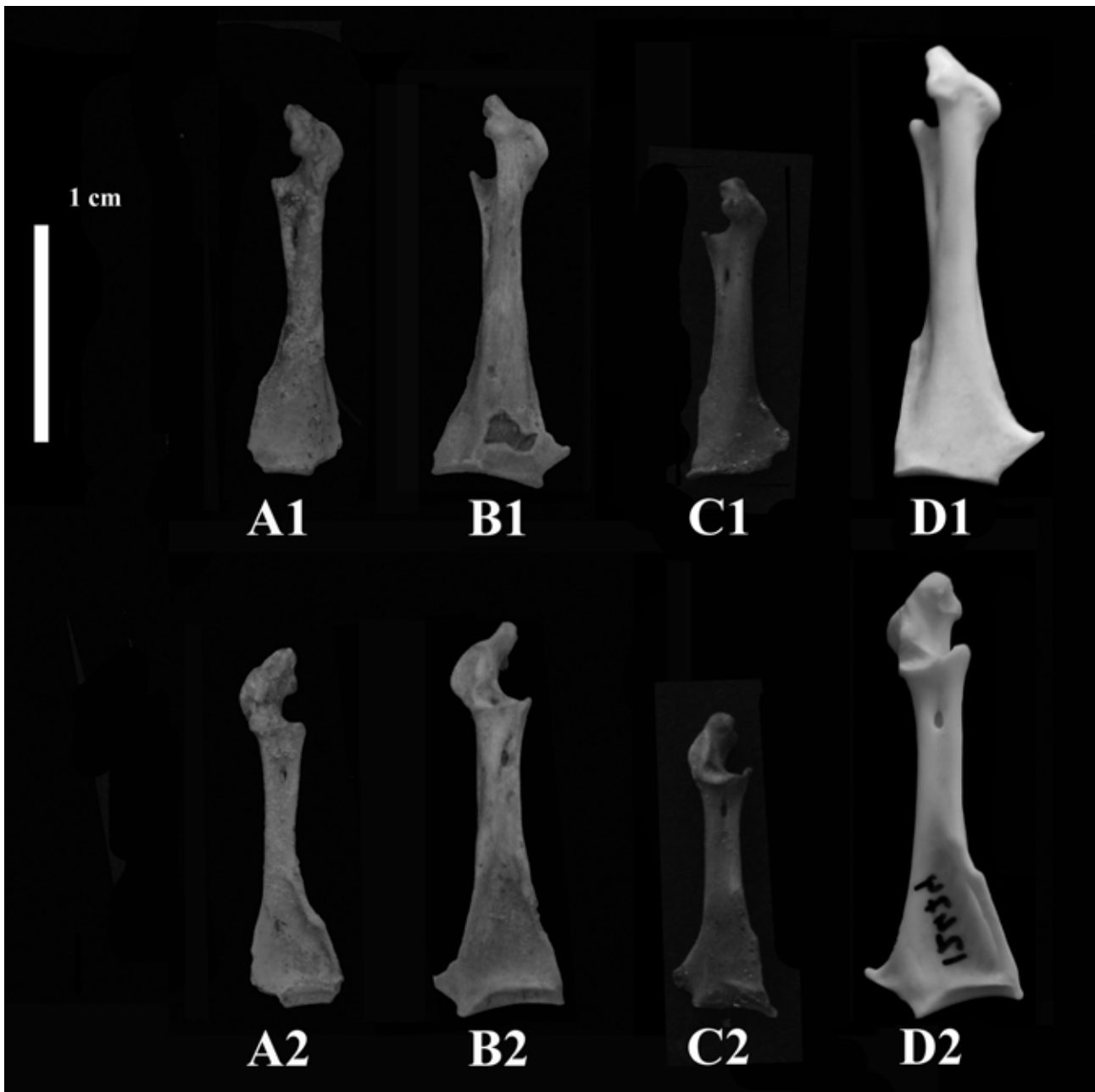
FIGURE 9. Coracoidea of *Rallus* spp. **A,** *Rallus carvaoensis* **n. sp.**, **MCMa 1805.013**, R coracoid (specular image). **B,** *Rallus montivagorum* **n. sp.**, **MCMa 1913.04**, L coracoid. **C,** *Rallus minutus* **n. sp.**, **MCMa 1950.014**, **D,** *Rallus aquaticus* **IMEDEA 12474**, R coracoid (specular image). 1, ventral view. 2, dorsal view. Scale bar: 1 cm.

Rallus minutus, **new species**
São Jorge rail
[Figures 7, 8I, 9C, 10D, 11E, 12D, 13C, 14C, 15E, 16E, 17E]
Artistic reconstruction: Figure 23

Holotype: **MCMa 1950.014**, associated skeleton (pmx frags, ste frag, LR cors, R scap frag, L hum, uln and uln frag, L cmc, fem frags, tbt and tbt frags, R tmt and prox L tmt, 3 ped phas).

Measurements of holotype (in mm): Humerus—length: 25.6; proximal width: 5.6; minimum shaft width: 1.5; distal width: 4.1. Ulna—length: 17.6; proximal width: 2.5; proximal diameter: 2.4; minimum shaft width: 1.3; distal width: 2.4. Carpometacarpus—length: 11.0; proximal width: 3.4. Femur—proximal width: 5.9; minimum

shaft width: 2.2; distal width: 5.7. <u>Tibiotarsus</u>—minimum shaft width: 2.2; distal width: 5.0. <u>Tarsometatarsus</u>—total length: 27.3; proximal width: 5.0; minimum shaft width: 2.5; distal width: 5.5. <u>Scapula</u>—proximal width: 3.6. Coracoid—length: 13.5.

**Type locality:** Gruta do Pasto do Engenheiro, São Jorge, collected 20 Sept 2014.

Known distribution: São Jorge, Central Azores.

Collectors: all the material was collected on 16–20 Sept 2014 by ET, FP, OT, DS and JAA.

Paratypes: **Gruta da Beira: MCMa 1951.014,** associated skeleton (pmx frag, man frag, ste frag, L cor, prox L uln, L hum, fem frags, R tbt, L tbt frag, LR tmt, 5 vert); **MCMa 1952.014,** associated skeleton (pmx frags, dist R tbt, distal R tmt, verts); **MCMa 1953.014,** associated skeleton (pmx frag, dis R hum, dis R tbt, tmt frag); **MCMa 1954.014,** associated skeleton (sku frag, pmx frag, man frag, LR fem, 2 LR tbt, LR tmt, 4 verts, 8 phas); **MCMa 1955.014,** associated skeleton (sku frags, man frag, pmx frags, femur frag, tbt frags, R and dis L tmt, syn frag, , 5 verts, 7 ped phas); **MCMa 1956.014,** associated material corresponding to two individuals (L uln, prox R fem, tbt frags, LR tmt, tmt frags, syn, 3 ped phas); **MCMa 1959.014,** associated skeleton (sku, man, dis L tmt, prox L tbt, sha L fem).
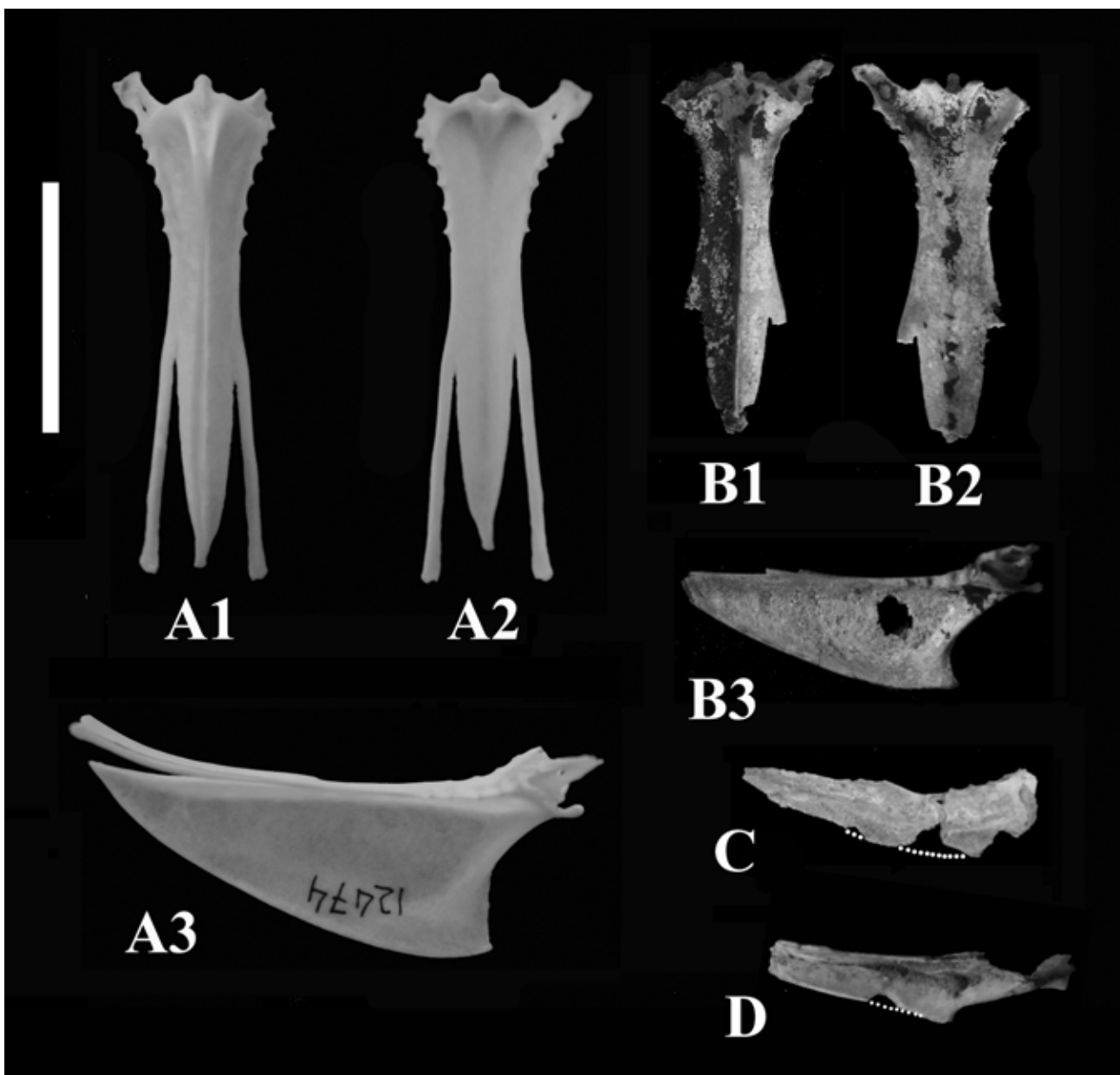
FIGURE 10. Sterna of *Rallus* spp. **A.** *Rallus aquaticus*, **IMEDEA 12474. B.** *Rallus montivagorum* **n. sp., MCMa 1831.014,** Pico. **C.** *Rallus carvaoensis* **n. sp., MCMa 1805.013. D.** *Rallus minutus* **n. sp., MCMa 1951.014.** 1, ventral view. 2, dorsal view. 3, lateral view. Scale bar: 2 cm.
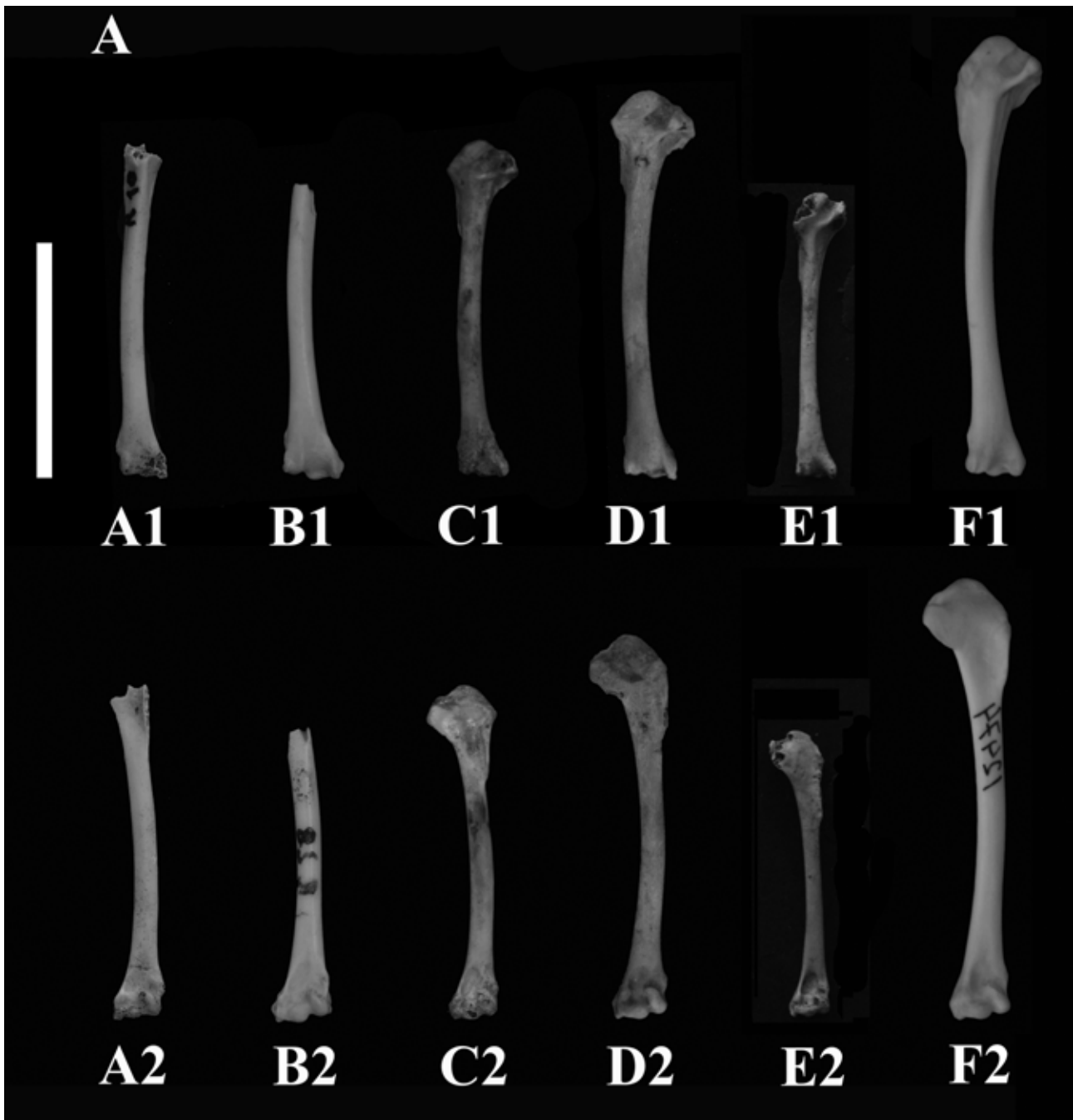
FIGURE 11. Humeri of *Rallus* spp. **A,** *Rallus lowei* **n. sp.**, **MMF 43414,** L humerus (paratype). **B,** *Rallus adolfocaesaris* **n. sp.**, **MMF 43451,** R humerus (specular image) (paratype). **C,** *Rallus carvaoensis* **n. sp.**, **MCMa 1801.013**, R humerus (specular image). **D,** Rallus *montivagorum* **n. sp.**, **MCMa 1943.014,** , R humerus (specular image). **E,** *Rallus minutus* **n. sp.** **MCMa 1951.014**. **F,** *Rallus aquaticus*, **IMEDEA 12474**, R humerus (specular image). 1, caudal view. 2, cranial view. Scale bar: 2 cm

Gruta do Pasto do Engenheiro: MCMa 1957.014, associated skeleton (sku frag, fem frags, tbt and tbt frags, tmt frags, syn frag, pha); **MCMa 1958.014**, associated skeleton (prox R tbt, R tmt, pha).

Measurements of paratypes: see Table 1.

Age: Probably Holocene-Recent.

Diagnosis. A very small species of *Rallus*. It is smaller than any other rail from Macaronesia and markedly smaller than *R. aquaticus*. The wing bones are relatively more reduced than in any other Azorean rail, including the São Miguel rail. The bill is very elongated and slightly curved. The humerus has a reduced fossa pneumotricipitalis, the crista bicipitalis is less expanded than in *R. aquaticus*, and has a reduced and relatively

flattened caput. All the bones, especially ulna, carpometacarpus and tarsometatarsus are very reduced in size relative to *R. aquaticus* (Figures 12, 13 and 17). The tarsometatarsus is relatively stout (Figure17). The synsacrum (Figure 14) is very broad, and the sternum (Figure 10) presents a very reduced depth to the carina sterni (the most reduced carina recorded among the species described herein).

Etymology. from the Latin, meaning little.
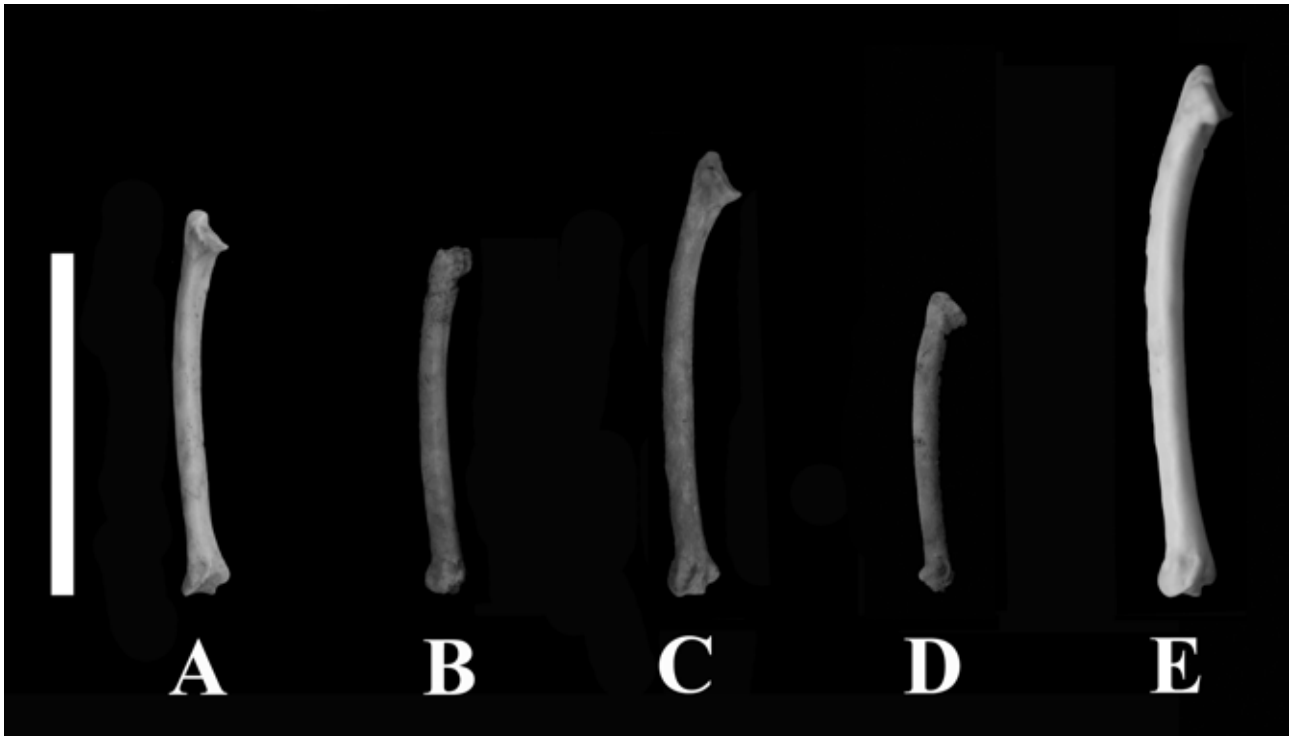
FIGURE 12. Ulnae of *Rallus* spp., dorsal view. **A,** *Rallus lowei* **n. sp.**, **MMF 43415**, R ulna (paratype). **B,** *Rallus carvaoensis* **n. sp.**, **MCMa 1801.013**, R ulna. **C,** *Rallus montivagorum* **n. sp.**, **MCMa 1867.014,** L ulna (specular image). **D,** *Rallus minutus* **n. sp.**, **MCMa 1950.014,** L ulna (specular image). **E,** *Rallus aquaticus*, **IMEDEA 12474**, R ulna. Scale bar: 1 cm.

Rallus **sp. A**
Graciosa rail
[Figure 19B]

The material from Graciosa consists of 21 bones (12 in a fragmentary condition). These bones probably also belong to an endemic species, convergent with the Pico rail, but we refer to them only as an indeterminate species of *Rallus* because the available material is insufficient to clearly establish its specific distinction from other taxa.

Material and collection information: Furna do Calcinhas: MCMa 1961.014, L hum; **MCMa 1962.014**, R hum frag; **MCMa 1963.014**, R hum frag; **MCMa 1964.014**, L cmc; **MCMa 1965.014,** R fem; **MCMa 1966.014**, R fem; **MCMa 1967.014**, L fem frag; **MCMa 1968.014**, L tmt; **MCMa 1969.014**, R cor; **MCMa 1970.014**, L cor; **MCMa 1971.014**, L cor; **MCMa 1972.014**, R cor frag; **MCMa 1973.014**, R cor frag; **MCMa 1974.014**, L cor frag; **MCMa 1975.014**, L cor frag juv; **MCMa 1976.014**, L cor frag juv; **MCMa 1977.014**, man frag; **MCMa 1978.014**, man frag; **MCMa 1979.014**, pmx frag; **MCMa 1980.014**, pmx frag; **MCMa 1981.014**, sku frag; **MCMa 1982.014,** L tbt frag.

All the material obtained on Graciosa was collected on 16–20 Sept 2014 by ET, FP and JAA.

Age: Holocene-Recent.

Known distribution: Graciosa, Central Azores.

Measurements: See Table 1.
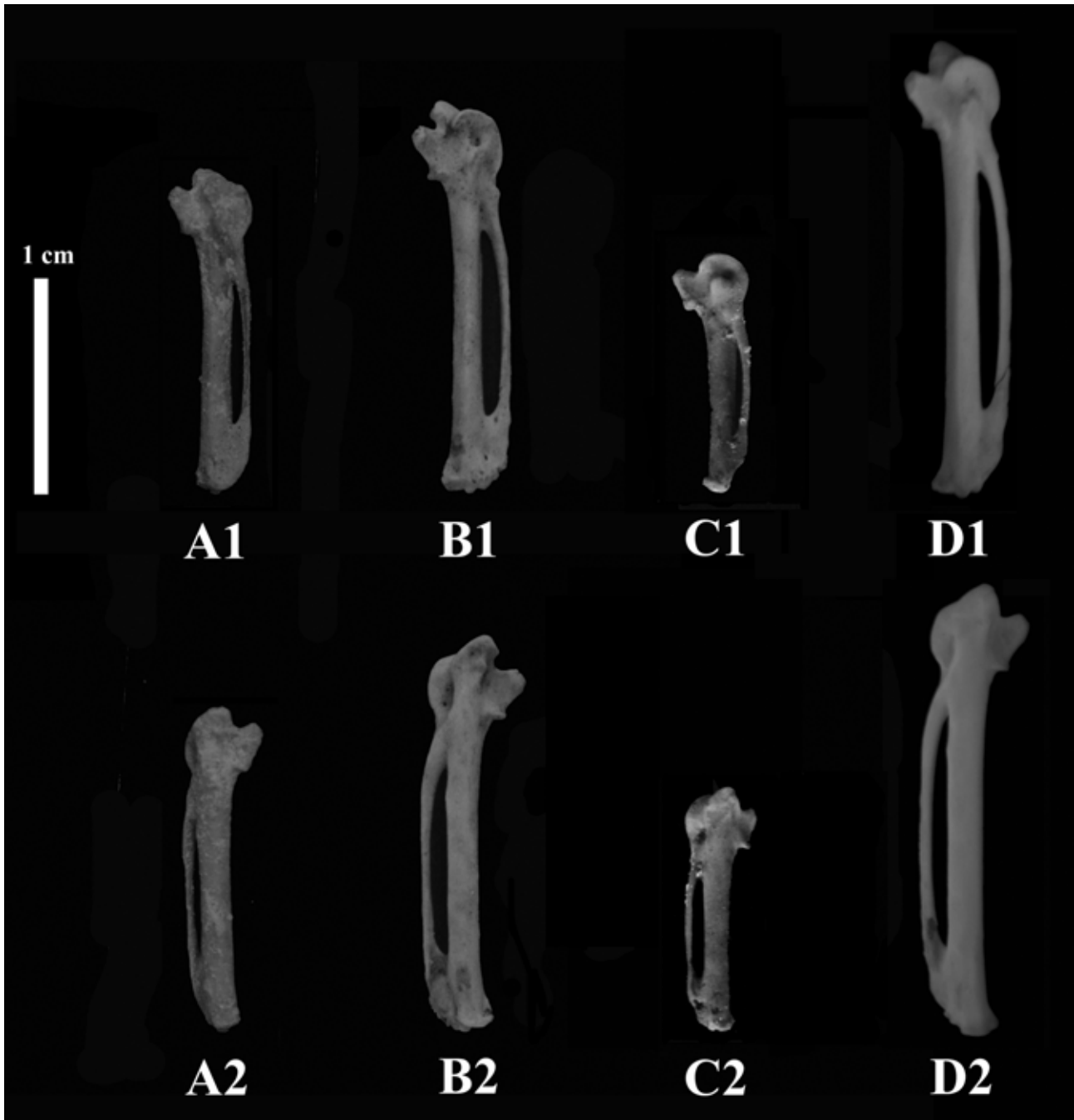
FIGURE 13. Carpometacarpi of *Rallus* spp. **A,** *Rallus carvaoensis* **n. sp.**, **MCMa 1805.013**, R carpometacarpus. **B,** *Rallus montivagorum* **n. sp.**, **MCMa 1856.014,** R carpometacarpus. **C,** *Rallus minutus* **n. sp. MCMa 1950.014,** L carpometacarpus (specular image). **D,** *Rallus aquaticus* **IMEDEA 12474**. R carpometacarpus. 1, ventral view. 2, dorsal view. Scale bar: 1 cm.
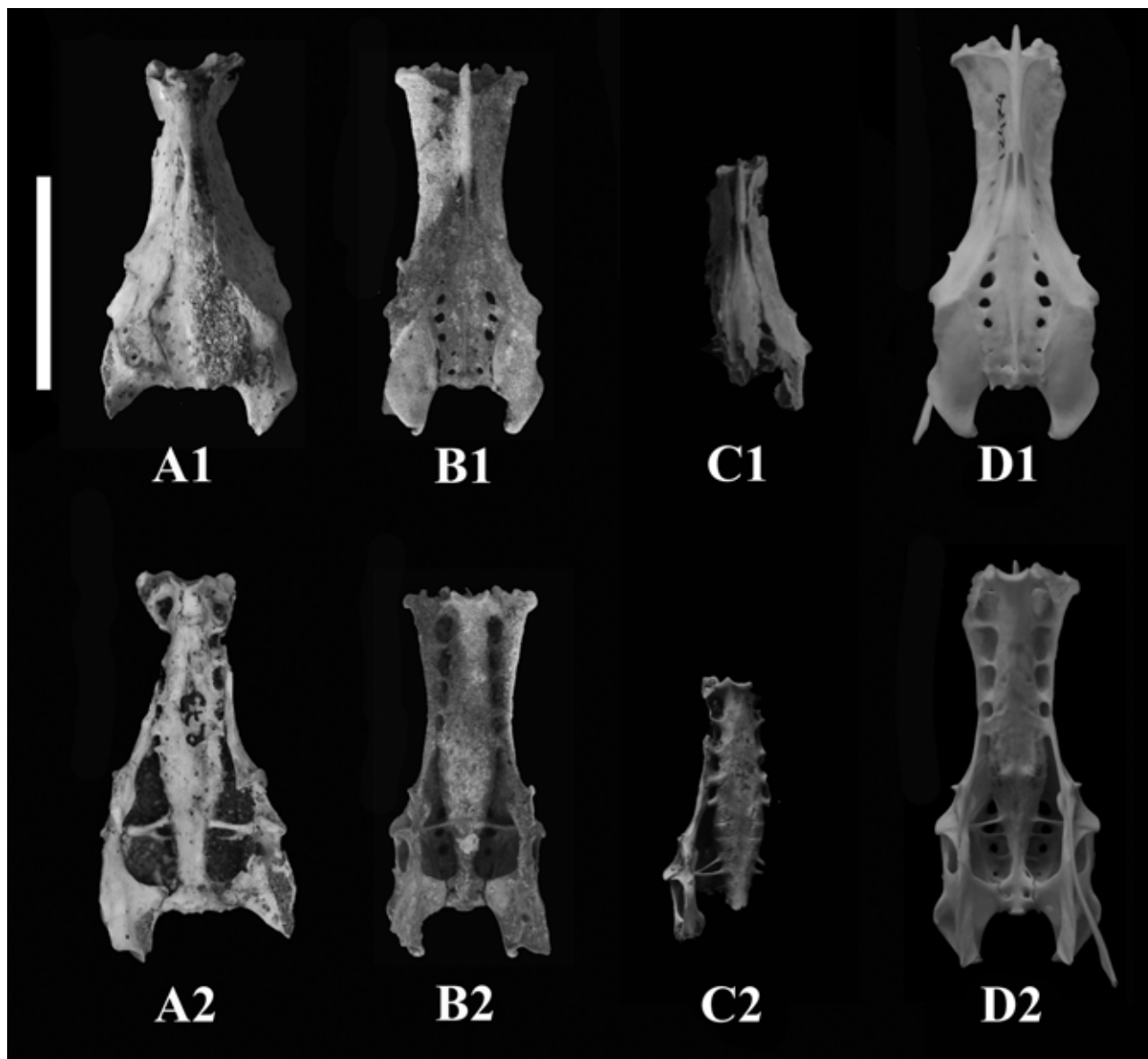
Rallus sp. B
Terceira rail
[Figures 18, 19C]

The material from Terceira consists of 13 associated skeletons (but most bones are very fragmentary). These bones probably also belong to an endemic species, convergent with the Pico rail, but the available material is very fragmentary and insufficient to establish clearly its specific distinction from known taxa, so we refer it as *Rallus* sp.

Material and collection information. Gruta do Natal: MCMa 1818.013, associated skeleton (LR tmt, R rad, L uln and R dis uln, 7 verts, LR cmc, fem frag, LR tbt frag, 6 ped phas); **MCMa 1819.013,** associated skeleton

(hum frags, R uln frags, rad frags, syn, verts, tbt frags, LR tmt, ped pha); **MCMa 1824.013,** associated skeleton (man frags, R tbt frag, R tmt, ped pha)

   Gruta de Santo Antonio: MCMa 1820.013, associated skeleton (sku, man frags, R cor, scap frag, R hum frag, syns frag, verts, quad, R fem frag, R tmt, R tbt frag, ped pha); **MCMa 1825.013,** associated skeleton (sku frags, R cor, syns frag, pel frags, L fem frag, LR tbt frags, tmt frags, verts); **MCMa 1827.013,** associated skeleton (sku frag, man frags, LR hum frags, uln frags, L cor and caudal part of R cor, sca frag, tbt frag, tmt frag, 10 vers, pha); **MCMa 1830.013,** associated skeleton (man frag, syn frag, LR fem frags, tbt frag, LR tmt frags, pha).

FIGURE 14. Synsacra of *Rallus* spp. **A,** *Rallus lowei* **n. sp.**, **MMF 43428,** (paratype). **B,** *Rallus montivagorum* **n. sp.**, **MCMa 1937.014. C,** *Rallus minutus* **n. sp. MCMa 1956.014.D,** *Rallus aquaticus*, **IMEDEA 12474**. 1, Dorsal view. 2, Ventral view. Scale bar: 2 cm.

   Gruta das Agulhas: MCMa 1821.013, associated skeleton (sku frag, LR hum, LR uln, R rad and L dis rad, LR cmc, LR cor, sca frag, fem frags, R tmt frags, LR tbt, 10 vers, 5 ped phas); **MCMa 1822.013,** associated skeleton (L hum frag, R uln, R cmc, L fem and R dis fem, tbt frag); **MCMa 1828.013,** associated skeleton (hum frag, tmt frag, LR tbt frag).

   Furna de Santa Maria: MCMa 1823.013, associated skeleton (sku frag, man frags, R hum frag, LR sca frags, R tbt frag, R tmt and L dis tmt, vers, ped phas); **MCMa 1826.013,** associated skeleton (sku frags, L hum frag, LR uln frag, rad frag, R cmc and L prox cmc, L cor and R cranial end of cor, LR fem frags, LR tbt frags, LR tmt frags, vers, ped phas); **MCMa 1829.013,** associated skeleton (sku frag, tbt frag, vers).

All the material was collected by FP, JCR and JAA on 17–22 Sept 2012, with the collaboration of IA in Furna de Santa Maria.

Measurements: See Table 1.

FIGURE 15. Femora of *Rallus* spp. **A,** *Rallus lowei* **n. sp.**, **MMF 43420,** L femur (specular image), (paratype). **B,** *Rallus adolfocaesaris* **n. sp.**, **MMF 43453,** R femur, (paratype). **C,** *Rallus carvaoensis* **n. sp.**, **DZUL 3183,** R femur. **D,** *Rallus montivagorum*, **MCMa 1880.014,** R femur. **E,** *Rallus minutus* **n. sp.** **MCMa 1954.014,** R femur. **F,** *Rallus aquaticus*, **IMEDEA 12474,** L femur (specular image). 1, cranial view. 2, caudal view. Scale bar: 2 cm.

FIGURE 16. Tibiotarsi of *Rallus* spp. **A,** *Rallus lowei* **n. sp.**, **MMF 43426/43427,** R tibiotarsus (paratype) (specular image). **B,** *Rallus adolfocaesaris* **n. sp.**, **MMF 43447,** L tibiotarsus, (paratype). **C,** *Rallus carvaoensis* **n. sp.**, **IMEDEA 104068**, L tibiotarsus. **D,** *Rallus montivagorum* **n. sp.**, **IMEDEA 104097,** R tibiotarsus (specular image). **E,** *Rallus minutus* **n. sp. MCMa 1951.014,** R tibiotarsus (specular image). **F,** *Rallus aquaticus*, **IMEDEA 12474**, R tibiotarsus (specular image). 1, cranial view. 2, caudal view. Scale bar: 2 cm.

FIGURE 17. Tarsometatarsi of *Rallus* spp. **A,** *Rallus lowei* **n. sp.**, **MMF 43419,** R tarsometatarsus (paratype). **B,** *Rallus adolfocaesaris* **n. sp.**, **MMF 43445,** R tarsometatarsus (paratype). **C,** *Rallus carvaoensis* **n. sp.**, **IMEDEA 104068,** R tarsometatarsus. **D,** *Rallus montivagorum* **n. sp.**, **MCMa 1949.014,** R tarsometatarsus. **E,** *Rallus minutus* **n. sp.**, **MCMa 1951.014**, R tarsometatarsus. **F,** *Rallus aquaticus* **IMEDEA 12474**, R tarsometatarsus. 1, dorsal view. 2, plantar view. Scale bar: 2 cm.
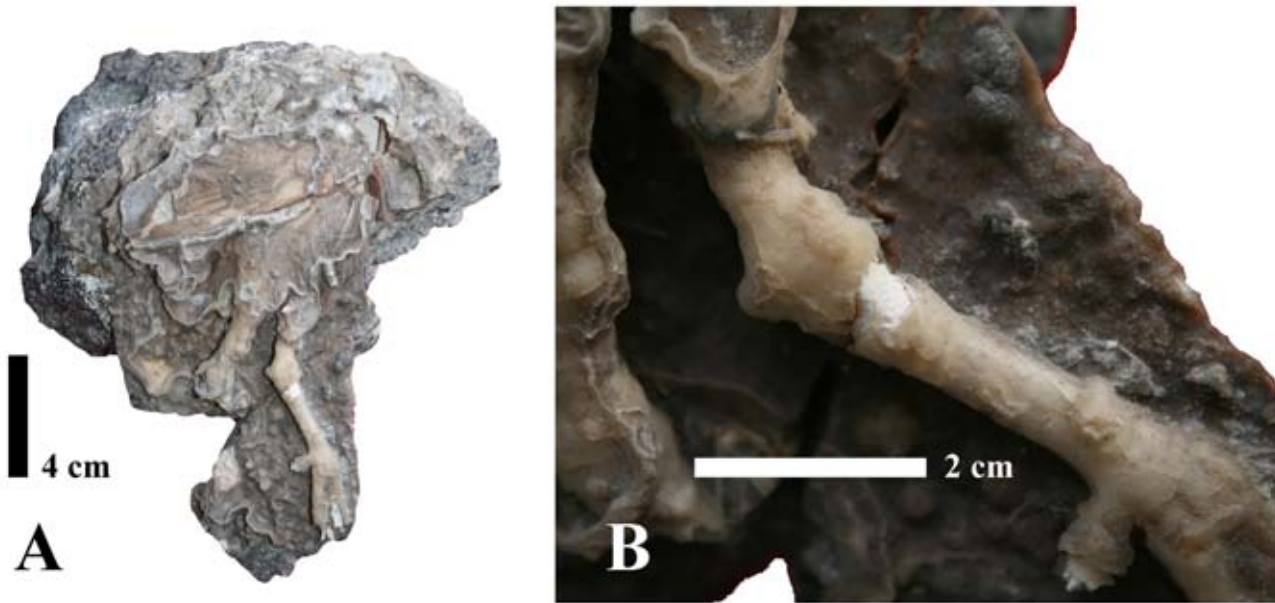
FIGURE 18. Photograph of a silicified specimen of *Rallus* sp. B from Algar do Carvão, Terceira. **A.** General view. **B.** Detail of the tarsometatarsus. The scales of the tarsometatarsus are visible in the section free of silica. Scale bar of **A**: 4 cm. Scale bar of **B**: 2 cm.

A silicified specimen of *Rallus* sp. B. We report here the first avian body fossil described from ancient siliceous sinter (opal) deposits in the Azorean Islands, curated at the Colecção dos Montanheiros. The specimen comes from the Algar do Carvão, Terceira. It is a 3D preservation of feathers and soft body morphology (Figure 18), derived from a silicification process that allows the preservation of features normally lost during fossilization. Silica (silicon oxide) is a mineral associated with exceptional preservation of fossils (e.g., Allison 1988; Channing *et al*. 2005; Manning *et al*. 2009). Some Azorean caves contain siliceous speleothems (stalactites, stalagmites and flowstone) made of opal. The opal is a hydrated amorphous form of silica that precipitates as hot water evaporates, becoming solid after drying. The silicification of a specimen results from its coating and encrustation by the dissolved opal and its subsequent drying. Exceptionally, the silification can affect carcasses of recently dead animals. Thesilica encrustation of the body of the dead specimen can occur within hours or days after death and before substantial soft tissue degradation takes place (i.e., before 2–3 days after death; Davis and Briggs 1998; Channing *et al*. 2005). It can preserve the feathers, nails, and the colonizing microbial communities.

Channing *et al*. (2005) described a silicified bird from Yellowstone Quaternary hot springs deposits. It consisted of an external mould of the body of a *Fulica*. According to the description of Nunes *et al*. (2004), Algar do Carvão is a volcanic cave located in the centre of Terceira Island, at 583 m above sea level. The entrance of the volcanic pit is 17 m x 27 m in size and connects with a vertical conduit, which drops ca. 45 m. After an uneven slope, the conduit [or passage] drops vertically once again and ends in a lake of clear water, at ca. 90 m below the mouth of the pit. The lake has a maximum depth of about 15 m and dries up almost completely in summer in years of low precipitation. The complex geological and biochemical phenomena which occur in the hydrogeological system of Algar do Carvão allowed the formation of stalactites and flowstone of amorphous silica (Si ≈ 77% to 82%). These are probably the most exuberant, rare and beautiful structures present in the volcanic caves of the Azores. These opal stalactites, milky-white coloured with reddish internal veins, cover a large area of the roof and walls of the pit and reach a length of about 1 m long and 40 cm to 50 cm in diameter. On the cave floor, opal flowstone coats several square meters. The presence of opal speleothems suggests the sporadic activity of a hot spring inside the cave.

Unlike the *Fulica* specimen described by Channing *et al.* (2005), which corresponds to an external cast that could have originated by the erosion of the body in a fully coated specimen or by the deposition of a carcass upon an opaline gum, the *Rallus* sp. B from the Algar do Carvão preserves its body. The specimen is a feathered carcass coated with a thin layer of opal. It suffered some damage during its extraction in the 1990s, and currently it is curated in the Museum of Os Montanheiros, at Angra do Heroísmo. The opal coat of the specimen was formed apparently as the result of a silica-enriched water flux upon a freshly dead specimen.

The specimen is 17.5 x 15.7 cm in size and apparently corresponds to an adult or to a full-grown specimen, preserving the body (abdomen and trunk), the two hindlimbs (the right is broken at the level of the proximal end of tarsometatarsus; the left is broken at the level of the toes), and the right wing. The tail is not visible and the specimen is broken at the level of the neck, lacking the entire head. A hole allows the right coracoid to be seen, fully formed, in its anatomical position. The tip of the wing is slightly broken, but the total length of the wing can be estimated at 9–10 cm. The length of the tarsosometatarsus is ca.4 cm, and the specimen might have attained a height of c.12 cm. It is possible to see the skin scales on the proximal right tarsometatarsus. The hindlimbs appear to wear fewer feathers than in *R. aquaticus*. The tibiotarsus seems to be naked until its upper third.

The plumage of the ventral part of the body has the appearance of a juvenile (i.e. loose feathers).

Age: Holocene-Recent. The silicified specimen of *Rallus* sp. B found in Algar do Carvão, (Terceira Island) a volcanic pit of a Late-Holocene age (Forjaz *et al.* 2004), indicates a very recent extinction. The radiometric dating analysis of charcoal found beneath the basaltic lava flow at Algar do Carvão rendered an age of 1730± 40 years BP for the lava flow (Forjaz *et al.* 2004), and the silicified specimen was apparently deposited at an indeterminate moment after this flow.
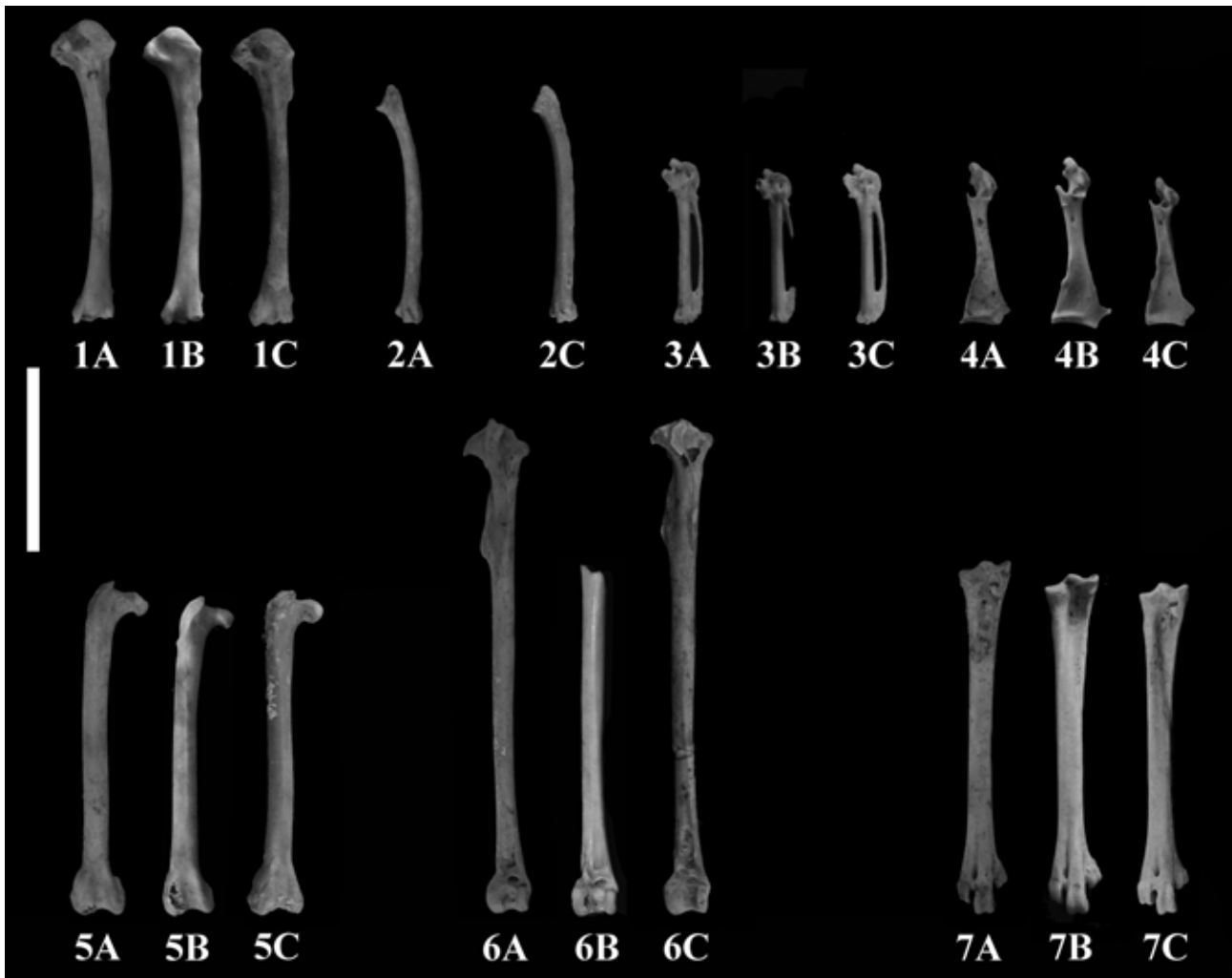
FIGURE 19. Bones of *Rallus* sp. A from Graciosa (**B**) and *Rallus* sp. B from Terceira (**C**) compared with the same bones of *Rallus montivagorum* **n. sp.** from Pico (**A**). From L to R: Humerus, caudal view: MCMa 1943.014; MCMa 1961.04 (L humerus, specular image), MCMa 1821.013. Ulna, dorsal view: MCMa 1867, MCMa 1821 (L ulna, specular image). Carpometacarpus, ventral view: MCMa 1856, MCMa 1821.013 (L carpometacarpus, specular image), MCMa 1964.014. Coracoid, dorsal view: MCMa 1918, MCMa 1969.014, MACa 1825. Femur, cranial view: MCMa 1880, MCMa 1965.014, MCMa 1822 (L femur, specular image). Tibiotarsus, cranial view: IMEDEA 104097, MCMa 1982.014, MCMa 1821.013. Tarsometatarsus, dorsal view: MCMa 1949, MCMa 1968.014 (L tarsometatarsus, specular image), MCMa 1820.013. Scale bar: 2 cm.
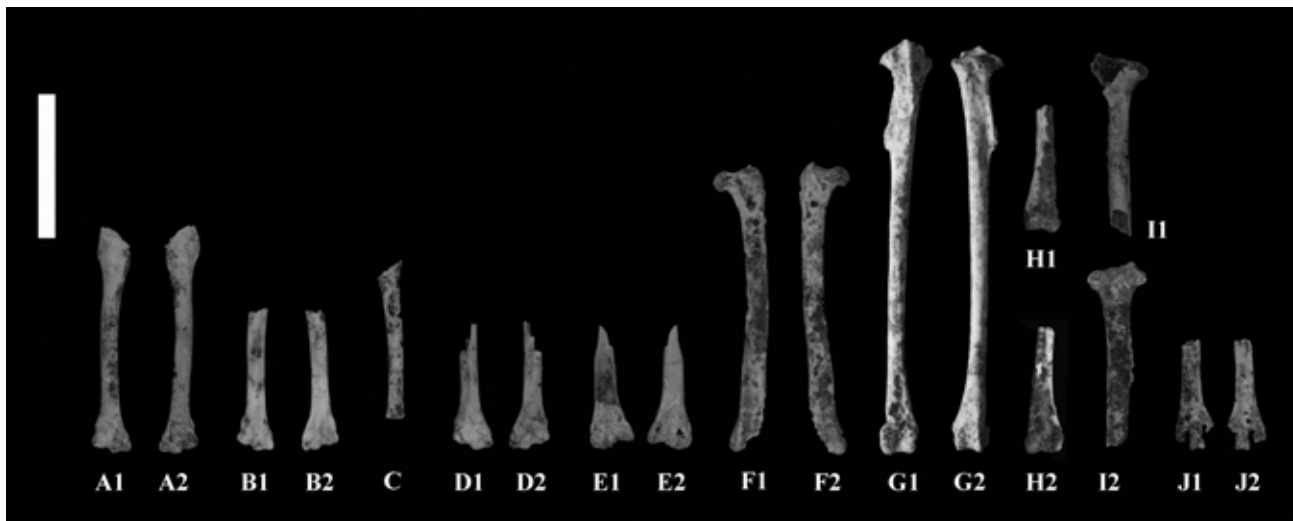
***Rallus* sp. C**
Santa Maria rail
[Figure 20]

We refer the material from Santa Maria, consisting of ten bones (eight of them in a fragmentary condition) to *Rallus* sp. They probably belong to an endemic species also, but the available material is insufficient as to establish clearly its specific status.

Age: Probably Holocene-Recent.

Material and collection information: Praia, coll. H. Pieper, 2001 and 2003: **MCMa 1816.13**, R tbt; **MCMa 1817.13**, dis L fem. Vinha Velha, coll. SA team, July of 2012 and July of 2013: **DBUAF 1080**, L hum frag; **R-1** [all the "R-" series here refered are provisional numbers of specimens to be curated at the DBUAF], dis L hum; **R-2**, dis L hum; **R-3**, sha L hum; **R-4**, L fem; **R-5**, prox R tbt; **R-6**, dis R tbt; **R-7**, dis R tbt.

Measurements: See Table 1

FIGURE 20. Material of *Rallus* sp. C from Santa Maria. **A, DBUAF 1080**, L humerus (1, caudal view; 2, cranial view). **B, R-1**, L humerus (1, caudal view; 2, cranial view). **C, R-3**, L humerus (cranial view). **D, R-2**, L humerus (1, caudal view; 2, cranial view). **E, MCMa 1817.13**, L femur (1, cranial view; 2, caudal view). **F, R-4**, L femur (1, cranial view; 2, posterior view). **G, MCMa 1816.13**, R tibiotarsus (1, anterior view; 2, caudal view). **H, R-6**, R tibiotarsus (1, cranial view; 2, caudal view). **I, R-5**, R tibiotarsus (1, cranial view; 2, caudal view). **J, R-7**, R tarsometatarsus (1, dorsal view; 2, plantar view). Scale bar: 2 cm.

Comparative morphology

All the new species from the Macaronesian islands are smaller than their presumed ancestor, *R. aquaticus*. Compared to the respective bones of *R. aquaticus*, we have detected in all the new species biometric changes in wing and hindleg. The magnitude of bone reduction in the Macaronesian rails compared to *R. aquaticus* differs among the species and the bones considered (both in linear lengths and robustness). The synsacrum and sternum (when available) differ among species. The shape of their bills differs also between the new species.

A MANOVA performed on the tarsometatarsus identified significant morphological differences between the new *Rallus* spp. (*R. lowei* **n. sp.**, *R. carvaoensis* **n. sp.**, *R. montivagorum* **n. sp.** and *R. minutus* **n. sp.**) and *R. aquaticus* (Wilks' lambda = 0.031, d.f. = 8, 126; p<0.001). These differences were detected in the total length (trait 26) ($F_{4,69}$= 87.39; p<0.001) and distal width (trait 29) ($F_{4,69}$= 34.74; p<0.001). The tarsometatarsus total length of *R. adolfocaesaris* **n. sp.** is smaller than that of *R. aquaticus* too (U = -2.84; p<0.001).

Rallus lowei

R. lowei **n. sp.** is a highly distinctive species. It belongs to a group that combines robust leg bones (especially the tarsometatarsus) with small wings. It is the largest and heaviest member of this group, which also includes *R. carvaoensis* **n. sp.** and *R. minutus* **n. sp.** Two almost complete humeri of *R. lowei* **n. sp.**, were available for study.

One of them is from an adult and measures ca. 29.7 mm, which represents about a 24% reduction compared with the average humerus length of *R. aquaticus* (Figure 11). This estimated humerus length falls between the average humerus lengths of the larger *R. montivagorum* **n. sp.** and *R. adolfocaesaris* and the smaller *R. carvaoensis* **n. sp.** and *R. minutus* **n. sp.** The ulna of *R. lowei* is shorter than in *R. aquaticus* (27% shorter), and than *R. montivagorum* **n. sp.** from Pico (14%), but longer than in *R. minutus* **n. sp.** (39%).

Its femur is slightly longer than in the *Rallus* species of Porto Santo, São Miguel and Pico, notably longer (28%) than in *R. minutus* **n. sp.** but shorter (8%) than that of *R. aquaticus*. Its tibiotarsus is longer (16%) than in *R. minutus* **n. sp.**, slightly longer than in *R. adolfocaesaris* **n. sp.**, close in size to those of the Pico, but shorter than in *R. aquaticus* (16%) (Table 1 & Figure 16). *R. lowei* **n. sp.** has a tarsometarsus similar in length to *R. montivagorum* **n. sp.** (p = 0.734), longer (12%) than in *R. carvaoensis* **n. sp.** (p = 0.003) and in *R. minutus* **n. sp.** (29%, p < 0.001), but shorter (18%) than in *R. aquaticus* (p< 0.001). The tarsometatarsus of the new species has the largest tarsometatarsus distal width (p<0.001 in all the cases) and proximal width reported within the species group (U = -3.745; p < 0.000, U = -3.337; p < 0.001, U = - 3; p = 0.001, and U = - 4.124; p < 0.000 respectively). In addition, the tarsometatarsus length is similar to *R. adolfocaesaris* **n. sp.** (U = - 0.342; p = 0.833), but has larger distal (U = - 2.449; p = 0.012) and proximal widths (U = - 2.646; p = 0.006) (Figure 17).

The quotient between the antitrochanterian width and the total length of the synsacrum is larger (20%) in *R. lowei* **n. sp.** than in *R. aquaticus*. This ratio is larger than in *R. montivagorum* **n. sp.**, but slightly smaller than in *R. minutus* **n. sp.**

The stout configuration of all the hindlimb bones gives them a peculiar shape (see Figure 17A), which combined with the very wide synsacrum, suggests the new species was a very robust bird (Figure 23). The species was flightless, as confirmed by the reduced wing bones compared to the hindlimb bones with a humerus-to-femur length ratio (0.78) (Livezey 2003). The short stout tarsometatarsus relative to the femur suggests that *R. lowei* **n. sp.** might have been a slow-pace runner.

Rallus adolfocaesaris

Rallus adolfocaesaris **n. sp.** forms with the rails from Pico, Graciosa, Terceira and Santa Maria, a Macaronesian group of species that share the display of legs less robust and wings less reduced than *R. lowei* **n. sp.** The humerus of *R. adolfocaesaris* **n. sp.** is slightly more gracile than in *R. aquaticus*, but considerably wider than in *R. lowei* **n. sp.**. Its size (c. 33 mm in length) is similar to that of the Pico rail, and much larger than the São Miguel rail (20%) and São Jorge (31%) rails. The smaller humerus in relation to *R. aquaticus* suggests a shortening of the primary remiges, although this reduction was probably not so extreme as in *R. lowei* **n. sp.**

The hindlimb bones are gracile compared to *R. lowei* **n. sp.**, and short in relation to *R. aquaticus*. *R. adolfocaesaris* **n. sp.** has a femur close in length to those of *R. lowei* **n. sp.**, and slightly longer than in the rails of São Miguel, Terceira and Pico, but shorter than in *R. aquaticus* (7%) and longer than in *R. minutus* **n. sp.** (28%, see Figure 15). Its tibiotarsus is slightly shorter than in *R. lowei* **n. sp.**, *R. carvaoensis* **n. sp.** and *R. montivagorum* **n. sp.**, shorter than in *R. aquaticus* (19%) and longer than in *R. minutus* **n. sp.** (11%, Table 1 & Figure 16). The ANOVA performed on the tibiotarsus distal width (trait 25) identified significant morphological differences ($F_{4,84}$=8.872; p < 0.001) between *R. adolfocaesaris* **n. sp.** and *R. carvaoensis* **n. sp.** (p = 0.007) and *R. minutus* **n. sp.** (p = 0.002) but not with *R. montivagorum* **n. sp.** (p = 0.262) and *R. aquaticus* (p = 0.504). *R. adolfocaesaris* **n. sp.** has a similar tarsometatarsus length (U = - 0.342; p = 0.833) but a smaller tarsometatarsus distal (U = -2.449; p = 0.012) and proximal width (U = - 2.646; p = 0.006) than *R. lowei* **n. sp.** The tarsometatarsus is shorter (20%) than in *R. aquaticus* (U = - 2.838; p < 0.001), and longer (25%, U = -2.236; p = 0.0.36) than in *R. minutus* **n. sp.** No differences were detected in tarsometarsus proximal (U = - 1.492; p = 0.171) and distal widths (U = -1.167; p = 0.262) between *R. adolfocaesaris* **n. sp.** and *R. minutus* **n. sp.** Seemingly, the ANOVA did not detect any relevant difference in tarsometatarsus length, and proximal and distal widths between *R. adolfocaesaris* **n. sp.** and the rails of São Miguel and Pico.

The ratio of humerus-to-femur length ratio (0.85) suggests that *R. adolfocaesaris* **n. sp.** was a flightless bird. According to this figure, and since the hindlimb bones are thinner than in *R. lowei* **n. sp.**, the loss of the flying capacity should have been less extreme in *R. adolfocaesaris* than in the Madeiran rail. The short stout tarsometatarsus (relative to the femur) suggests that *R. adolfocaesaris* **n. sp.** could be a slow-pace runner.

Rallus carvaoensis

R. carvaoensis **n. sp.** belongs to the group of species that combine robust leg bones (in this case, excluding the femur) with reduced wings. It is smaller than *R. lowei* **n. sp.** from Madeira and larger than *R. minutus* **n. sp.** from São Jorge.

Although no complete skulls are available, the premaxilla is longer and more curved than in *R. aquaticus* and *R. montivagorum* **n. sp.** (see Figure 8B–E). The bill shape was probably similar to that of *R. minutus* **n. sp.**
R. carvaoensis **n. sp.** has a shorter coracoid and humerus than *R. montivagorum* **n. sp.** from Pico (12% and 19% shorter, respectively; U = -2.448; p = 0.007, U = -2.714; p = 0.002) and *R. aquaticus* (26% and 29% shorter, respectively; U = -2.833; p < 0.001, U = -2.842; p < 0.001). The available forelimb bones (humerus and carpometacarpus) are around 30% smaller than in *R. aquaticus*, while the femur, tibiotarsus and tarsometatarsus are 12%, 17% and 26% smaller than in *R. aquaticus*, respectively.

The humerus is longer (9%) than in *R. minutus* **n. sp.** The carpometacarpus is smaller than in the Pico rail (21%) and in *R. aquaticus* (30%) (Table 1), and it is longer than in *R. minutus* **n. sp.** (35%). Despite all the known ulnae being incomplete, its extreme reduction in size is clear based on their width measurements (see Table 1).

The femur length of *R. carvaoensis* **n. sp.** is close to *R. lowei* **n. sp.** and *R. adolfocaesaris* n.sp (Table 1). The ANOVA of femur length (trait 17) of the *Rallus* from São Miguel, Pico, and *R. aquaticus*, reveal significant differences among them ($F_{2,66}$ = 75,664; p < 0.001). These differences were significant between *R. carvaoensis* **n. sp.** and *R. aquaticus* (p < 0.001) (12%), but not between *R. carvaoensis* n. sp and the *Rallus* from Pico (p = 0.601). The tibiotarsus of *R. carvaoensis* **n. sp.** is longer than in *R. minutus* **n. sp.** (14%), slightly longer than in *R. adolfocaesaris* **n. sp.**, close in length to *R. lowei* **n. sp.** and the *Rallus* from Pico, and smaller (17%) than in *R. aquaticus*.

The ANOVA of the tibiotarsus distal width (trait 25) identified morphological differences between *R. carvaoensis* **n. sp.** and *R. adolfocaesaris* **n. sp.** (p = 0.007), *R. aquaticus* (p < 0.001), and *R. minutus* **n. sp.** (p = 0.002), but not with *Rallus montivagorum* **n. sp.** (p = 0.262).

The MANOVA of tarsometatarsus lengths (total length and distal width; traits 26 and 29) showed that *R. carvaoensis* **n. sp.** has a shorter tarsometatarsus than in *R. lowei* **n. sp.** (11%) (p = 0.003), *R. montivagorum* **n. sp.** (11%) (p < 0.001), and *R. aquaticus* (26%) (p < 0.001), but it is longer than in *R. minutus* **n. sp.** (p < 0.001). The tarsometatarsus distal width of *R. carvaoensis* **n. sp.** is shorter than in *R. lowei* **n. sp.** (p < 0.001) and *R. aquaticus* (p < 0.001), but similar to *R. montivagorum* **n. sp.** (p = 0.795) and *R. minutus* **n. sp.** (p = 0.871). The length and distal width of the tarsometatarsus of *R. carvaoensis* **n. sp.** is similar to *R. adolfocaesaris* **n. sp.** (U = - 1,837; p = 0.085, U = - 1,829; p = 0.067), whereas its proximal width is narrower than in *R. lowei* **n. sp.** (U = 3.337; p < 0.001), but similar to *R. adolfocaesaris* **n. sp.** (U = - 0,155; p = 0.94), *R. montivagorum* **n. sp.** (U = - 0,907; p = 0.388), *R. minutus* **n. sp.** (U = -1.533; p = 0.145) and *R. aquaticus* (U = - 1,911; p = 0.057).

The leg bones of *R. carvaoensis* **n. sp.** indicate that it was more stout than *Rallus aquaticus*. The low humerus-to-femur length ratio (0.76) –the smallest among all the species here described—is clearly indicative of flightlessness. The short stout tarsometatarsus (relative to the femur) suggests that *R. carvaoensis* **n. sp.** could be a slow-pace runner

Rallus montivagorum

Rallus montivagorum **n. sp.** has a longer coracoid (14%) and humerus (23%) than *R. carvaoensis* **n. sp.** from São Miguel (U = -2.448; p = 0.007, U = -2.714; p = 0.002) and *R. minutus* **n. sp.** from São Jorge (34% and 35%), and a smaller coracoid than *R. aquaticus* ($F_{1,54}$ = 167.293; p = < 0.001, $F_{1,53}$ = 123.804; p = 0.001) (16% and 13% respectively). The ulna is longer (16%) than in *R. lowei* **n. sp.** and in *R. minutus* **n. sp.** (60% longer; U = -2.646; p = 0.003) (Table 1), but smaller (15%) than in *R. aquaticus* ($F_{1,50}$ = 124.784; p = < 0.001). The carpometacarpus is longer (27%) than in *R. carvaoensis* **n. sp.** and *R. minutus* **n. sp.** (71%) (Table 1), but shorter (12%) than in *R. aquaticus* (U = -4.861, p < 0.001). The femur length is similar to *R. lowei* **n. sp.**, *R. adolfocaesaris* **n. sp.** and *R. carvaoensis* **n. sp.** (Table 1) (p = 0.601), but shorter (13%) than in *R. aquaticus* (U = -6.709, p < 0.001). The tibiotarsus of *R. montivagorum* **n. sp.** is close in length to that of *R. lowei* **n. sp.** and *R. carvaoensis* **n. sp.**, but it is slightly longer than in *R. adolfocaesaris* **n. sp.** (Table 1), and shorter (16%) than in *R. aquaticus* ($F_{1,51}$ = 153,334, p < 0.001). The MANOVA of traits 26 and 29 showed that *R. montivagorum* **n. sp.** has a longer (12%) tarsometatarsus than *R. carvaoensis* **n. sp.** (p < 0.001) and *R. minutus* **n. sp.** (29% longer; p < 0.001), being similar in total length to that of *R. lowei* **n. sp.** (p = 0.734), but shorter (17%) than in *R. aquaticus* (p < 0.001). The distal

tarsometatarsus width is narrower than in *R. lowei* **n. sp.** and *R. aquaticus* (p < 0.in both cases), but similar to *R. carvaoensis* **n. sp.** and *R. minutus* **n. sp.** (p = 0.795 and p = 0.678 respectively). *R. montivagorum* **n. sp.** has a similar tarsometatarsus length (U = -1.095; p = 0.309), distal (U = - 1.048; p = 0.310), and proximal width (U = -0.334; p = 0.748) to *R. adolfocaesaris* **n. sp.**

The humerus+ulna+carpometacarpus to femur length ratio (2.2:1) and the humerus-to-femur length ratio (0.94) indicates that *R. montivagorum* **n. sp.** was a species capable of flying, although with this capability somewhat reduced, as suggested by the small sternum, which in turn displays a shortened carina sterni (Figure 10).
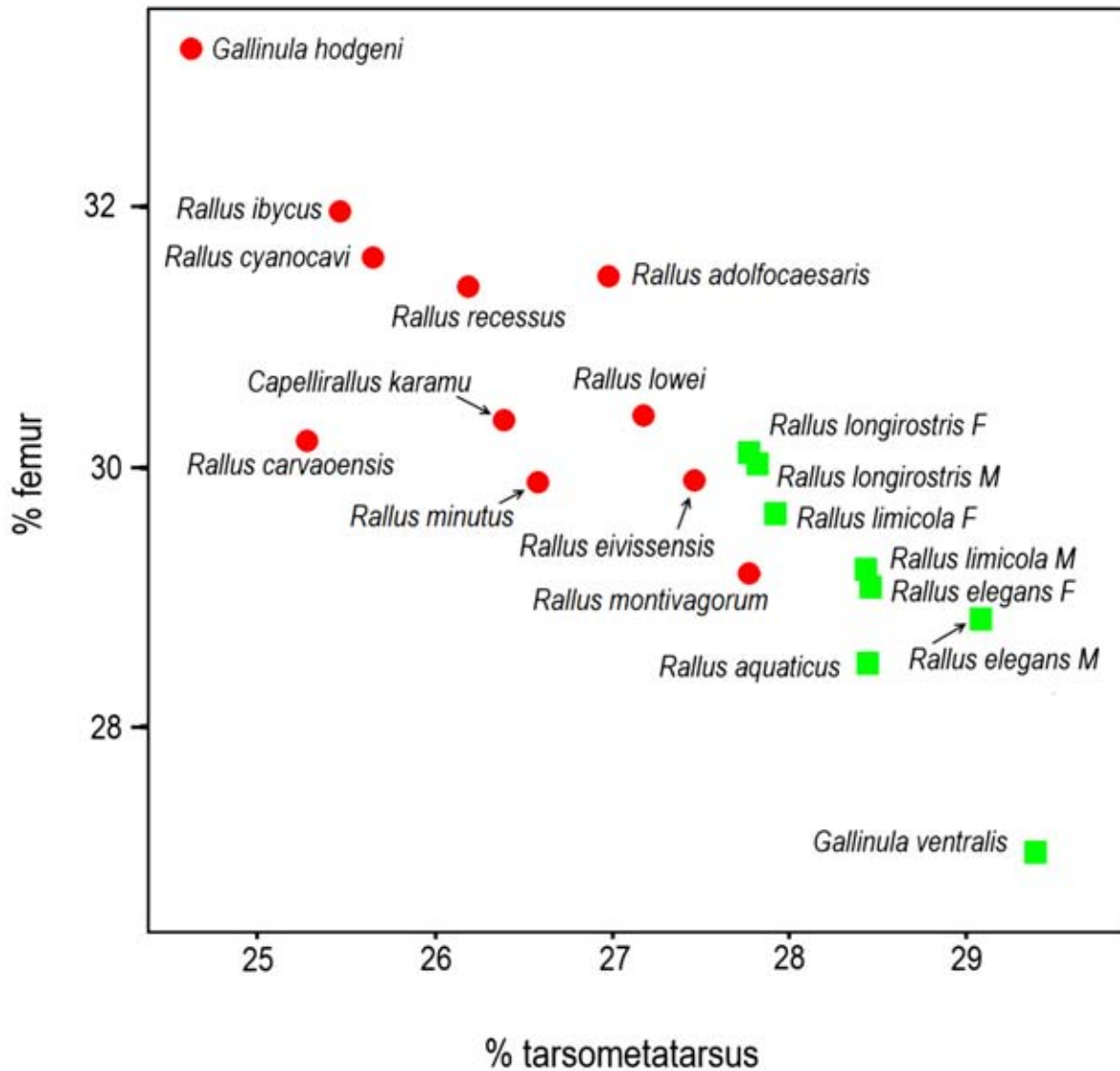
FIGURE 21. Plot of percentage of femur vs. tarsometatarsus length in relation to total length of the leg bones (femur+tibiotarsus+tarsometatarsus) of the Macaronesian rail taxa and other extinct (circles) and extant (squares) rails. Data from Table 2.

Rallus minutus

R. minutus **n. sp.** is one of the most distinctive species found. It is a dwarf rail, the smallest among the Macaronesian species, only slightly larger than *Atlantisia rogersi*, with robust leg bones (especially tarsometatarsus) and reduced wings. Its bill is relatively curved and the bill to total skull length ratio is slightly larger than in *R. aquaticus*. A long and curved bill in insular rails might be related to foraging by probing in soft soil, deep litter and mosses, as suggested elsewhere for *Capellirallus karamu* from New Zealand (Worthy and Holdaway 2002).
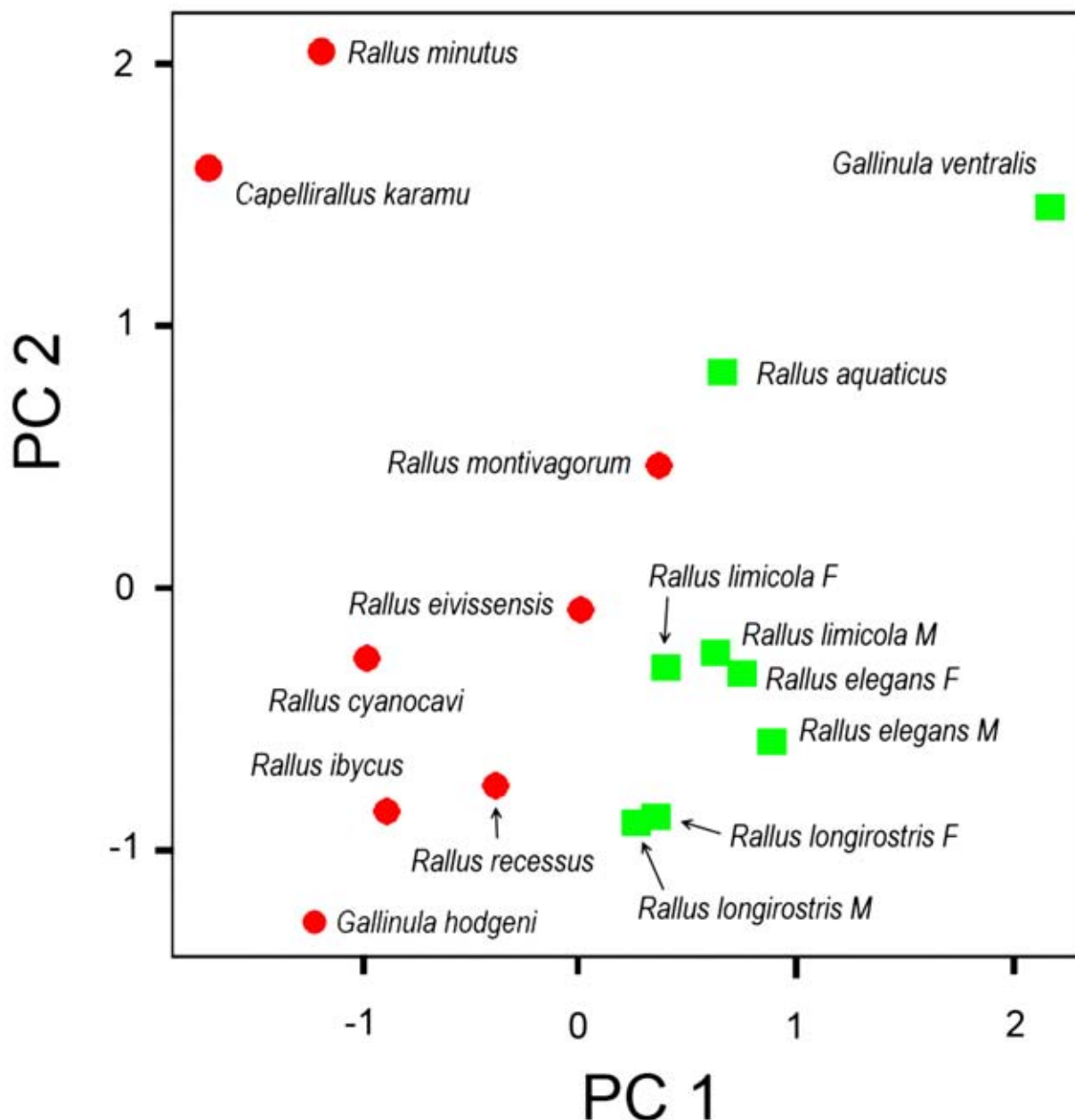
FIGURE 22. PCA plot for the two principal components obtained from wing (humerus, ulna and carpometacarpus) and leg bone (femur, tibiotarsus and tarsometatarsus) proportions of extinct (circles) and extant (squares) rails. Data from Table 2.

The bones of *R. minutus* **n. sp.** are generally similar to those of *R. aquaticus*, but differ considerably in size and proportions. All the bones are clearly shorter than their respective *R. aquaticus* counterparts. *R. minutus* **n. sp.** combines reduced wing bones (mainly carpometacarpus and ulna) with relatively short and massive leg bones (mainly tarsometatarsus). The humerus, ulna and carpometacarpus are 35%, 47% and 49% shorter than in *R. aquaticus*, while the femur, tibiotarsus and tarsometatarsus are 28%, 28% and 36% shorter.

R. minutus **n. sp.** has a shorter coracoid, scapula, humerus, ulna and carpometacarpus than in *R. montivagorum* **n. sp.** and *R. aquaticus*. The reduction of humerus length is of about 26% compared to the coracoid and 35% with respect to the scapula. The ulna is smaller than in *R. lowei* **n. sp.** (28%), *R. montivagorum* **n. sp.** (37%; U = -2.646; p = 0.003) and *R. aquaticus* (47%; U = -2.838; p < 0.001). The carpometacarpus is 42% and 49% shorter than in *R. montivagorum* **n. sp.** and *R. aquaticus* respectively (the carpometacarpus of *R. lowei* **n. sp.** is not available). *R.*

minutus **n. sp.** also exhibits the most reduced *carina sterni* of all the Macaronesian rails. The carpometacarpus is much shorter relative to the humerus (Cmc/H=0.44) than in the rest known species of *Rallus* (including *R. cyanocavi*), which is an indication of extremely weak development of primary flight feathers.
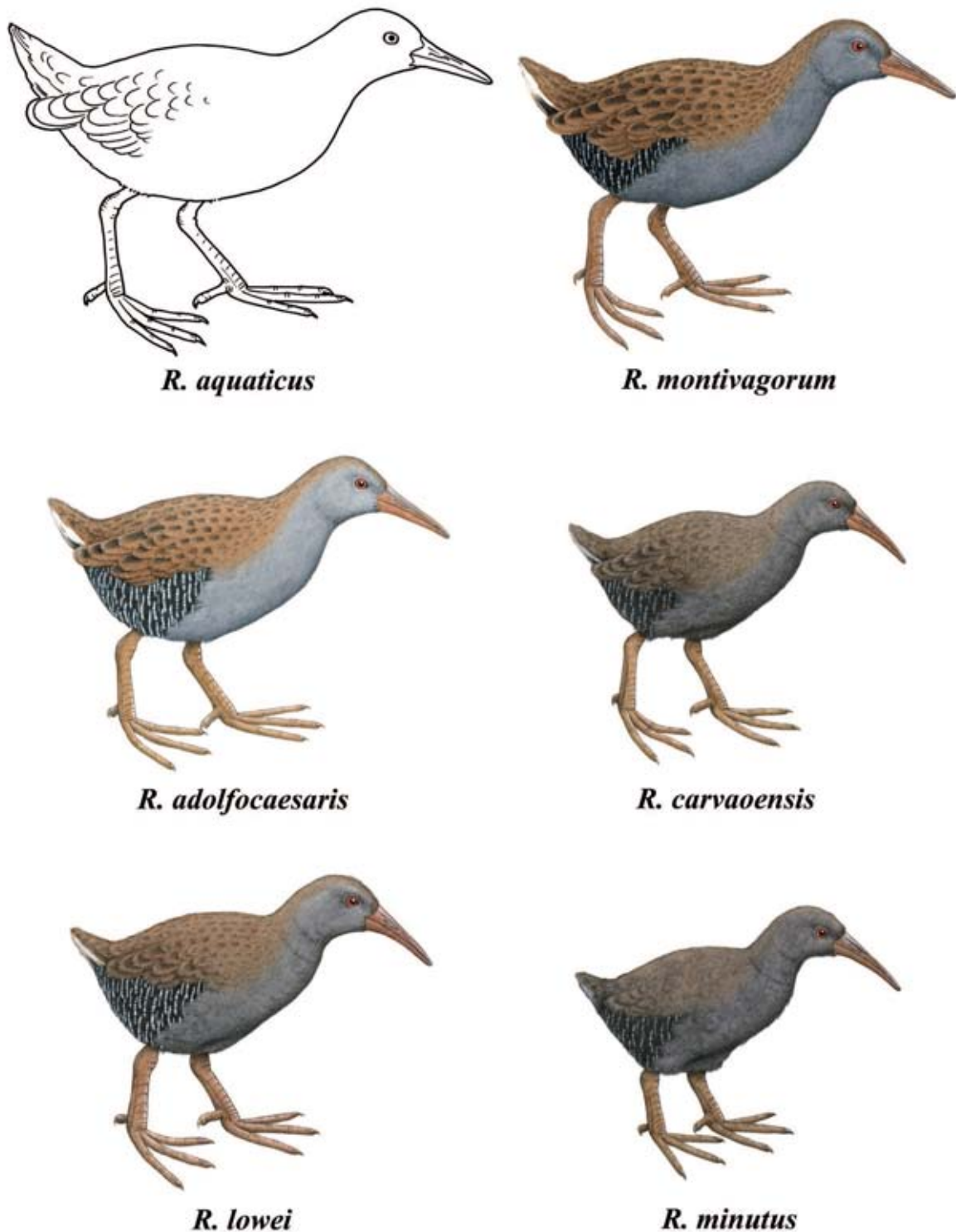
FIGURE 23. Artist reconstruction of the *Rallus* species described. Colours are speculative. Art: Pau Oliver.

The femur and the tibiotarsus are shorter than in *R. lowei* **n. sp.** (22% and 14%, respectively), *R. adolfocaesaris* **n. sp.** (23% and 10%), *R. carvaoensis* **n. sp.** (18% and 13%), *R. montivagorum* **n. sp.** (17% and 14%) and *R. aquaticus* (28% for both bones). The tarsometatarsus is robust (Figure 17). This bone is shorter than in *R. lowei* **n. sp.** (47% smaller), *R. carvaoensis* **n. sp.** (13%), *R. montivagorum* **n. sp.** (23%; $p < 0.005$ in the three

cases) and *R. adolfocaesaris* **n. sp.** (20%; U = -2.236; p = 0.036). In addition, the tarsometatarsus distal width is smaller than in *R. lowei* **n. sp.** (p < 0.001) and *R. aquaticus* (p = 0.001), but similar to *R. carvaoensis* **n. sp.** (p = 0.871), *R. montivagorun* **n. sp.** (p = 0.678) and *R. adolfocaesaris* **n. sp.** (U = -1.167; p = 0.262).

The humerus-to- length to femur length ratio (0.84) and the humerus+ulna+carpometacarpus to femur length ratio (1.8:1) show that *R. minutus* **n. sp.**, was a flightless species (Livezey 2003).

The Figure 21 shows the femur vs. tarsometatarsus relative lengths, in relation to total length of leg bones, in the Macaronesian taxa and other extant and extinct rails (Table 2). This plot shows that rails with a tarsometatarsus relative length above 27.5% survive, the only exception being the extinct *R. montivagorum* **n. sp.** from Pico (Figure 21). The PCA performed on the proportions of hind and forelimb bones (Table 2; Figure 22) produced two principal components explaining 88.6% of the total variance. 64.1% is explained by PC1, which shows a high positive weighting for ulna, carpometacarpus and tarsometatarsus, and a high negative weighting for humerus and femur proportions. PC2 explains 24.5% of the variance and shows a high positive weighting for tibiotarsus, and a moderate negative weighting for ulna and femur proportions. All the extinct species score zero or below on PC1 with the only exception of *R. montivagorum* n.sp (the only flying species among the Macaronesian rails).

Discussion

Here we describe the first five endemic rail species known from Macaronesia. The presence of rails in the remote archipelagos of the Azores and Madeira fits well with the fact that these birds are among the species more prone to reach remote islands and to evolve into endemic and flightless birds (Olson 1977; Livezey 2003; Steadman 2006). Our study draws attention to the absence of these birds from the fossil record of Canary Islands. The apparent absence of endemic rails in the Canary Islands could be related to the fact that this archipelago lies too close to the mainland (ca. 100 km). However, the distance separating the eastern Canary Islands (Fuerteventura and Lanzarote) from the mainland is not enough to prevent rails from reaching them (as documented by the recent sporadic records of *Rallus aquaticus* on these islands; Martin & Lorenzo 2001). Moreover, theshort distance separating the Canary islands from the mainland would not impede the differentiation of endemic species, as demonstrated by endemic rails on the Mediterranean island of Eivissa, placed only 95 km far from the Iberian mainland, and devoid of terrestrial mammals during the Pleistocene (McMinn *et al.* 2005). Instead, we suggest that the presence of an endemic rodent on the eastern Canary islands, *Malpaisomys insularis*, might have been a key factor precluding the evolution of an ancient insular population of rails. The central Canary Islands (Tenerife and Gran Canaria) also harboured insular endemic rodents (genus *Canariomys*) during the Pleistocene, and no endemic rails have been found there thus far. Finally, the apparent absence of rails in the fossil record of the rodent-free western Canary Islands (La Gomera, La Palma and El Hierro) suggests that these islands could have been out of the regular dispersal zones of rails flying over the Atlantic. Thus, we consider that the Canarian archipelago might never have harboured any endemic species of rail, due to the combined effect of the presence of rodents on the eastern and central islands and the remote placement of the remaining Canary Islands. In contrast, the recurrent presence of rails in the Madeiran and Azorean islands suggests that extinct rail species await to be discovered on other Azorean islands (like Faial, and perhaps Corvo and Flores), and on the Desertas. Additionally it is probable that future research will allow new species of rails to be described from the islands dealt with in this article.

The distribution of the genus *Rallus* is similar to that of the genus *Otus* in Macaronesia. Two extinct species of Scops owls are known from these archipelagos: *O. mauli* Rando, Pieper, Alcover & Olson, 2012 from Madeira and *O. frutuosoi* Rando, Alcover, Olson & Pieper, 2013 from São Miguel Island (Azores). However this genus is absent, both as a current breeder and in the fossil record, from the other Macaronesian archipelagos (Illera *et al*. 2012).

The leg bone proportions of *R. lowei*, *R. adolfocaesaris, R. carvaoensis* and *R. minutus* are close to those of other extinct flightless rails like *R. recessus* from Bermuda Island (Olson & Wingate 2001) and *Capellirallus karamu* from New Zealand (Olson 1975) (Table 2; Figure 21). In addition, *R. lowei*, *R. carvaoensis* and *R. minutus* have very robust leg bones, suggesting that they evolved in a convergent way and had a similar lifestyle. However, leg bone proportions of *R. montivagorum* differ from these species and are close to those of current flying species like *R. limicola* and *R. elegans* (Table 2; Figure 21). This similarity is also observed in the PCA analysis where the results for *R. montivagorum* are closer to current flying species than to extinct flightless birds (Table 2; Figure 22).

TABLE 2. Mean length (mm) and proportions (%) of each limb bone of extant and extinct (†) rails: mean length (M) of limb bones (H: humerus; Ul: ulna; Car: carpometacarpus; F: femur; Tbt: tibiotarsus; Tmt: tarsometatarsus). f: female; m: male. Data from this paper, Steadman et al. (2013) and Olson (1975).

	†Rallus lowei n. sp.		†R. adolfocaesaris n. sp		†R. carvaoensis n. sp.		†R. montivagorum n. sp.		†R. minutus		†R. eivissensis	
	M	%	M	%	M	%	M	%	M	%	M	%
H	-	-	-	-	27.41	-	33.8	42.62	25.1	47.59	34.8	43.66
Ul	22.9	-	-	-	-	-	26.6	33.58	16.6	31.55	27.2	34.10
Cmc	-	-	-	-	14.94	-	18.9	23.80	11.0	20.86	17.7	22.24
F	38.1	30.38	38.6	31.46	36.3	30.19	35.8	29.30	29.8	29.79	37.3	29.92
Tbt	52.2	42.47	51.1	41.59	53.5	44.50	54.3	42.85	43.8	43.76	53.1	42.61
Tmt	34	27.15	33.1	26.96	30.4	25.31	34.1	27.85	26.4	26.45	34.3	27.47

	†R. recessus		†R. cyanocavi		†R. ibycus		†R. longirostris[m]		†R. longirostris[f]		R. elegans[m]		R. elegans[f]		†R. limicola[m]	
	M	%	M	%	M	%	M	%	M	%	M	%	M	%	M	%
H	42.7	43.39	39.9	45.44	32.3	44.92	56.6	42.88	54.6	42.49	61.5	41.98	56.3	41.89	37	42.24
Ul	34.1	33.86	29.3	33.37	24.8	34.49	45.9	34.77	44.6	34.71	51.1	34.88	47.2	35.12	30.4	34.7
Cmc	22.9	22.74	18.6	21.18	14.8	20.58	29.5	22.35	29.3	22.80	33.9	23.14	30.9	22.99	20.2	23.06
F	49.1	31.41	45.1	31.60	37.9	31.96	56	30.07	54.1	30.11	61	28.83	56.1	29.11	37.6	29.15
Tbt	66.3	42.42	61	42.75	50.5	42.58	78.4	42.11	75.7	42.13	89	42.06	81.8	42.45	54.7	42.4
Tmt	40.9	26.17	36.6	25.65	30.2	25.46	51.8	27.82	49.9	27.77	61.6	29.11	54.8	28.44	36.7	28.45

	R. limicola		Gallinula ventralis		†G. hodgeni		†Capellirallus karamu		R. aquaticus	
	M	%	M	%	M	%	M	%	M	%
H	34.7	42.58	54.9	37.45	40.4	44.74	25.9	49.52	38.9	42.36
Ul	28.1	34.48	52	35.47	29.4	32.56	16.3	31.17	31.4	34.22
Cmc	18.7	22.94	39.7	27.08	20.5	22.7	10.1	19.31	21.5	23.42
F	35.4	29.65	55.3	27.02	57.9	33.22	46.5	30.31	41.3	28.49
Tbt	50.7	42.46	89.4	43.67	73.5	42.17	66.5	43.35	62.5	43.07
Tmt	33.3	27.89	60	29.31	42.9	24.61	40.4	26.34	41.3	28.44

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The ratio humerus+ulna+carpometacarpus to femur length ratio in *R. montivagorum* (2.2:1) is similar to those of flying rails (*R. longirostis* and *R. limicola*, 2.3:1; *R. elegans*, 2.4:1; *R. aquaticus*, 2.2:1) and larger than those of *Atlantisia rogersi* (1.7:1)—a flightless rail that survives on Inaccessible Island (14 km^2), where alien mammals have not been introduced (BirdLife International 2012). In the same way, the humerus/femur length ratio in *R. montivagorum* (0.94) is very close to those of flying rails (*R. longirostis* and *R. elegans*, 1.01; *R. limicola*, 0.98; *R. aquaticus*, 0.94) whereas these ratios for *R. lowei*, *R. norhonai*, *R. carvaoensis* and *R. minutus* (0.78, 0.85, 0.76 and 0.84 respectively) are close to those of other extinct insular rails like *R. recessus*, *R. cyanocavi*, *R. ibycus* (0.87, 0.88 and 0.85) and to those of *Atlantisia rogersi* (0.78) (data from Table 2 and Olson 1973b).

These morphological traits and bone proportions support the conclusion that *R. minutus*, *R. carvaoensis*, *R. adolfocaesaris* and *R. lowei* were flightless birds and each inhabited only a single island (São Jorge, São Miguel, Porto Santo and Madeira respectively), as other flightless rails did (e.g., McMinn et al 2005; Steadman et al 2013). In contrast, *R. montivagorum* was a flying rail, although with a somewhat reduced flying ability and it probably lived at least on the islands of Pico and Faial (a still paleontologically unexplored island). Both were merged between 30 and 14 kyr during this period of lower sea level (Rijsdijk *et al*. 2014).

The presence of flying and flightless species of *Rallus* on geographically close islands of the Azores, suggest independent colonization events from the continent rather than a single origin with subsequent radiation. This idea is supported by the fact that multiple colonization events by several modern avian genera have taken place in Macaronesia (i.e., *Regulus*, *Erithacus* and *Fringilla*; Dietzen *et al*. 2003; Päckert *et al*. 2006; Rando *et al*. 2010).

Endemic species of *Rallus* from Macaronesia, like many other island naive vertebrates, probably disappeared quickly after the arrival of humans and the introduction of alien species to the islands. The extinction of several species of endemic vertebrates due to human perturbations has been documented in the Canary Islands (Rando & Alcover 2008, 2010; Rando *et al*. 2008, 2012a, 2012b), and has been suggested as the reason for the extinction of endemic scops owls in Madeira and São Miguel islands (Rando *et al*. 2012b, 2013). The young age (3,200 ± 40 years BP) of the cave Algar do Carvão (Forjaz *et al*. 2004), where remains of *Rallus* sp. B have been found in Terceira, indicate a very recent extinction event for this unnamed species. The ages obtained from *R. montivagorum* **n. sp.** bones from Furna das Torres provide the most recent evidence of survival of an endemic rail in Macaronesia (Lab code: RICH 21396; 489±29 BP, 1405–1450 cal AD), documenting that the rail from Pico Island survived until at least the arrival of Portuguese colonizers in the first half of the 15th century (Newitt 2005).

Acknowledgements

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