



<http://dx.doi.org/10.11646/zootaxa.4057.2.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:BADD5843-1566-4BF8-A507-7369C1F5B950>

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

JOSEP ANTONI ALCOVER¹, HARALD PIEPER², FERNANDO PEREIRA³ & JUAN CARLOS RANDO⁴

¹Departament de Biodiversitat i Conservació, Institut Mediterrani d'Estudis Avançats, Cr Miquel Marquès 21, 07190 Esporles, Mallorca, Balearic Islands (Spain). E-mail: jaalcover@imedea.uib-csic.es

²Ulmenstr. 21, D-24223 Schwentinental (Germany). E-mail: orunzehpieper@condaservices.com

³Centre for Ecology, Evolution and Environmental Changes (Ce3C) and Azorean Biodiversity Group, Universidade dos Açores, Rua Capitão João d'Ávila, Pico da Urze, 9700-042 Angra do Heroísmo, Terceira, Açores, Portugal. E-mail: morcegomaluco@gmail.com

⁴Departamento de Biología Animal (UDI Zoología), Universidad de La Laguna E-38206, La Laguna, Tenerife – Canary Islands (Spain). E-mail: canariomys@yahoo.es; jcrando@ull.es

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 carvaensis* 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. carvaensis* 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 capacidade de 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 encontramos fósseis de Frangos-de-água. Em três das ilhas encontramos material suficiente para uma descrição adequada das suas espécies de Frango-de-água actualmente extintos. *Rallus montivagorum* n. sp., com reduzida capacidade de voo, mais pequeno que *Rallus aquaticus*, viveu na ilha do Pico. *Rallus carvaensis* 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, descrevemos um fóssil notável de um *Rallus* encontrado no Algar do Carvão na ilha Terceira.

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. Sarmiento "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.

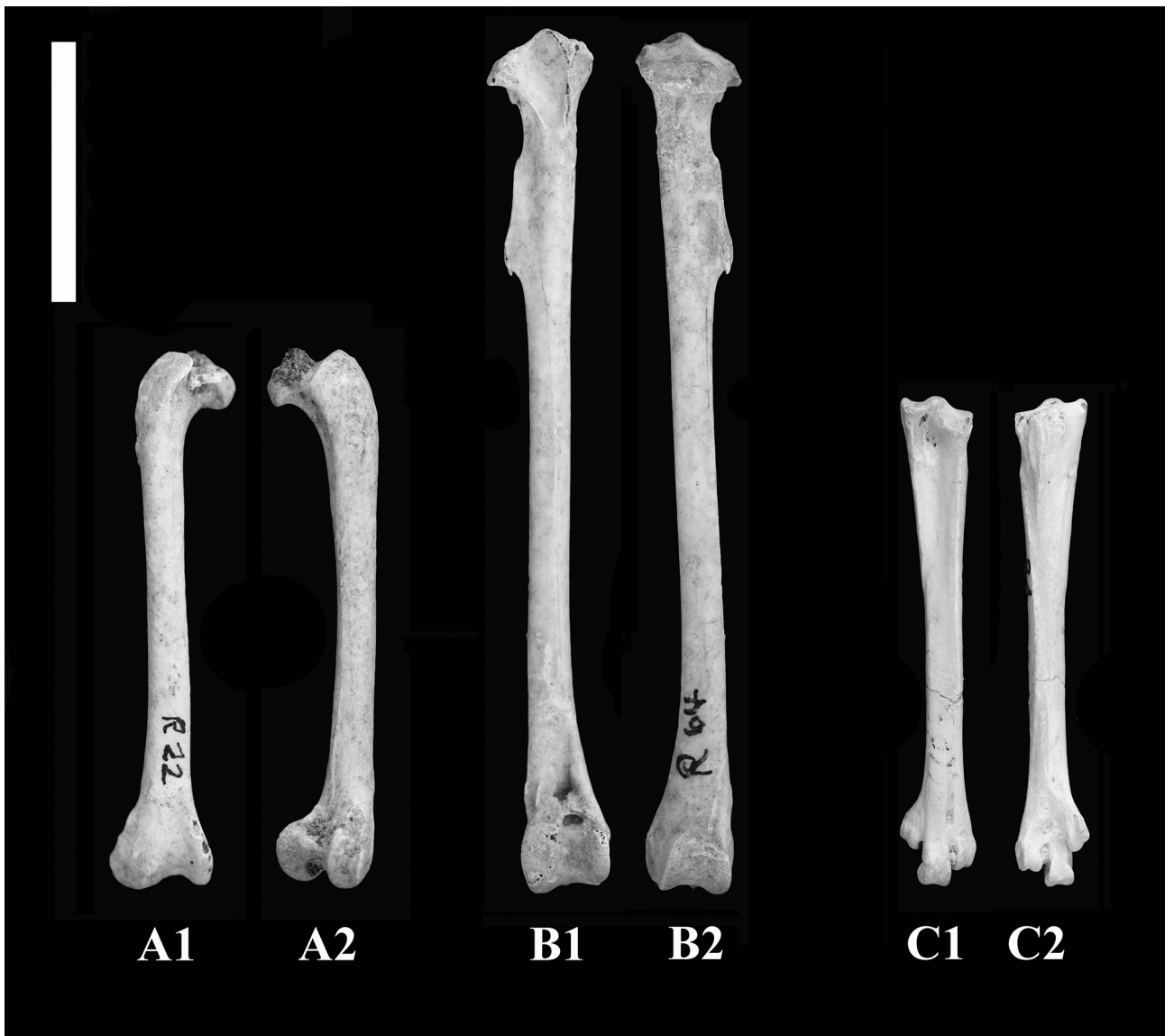


FIGURE 4. Bones of *Rallus* sp. from Madeira and Porto Santo. **A**, MMF 43479, R femur (1, cranial view; 2, caudolateral view). **B**, MMF 43478, R tibiotarsus (1, cranial view; 2, caudal view). **C**, MMF 43480, L tarsometatarsus. (1, dorsal view; 2, plantar view). Scale bar: 2 cm.

PART 2. RAILS FROM THE ARCHIPELAGO OF THE AZORES

Rallus carvaensis, 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 carvaensis* 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): Humerus—length: 28.5, 28.6; proximal width: 6.2, 6.3; minimum shaft width: 1.9, 1.9; distal width: 4.1, 4.1. Ulna—minimum shaft width: 1.2, 1.3; distal width: 2.4, -. Femur—length: -, 36.0; minimum shaft width: ~2.0, ~2.0; distal width: ~5.0, ~7.0. Tibiotarsus—minimum shaft width: 2.5, 2.5; distal width: 4.6, 4.6. Tarsometatarsus—length: -, 31.7; minimum shaft width: 2.6, 2.5; distal width: -, 5.5. Scapula—length: 25.6, -; proximal width: 3.6, -.

Type locality and collection information: Gruta do Carvão, São Miguel; all the material of *R. carvaensis* **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. adolfocesaris* **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): Humerus—length 32.9, proximal width 6.7, minimum shaft width 2.2, distal width 4.7. Ulna—length: 25.8; proximal width: 3.1; proximal diameter: 2.9; minimum shaft width—2.0; distal width: 3.0. Carpometacarpus—length: 16.8; proximal width: 4.2; distal width: 2.4. Femur—length: 35.8; proximal width: 5.7; minimum shaft width: 2.5; distal width: 5.6. Tibiotarsus—total length: 55.0; medial length: 53.1; proximal width: 5.7; minimum shaft width: 2.4; distal width: 4.9. Tarsometatarsus—length: 33.3; proximal width: 5.1; minimum shaft width: 2.4; distal width: 5.0. Scapula—length: 29.0; proximal width: 4.5. Coracoid: length: 16.8. Cranial length (without the bill)—26.8; cranial width: 14.9; interorbitalium width: 3.7; cranial height:

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

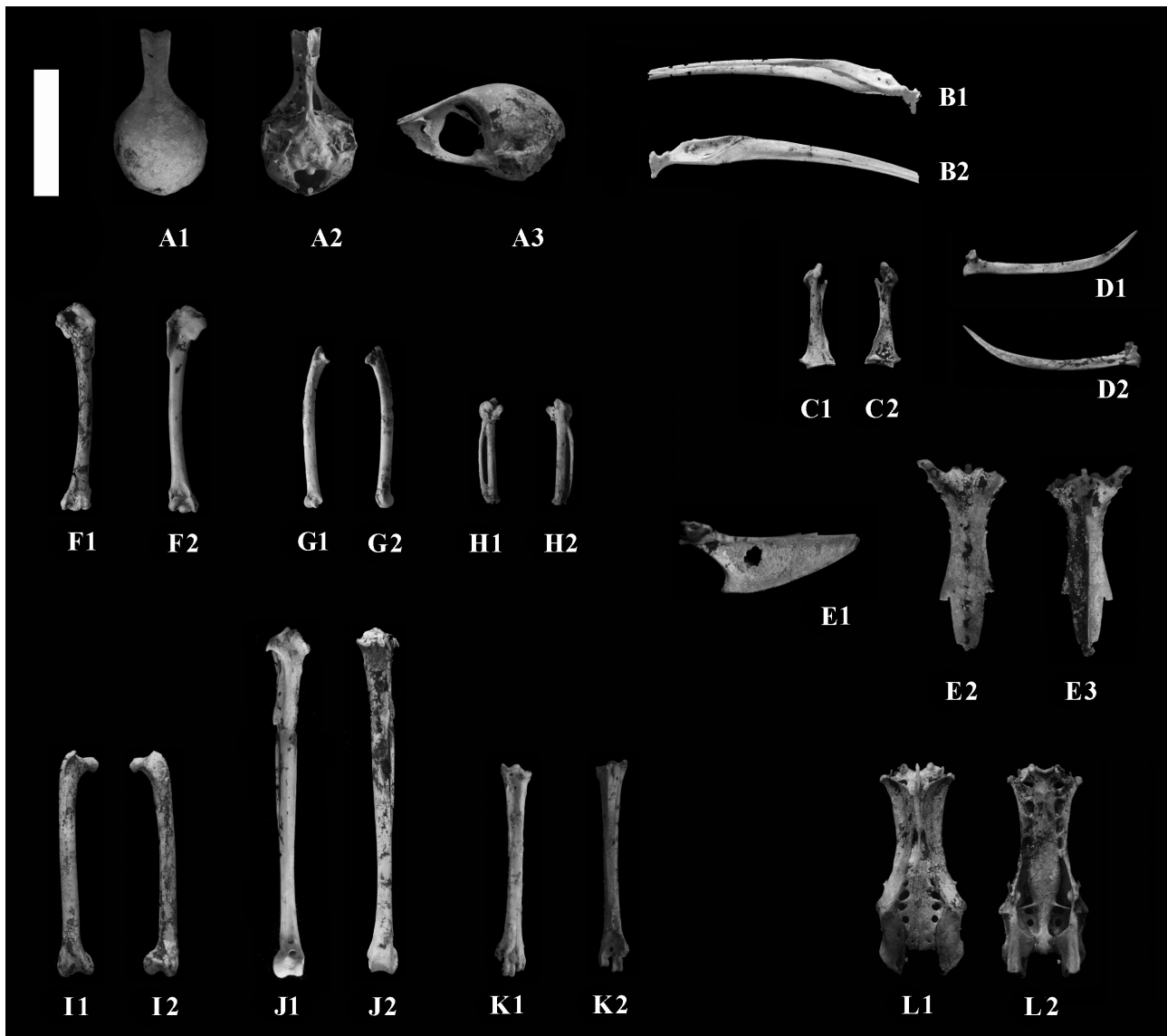


FIGURE 6. Bones of the associated skeleton of the holotype of *Rallus montivagorum* n. sp. **McMa 1831.014.** **A**, skull (1, dorsal view; 2, ventral view; 3, lateral view). **B**, mandible. **C**, R coracoid (1, ventral view; 2, dorsal view). **D**, R scapula (1, lateral view; 2, internal view). **E**, 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 ¹⁴C 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. carvaensis* 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.

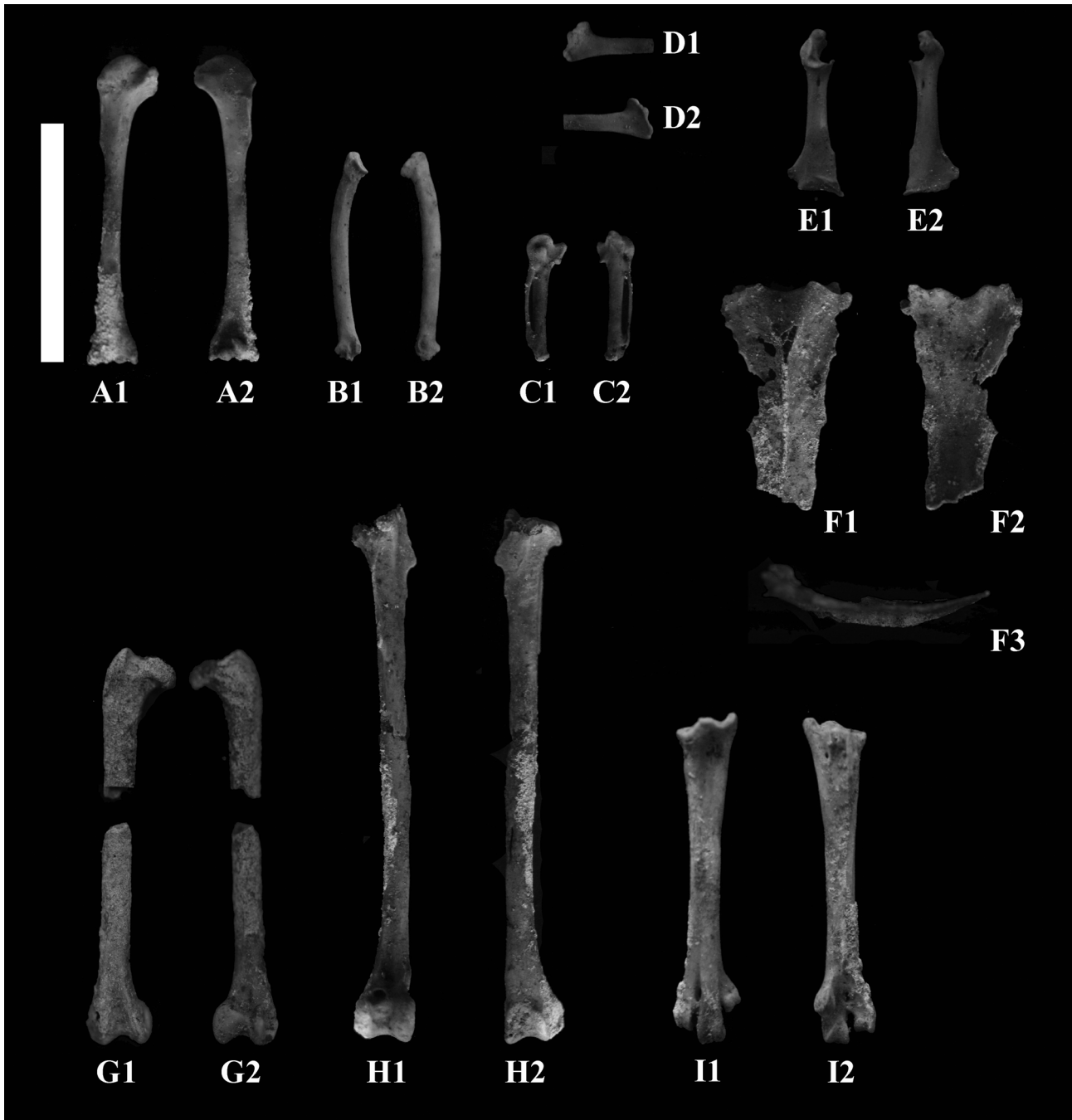


FIGURE 7. Bones of the associated skeleton of the holotype of *Rallus minutus* n. sp. MCMa 1950.014. **A**, L humerus (1, caudal view; 2, ventral view). **B**, L ulna (1, ventral view; 2, dorsal view). **C**, L carpometacarpus (1, ventral view; 2, dorsal view). **D**, R scapula (1, lateral view; 2, internal 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.

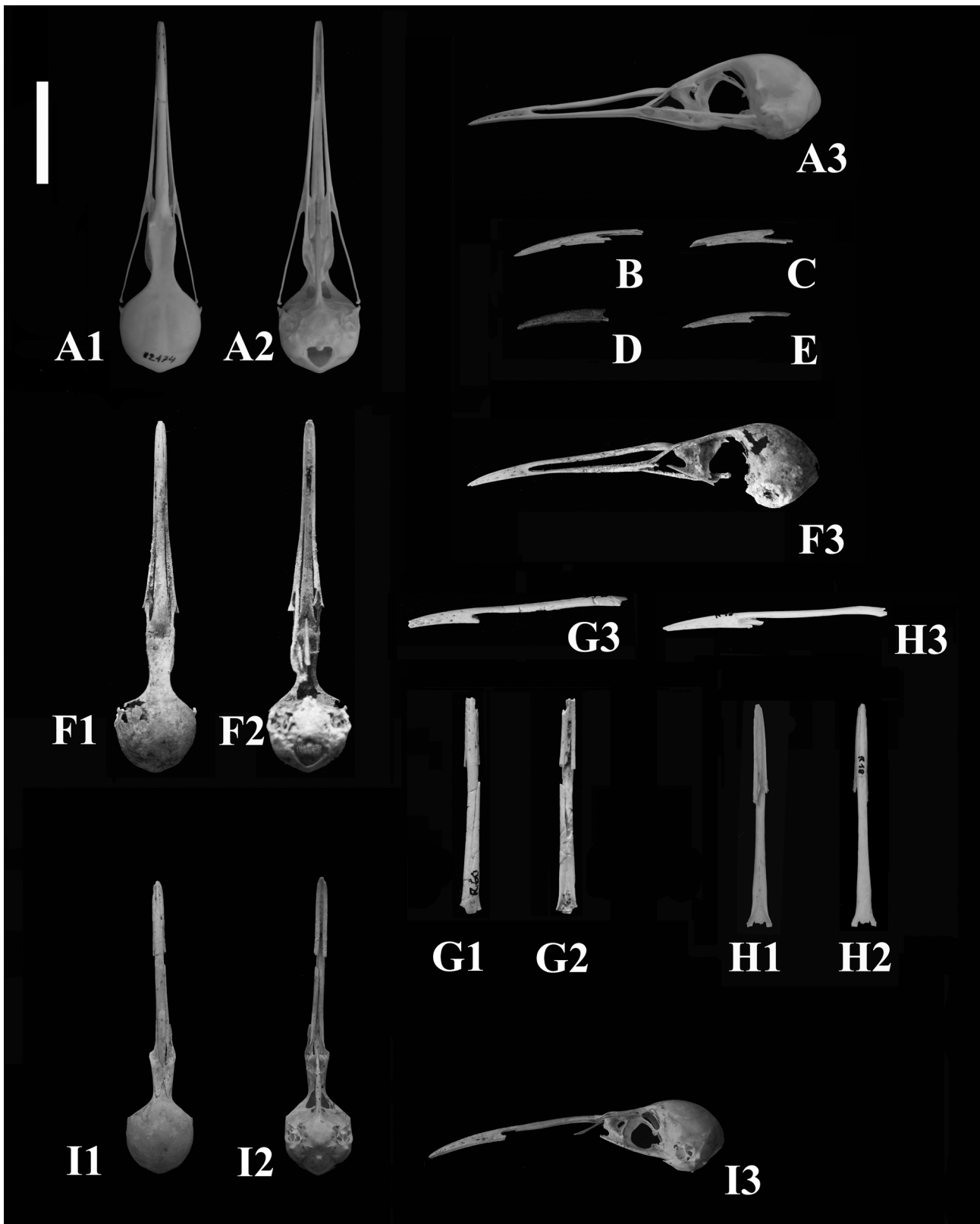


FIGURE 8. Skulls and premaxillae of *Rallus* spp. **A**, *Rallus aquaticus* IMEDEA 12474. **B**, *Rallus carvaoensis* n. sp. IMEDEA 104069. **C**, *Rallus carvaoensis* n. sp. MCMa 1801.013. **D**, *Rallus carvaoensis* n. sp. MCMa 1804.013. **E**, *Rallus carvaoensis* n. sp. MCMa 1812.013. **F**, *Rallus 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.

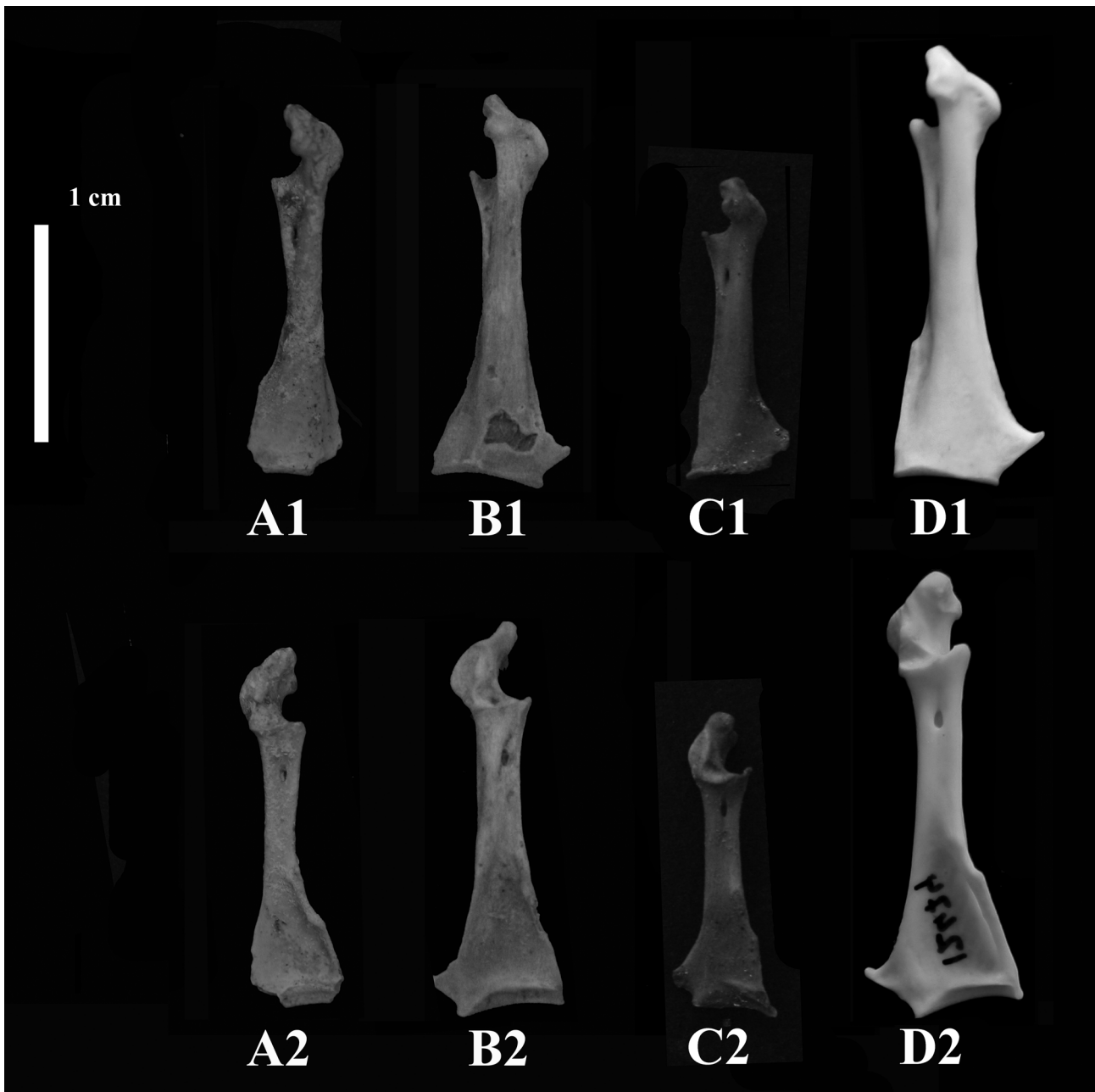


FIGURE 9. Coracoidea of *Rallus* spp. **A**, *Rallus carvaensis* n. sp., MCMa 1805.013, R coracoid (specular image). **B**, *Rallus montivagorum* n. sp., MCMa 1913.04, L coracoid. **C**, *Rallus minutus* n. sp., MCMa 1950.014, **D**, *Rallus aquaticus* IMEDEA 12474, R coracoid (specular image). 1, ventral 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. Tibiotarsus—minimum shaft width: 2.2; distal width: 5.0. Tarsometatarsus—total length: 27.3; proximal width: 5.0; minimum shaft width: 2.5; distal width: 5.5. Scapula—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).

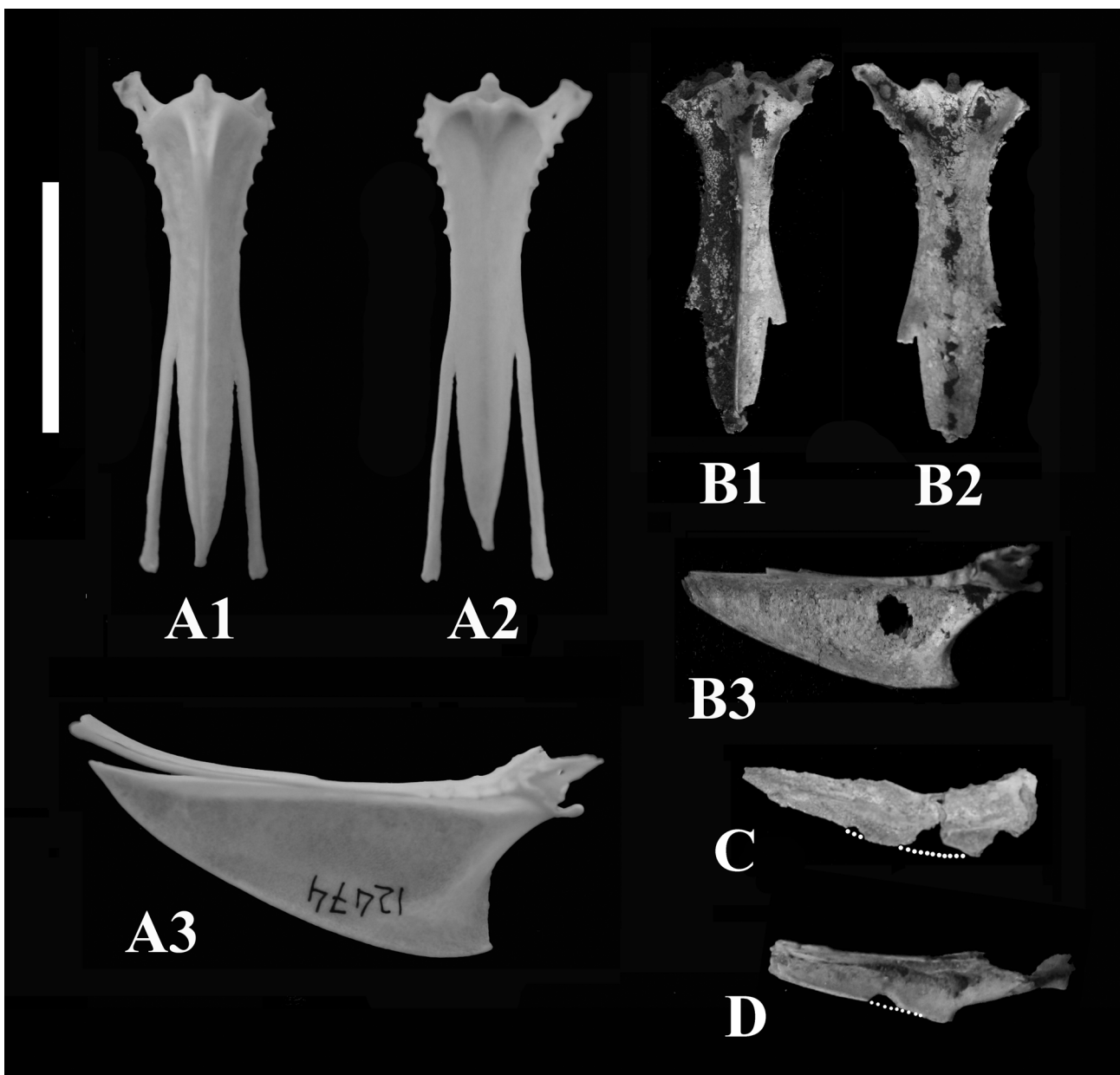


FIGURE 10. Sterna of *Rallus* spp. **A.** *Rallus aquaticus*, IMEDEA 12474. **B.** *Rallus montivagorum* n. sp., MCMa 1831.014, Pico. **C.** *Rallus carvaensis* n. sp., MCMa 1805.013. **D.** *Rallus minutus* n. sp., MCMa 1951.014. 1, ventral view. 2, dorsal view. 3, lateral view. Scale bar: 2 cm.

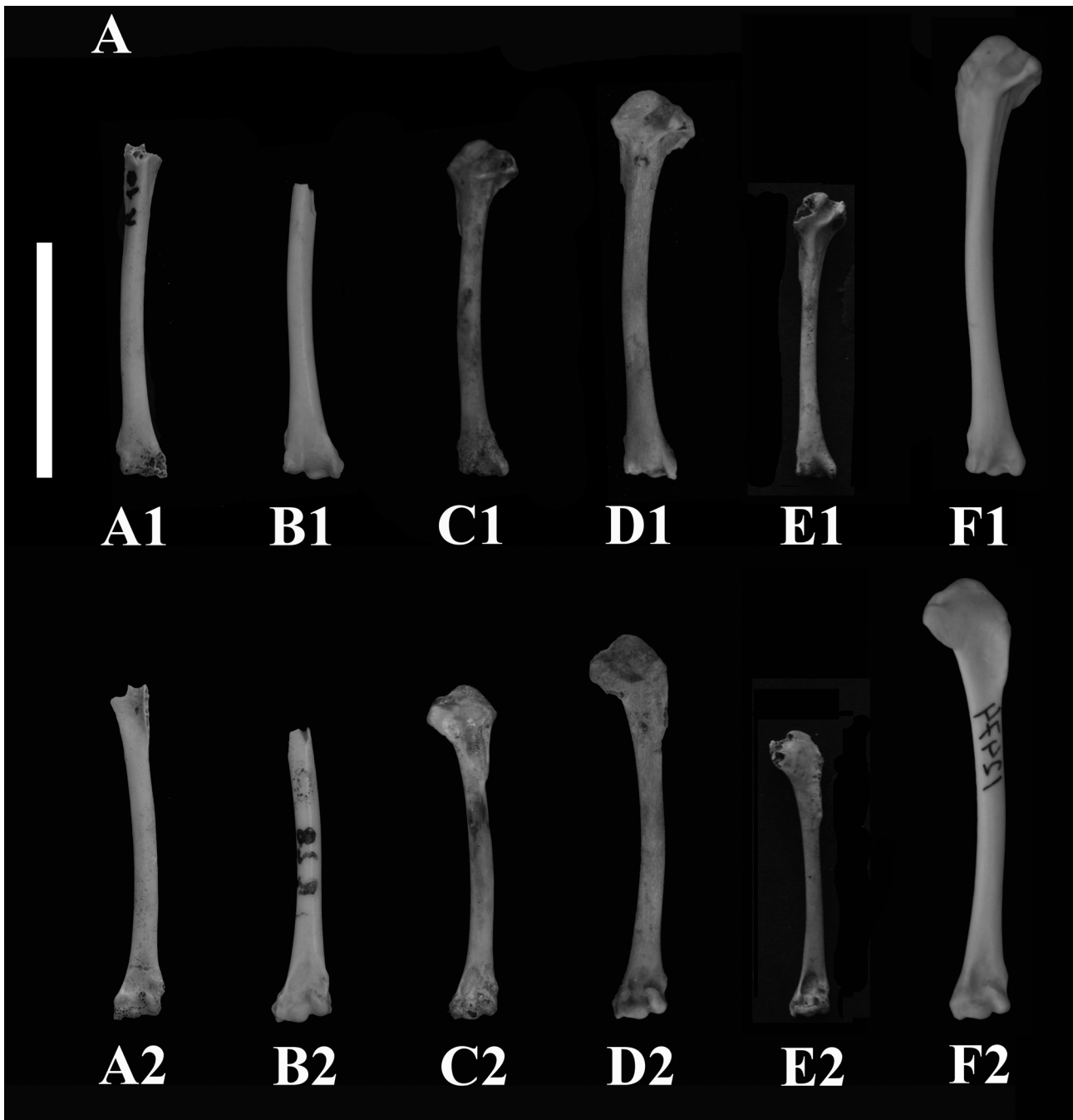


FIGURE 11. Humeri of *Rallus* spp. **A**, *Rallus lowei* n. sp., MMF 43414, L humerus (paratype). **B**, *Rallus adolfcaesaris* n. sp., MMF 43451, R humerus (specular image) (paratype). **C**, *Rallus carvaensis* n. sp., MCMa 1801.013, R humerus (specular image). **D**, *Rallus montivagorum* n. sp., 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 (Figure 17). 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.

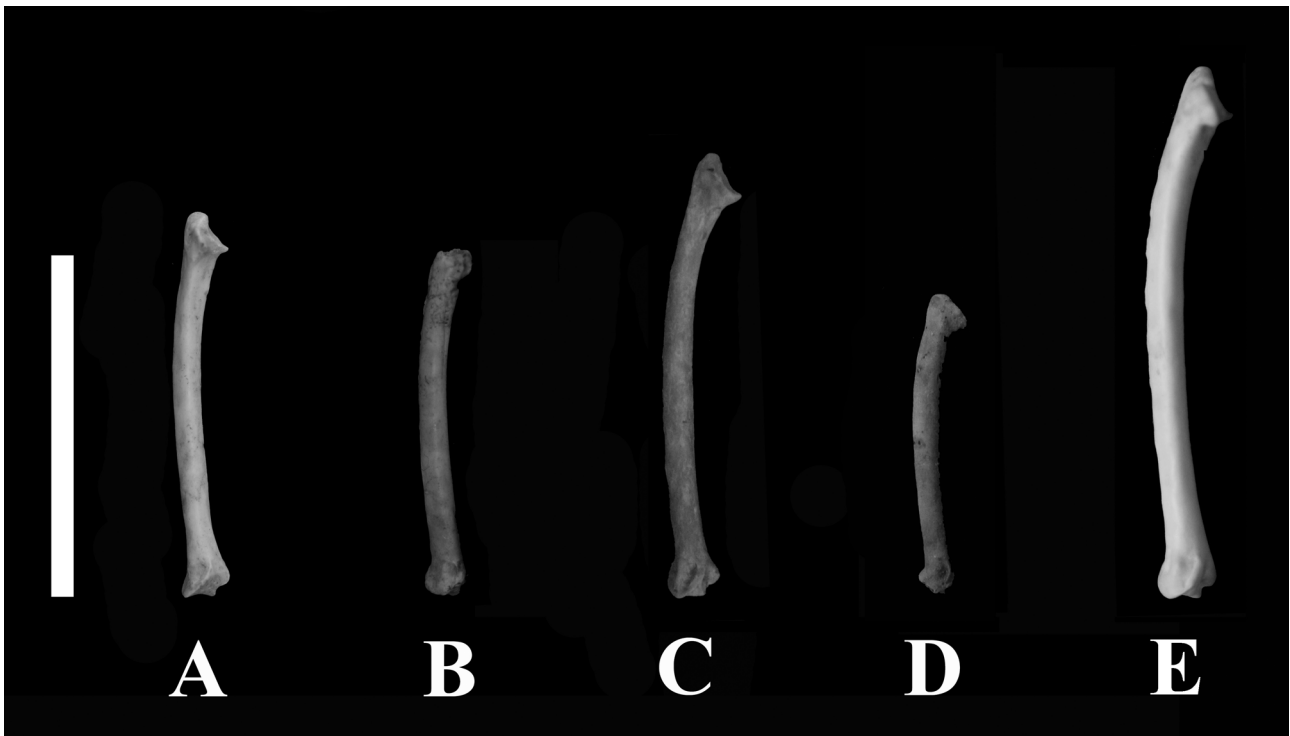


FIGURE 12. Ulnae of *Rallus* spp., dorsal view. **A**, *Rallus lowei* n. sp., MMF 43415, R ulna (paratype). **B**, *Rallus carvaensis* n. sp., MCMa 1801.013, R ulna. **C**, *Rallus montivagorum* n. sp., MCMa 1867.014, L ulna (specular image). **D**, *Rallus minutus* n. sp., MCMa 1950.014, L ulna (specular 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.

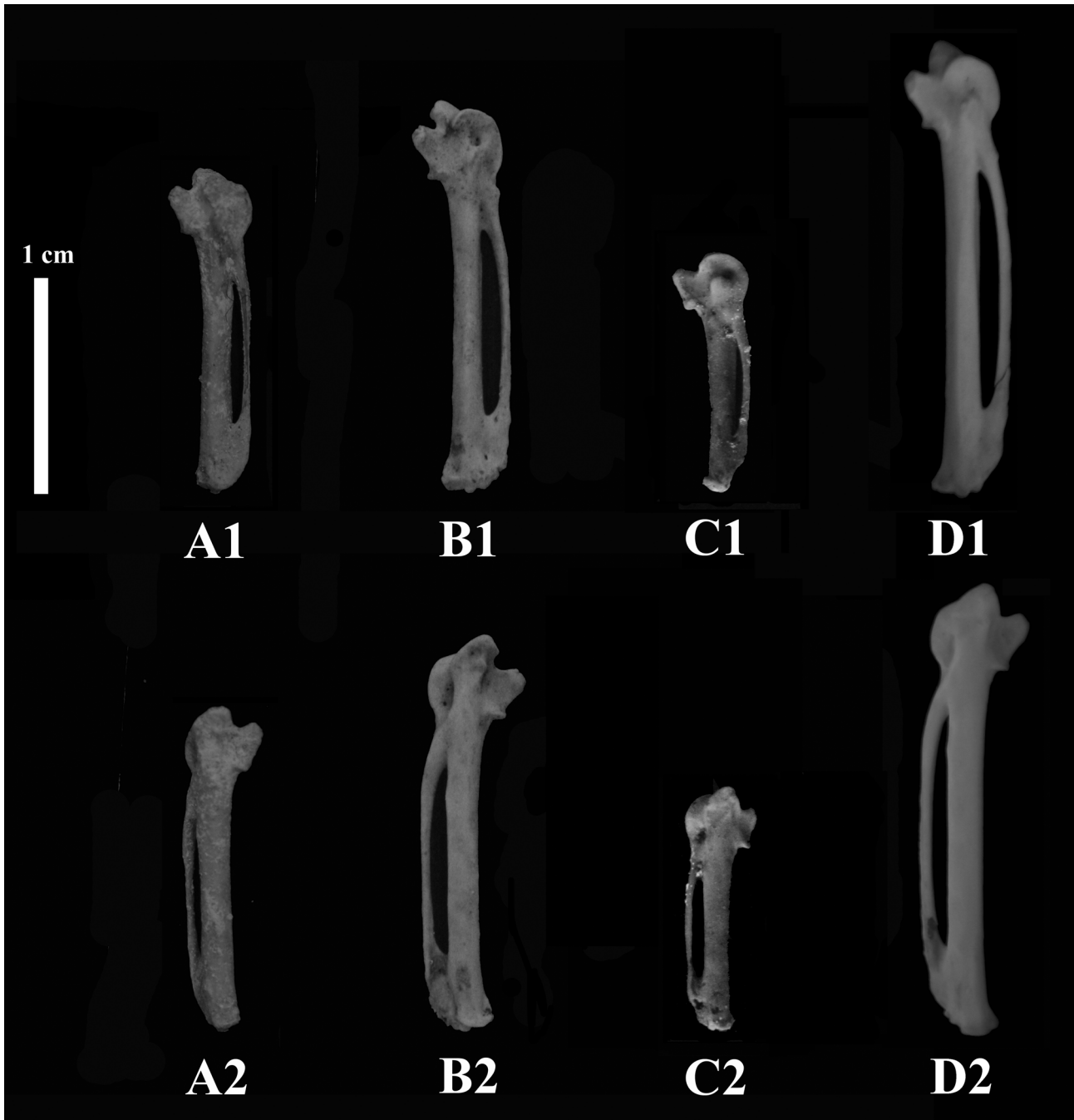


FIGURE 13. Carpometacarpi of *Rallus* spp. **A**, *Rallus carvaensis* n. sp., MCMa 1805.013, R carpometacarpus. **B**, *Rallus montivagorum* n. sp., MCMa 1856.014, R carpometacarpus. **C**, *Rallus minutus* n. sp. MCMa 1950.014, L carpometacarpus (specular image). **D**, *Rallus aquaticus* IMEDEA 12474. 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 vert, 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 carvaensis* 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 tibia-tarsus (paratype) (specular image). **B**, *Rallus adolfocaesaris* n. sp., MMF 43447, L tibia-tarsus, (paratype). **C**, *Rallus carvaoensis* n. sp., IMEDEA 104068, L tibia-tarsus. **D**, *Rallus montivagorum* n. sp., IMEDEA 104097, R tibia-tarsus (specular image). **E**, *Rallus minutus* n. sp. MCMa 1951.014, R tibia-tarsus (specular image). **F**, *Rallus aquaticus*, IMEDEA 12474, R tibia-tarsus (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.

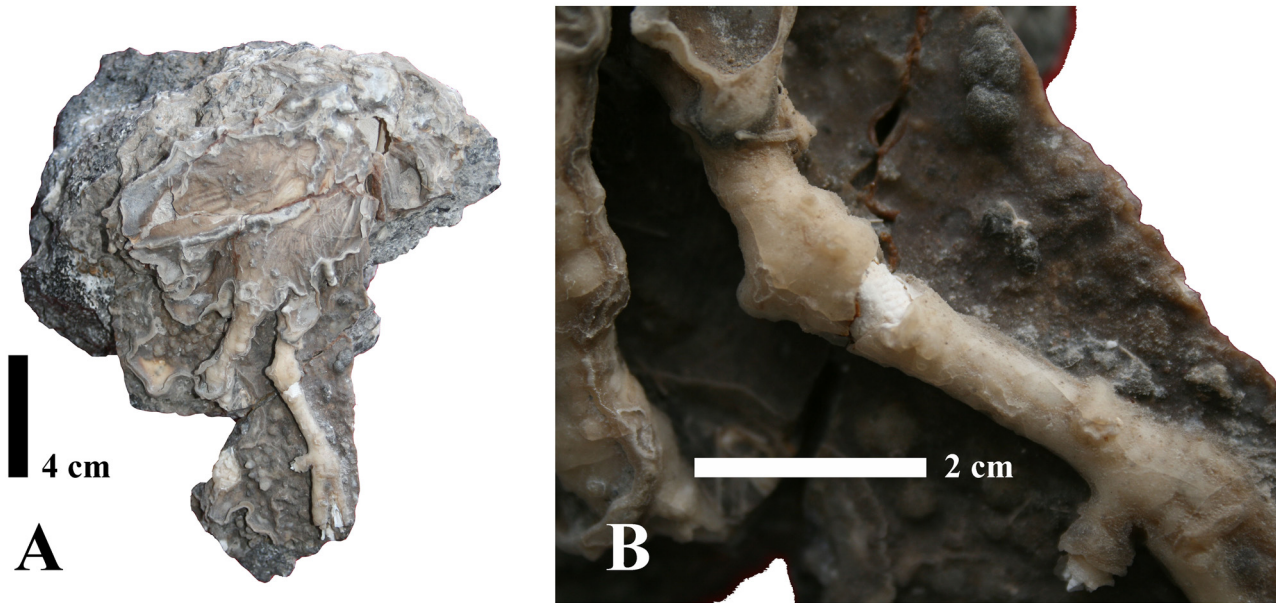


FIGURE 18. Photograph of a silicified specimen of *Rallus* sp. B from Algar do Carvão, Terceira. **A.** General view. **B.** Detail of the tarsometatarsus. The scales of the tarsometatarsus are visible in the section free of silica. Scale bar of **A**: 4 cm. Scale bar of **B**: 2 cm.

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. The silica 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 \approx 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.

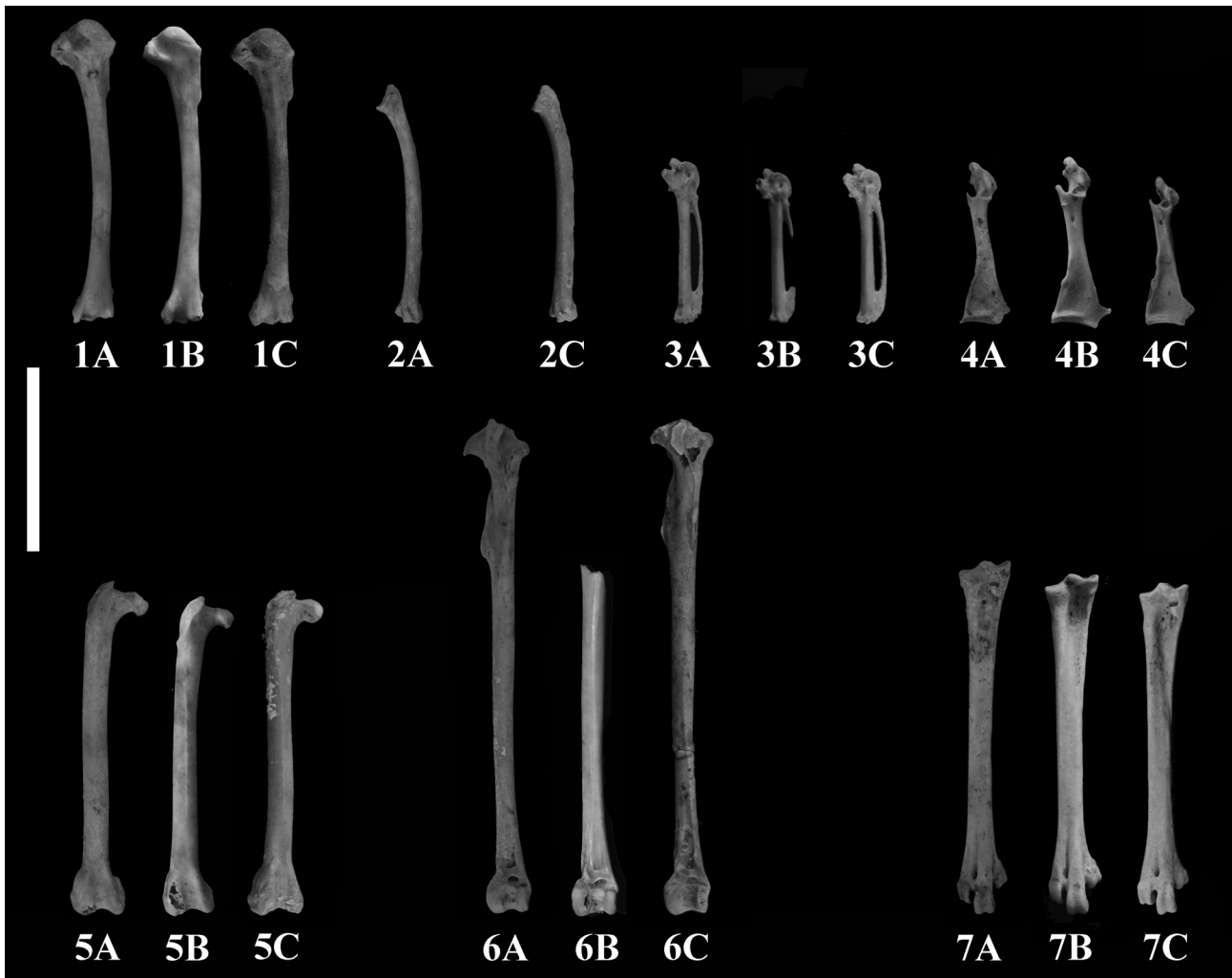


FIGURE 19. Bones of *Rallus* sp. A from Graciosa (**B**) and *Rallus* sp. B from Terceira (**C**) compared with the same bones of *Rallus montivagorum* n. sp. from Pico (**A**). From L to R: Humerus, caudal view: MCMa 1943.014; MCMa 1961.04 (L humerus, specular image), MCMa 1821.013. Ulna, dorsal view: 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 referred 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

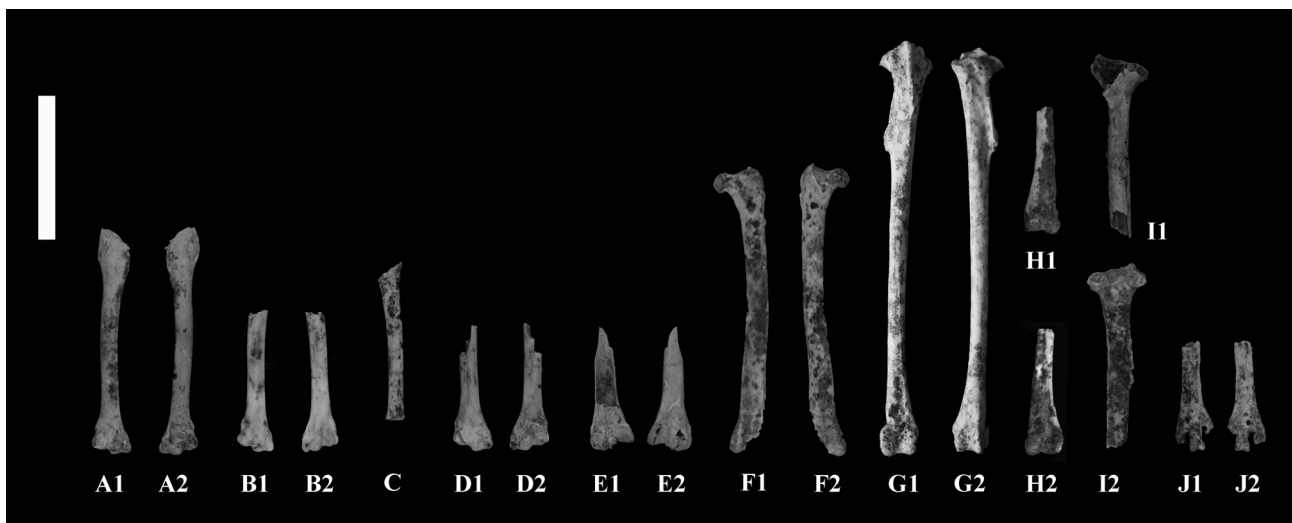


FIGURE 20. Material of *Rallus* sp. C from Santa Maria. **A**, **DBUAF 1080**, L humerus (1, caudal view; 2, cranial view). **B**, **R-1**, L humerus (1, caudal view; 2, cranial view). **C**, **R-3**, L humerus (cranial view). **D**, **R-2**, L humerus (1, caudal view; 2, cranial view). **E**, **MCMa 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. carvaensis* 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. adolfocaezaris* 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. carvaensis* 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. carvaensis 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 tarsometatarsus similar in length to *R. montivagorum n. sp.* ($p = 0.734$), longer (12%) than in *R. carvaensis 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. carvaensis 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. carvaensis 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%, $U = -2.236$; $p = 0.036$) than in *R. minutus n. sp.* No differences were detected in tarsometatarsus 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 carvaensis

R. carvaensis **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. carvaensis **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. carvaensis* **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. carvaensis* **n. sp.** and *R. aquaticus* ($p < 0.001$) (12%), but not between *R. carvaensis* **n. sp.** and the *Rallus* from Pico ($p = 0.601$). The tibiotarsus of *R. carvaensis* **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. carvaensis* **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. carvaensis* **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. carvaensis* **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. carvaensis* **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. carvaensis* **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. carvaensis* **n. sp.** could be a slow-pace runner

Rallus montivagorum

Rallus montivagorum **n. sp.** has a longer coracoid (14%) and humerus (23%) than *R. carvaensis* **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. carvaensis* **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. carvaensis* **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. carvaensis* **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. carvaensis* **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).

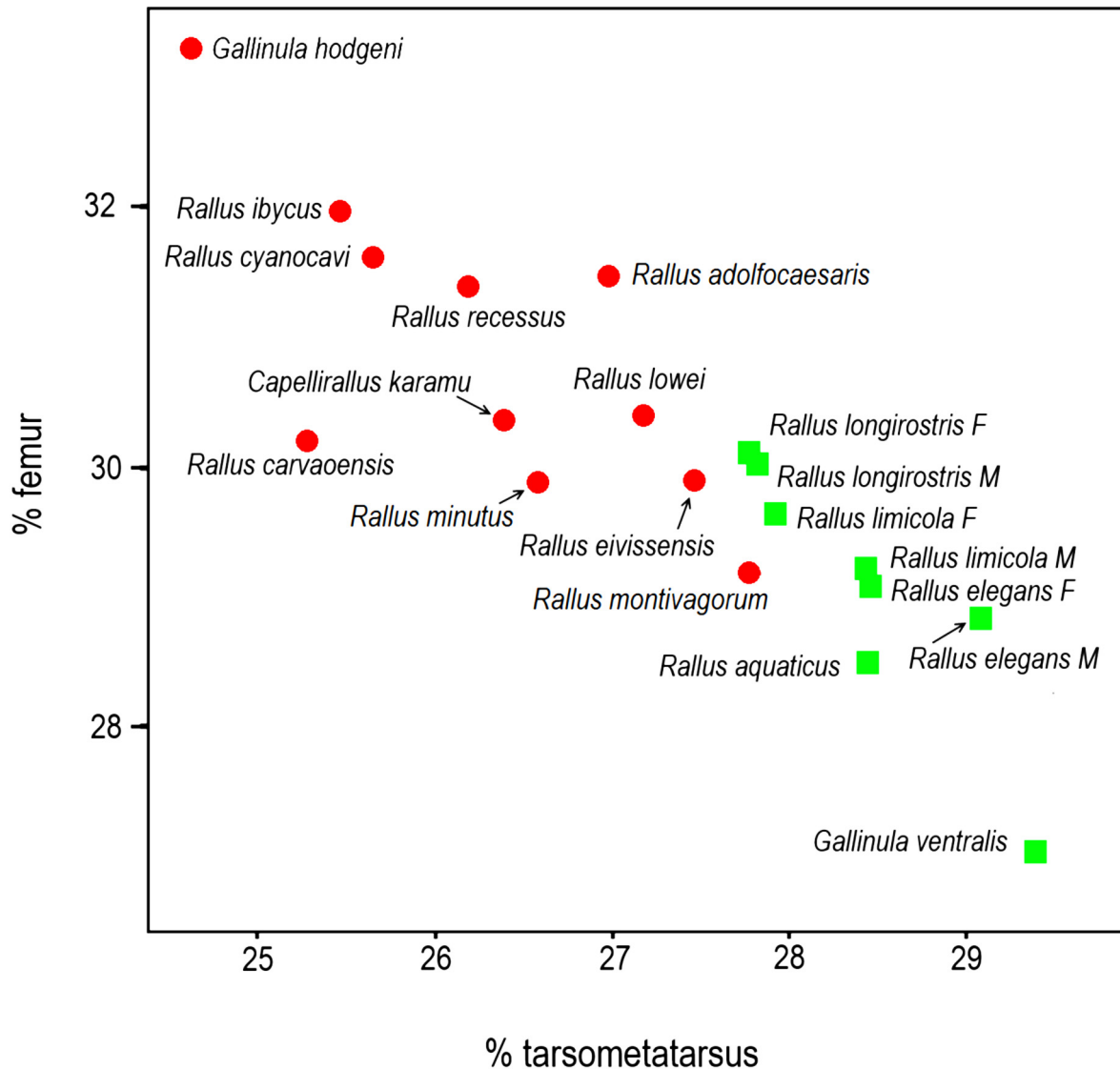


FIGURE 21. Plot of percentage of femur vs. tarsometatarsus length in relation to total length of the leg bones (femur+tibiotarsus+tarsometatarsus) of the Macaronesian rail taxa and other extinct (circles) and extant (squares) rails. Data from Table 2.

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).

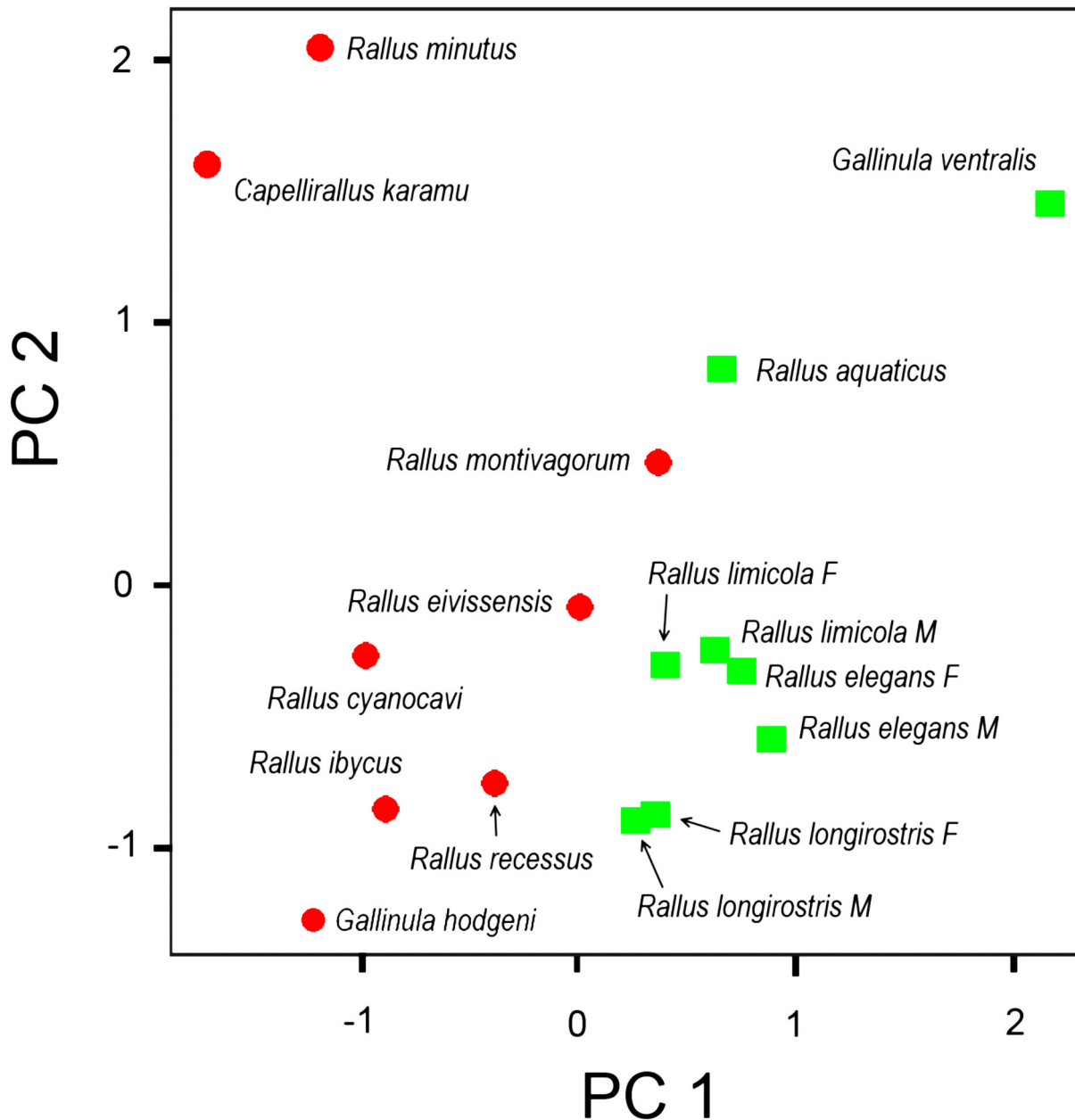


FIGURE 22. PCA plot for the two principal components obtained from wing (humerus, ulna and carpometacarpus) and leg bone (femur, tibiotarsus and tarsometatarsus) proportions of extinct (circles) and extant (squares) rails. Data from Table 2.

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.

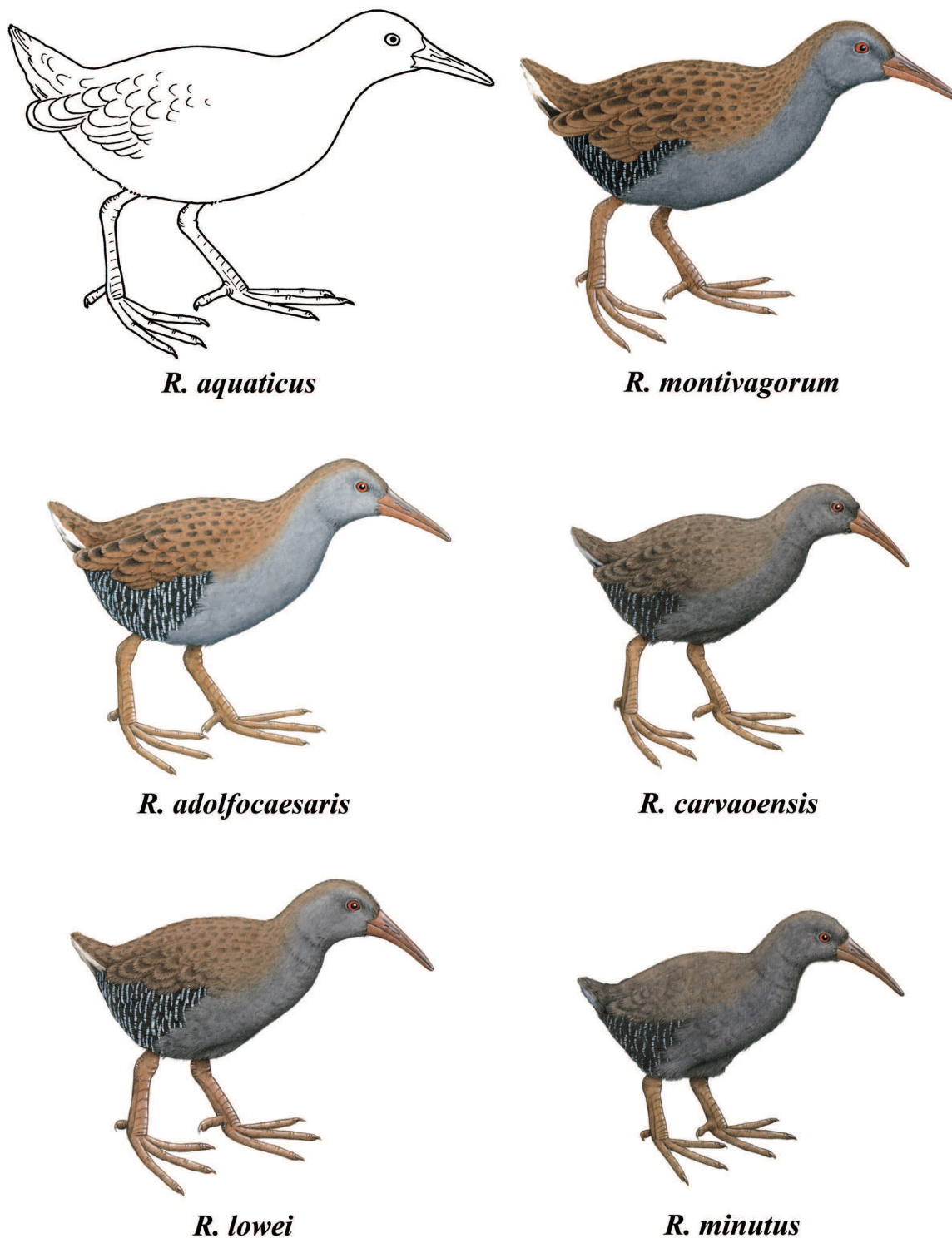


FIGURE 23. Artist reconstruction of the *Rallus* species described. Colours are speculative. Art: Pau Oliver.

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. carvaensis* **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. carvaensis* **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. montivagorum* **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, the short 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. maui* Rando, Pieper, Alcover & Olson, 2012 from Madeira and *O. fruticosi* 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).

	† <i>Rallus lowei</i> n. sp.		† <i>R. adolfocesaris</i> n. sp.		† <i>R. carvaensis</i> n. sp.		† <i>R. montivagorum</i> n. sp.		† <i>R. minutus</i>		† <i>R. eivissensis</i>	
	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

	† <i>R. recessus</i>		† <i>R. cyanocavi</i>		† <i>R. ibycus</i>		† <i>R. longirostris</i> [†]		† <i>R. longirostris</i> ^m		† <i>R. elegans</i> ^m		† <i>R. elegans</i> ^f		† <i>R. limicola</i> ^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

	<i>R. limicola</i> ^f		<i>Gallinula ventralis</i>		† <i>G. hodgengi</i>		† <i>Capellirallus karamu</i>		<i>R. aquaticus</i>	
	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

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 km²), 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. carvaensis* 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. carvaensis*, *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

We thank Dr J.C. Illera for his assistance with the statistical analysis. Himself, Elisa Blanco (Tenerife), Miquel Trias (Mallorca), Enric Torres (Eivissa), Dra Isabel Amorim, (Universidade dos Açores in Terceira), Odilia Teixeira and David Silva (São Jorge), helped us considerably during the fieldwork in Azores. HP thanks his wife, Ortrud Runze, for all her indefatigable help during the visits to Madeira and the Azores, including collecting bones included in this study, and the remaining authors want to acknowledge her assistance also. Mr Klaus Groh / Hackenheim (Germany) provided several rail bones used in this study. We received great logistic support from Dr Paulo Borges (Universidade dos Açores in Terceira), Dr Sergio Ávila and all his team (Universidade dos Açores in São Miguel), Os Amigos dos Açores (specially Diogo Caetano in São Miguel, and Jose Melo in Santa Maria) and Os Montanheiros (Terceira, Pico and Sao Jorge). We are indebted to the curators of the Museu Municipal do Funchal (MMF, Funchal), Dr Manuel Biscoito, and the Museu Carlos Machado (MCMa, São Miguel), Dr Joao Paulo Constança, for their facilities and patience. Clara Vignolo (Institut Mediterrani d'Estudis Avançats) prepared Figure 19. Anna Díaz (Institut Mediterrani d'Estudis Avançats) helped us catalogue material. Dr Storrs L. Olson (Washington) edited a first version of this paper and enriched it with very valuable comments. Dr Damià Jaume (Palma) improved considerably our English text. Finally, we acknowledge Dr David W. Steadman (Gainesville), Alan Tennyson (Wellington), a third anonymous reviewer and the editor Dr Trevor H. Worthy for their valuable comments and improvements to our initial text. This paper is included in the Research Project CGL2012-38087, "Cambios holocénicos en la biodiversidad animal de las islas de la Macaronesia y de Baleares" (Dirección General de Investigación Científica y Técnica, Ministerio de Economía y Competitividad).

Literature

- Allison, P.A. (1988) Konservat-Lagerstätten: Cause and Classification. *Paleobiology*, 14, 4, 331–344.
- Baumel, J.L. & Witmer, L.M. (1993) Osteology. In: Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E. & van den Berge, J.C. (Eds), *Handbook of Avian Anatomy: Nomina Anatomica Avium*, 2nd ed. Cambridge, Massachusetts: *Publications of the Nuttall Ornithological Club*, 23, 45–132.
- Channing, A., Schweitze, M.H., Horner, J.R. & McEneaney, T. (2005) A silicified bird from Quaternary hot spring deposits. *Proceedings of the Royal Society B*, 272, 905–911.
<http://dx.doi.org/10.1098/rspb.2004.2989>
- Clode, L.P. (1984) *Registo bio-bibliográfico de madeirenses : sécs XIX e XX*. Funchal : Caixa Económica do Funchal, 515 pp.
- da Silva, F.A. & de Meneses, C.A. (1984) *Elucidário Madeirense*. (reprinted from the first edition of 1946). Funchal, 3 volumes.
- Davis, P.G. & Briggs, D.E.G. (1998) The impact of decay and disarticulation on the preservation of fossil birds. *Palaios*, 13, 3–13.
<http://dx.doi.org/10.2307/3515277>
- Dietzen, C., Witt, H.-H. & Wink, M. (2003) The phylogeographic differentiation of the European robin, *Erithacus rubecula*, on the Canary Islands revealed by mitochondrial DNA sequence data and morphometrics: evidence for a new robin taxon on Gran Canaria? *Avian Science*, 2–3, 115e131.
- Driesch, A. von den (1976) A guide to the measurement of animal bones from archaeological sites. *Bulletin of the Peabody Museum*, 1, 1–137.
- Forjaz, V.H., Nunes J.C. & Bancelos, P. (2004) Algar do Carvão pit, Terceira Island (Azores): Geology and Vulcanology. In: Nunes J.C. & Halliday W. (Eds), *XI International Symposium on Volcanospeleology*. Maio, Madalena, Pico, pp. 71–72.
- França, Z., Cruz, J.V., Nunes, J.C. & Forjaz, V.H. (2003) Geologia dos Açores: uma perspectiva actual. *Açoreana*, 10, 11–140.
- Geldmacher, J., Hoernle, K., van den Bogaard, P., Zankl, G. & Garbe-Schönberg, D. (2001) Earlier history of the 70-Ma-old Canary hotspot based on the temporal and geochemical evolution of the Selvagen Archipelago and neighboring seamounts in the eastern North Atlantic. *Journal of Volcanology and Geothermal Research*, 111, 55–87.
[http://dx.doi.org/10.1016/S0377-0273\(01\)00220-7](http://dx.doi.org/10.1016/S0377-0273(01)00220-7)
- Illera, J.C., Rando, J.C., Richardson, D.S. & Emerson, B.C. (2012) Age, origin and extinctions of the avifauna of Macaronesia: a synthesis of phylogenetic and fossil information. *Quaternary Science Reviews*, 50, 14–22.
<http://dx.doi.org/10.1016/j.quascirev.2012.07.013>
- Kirchman, J.J. & Steadman, D.W. (2005) Rails (Aves: Rallidae: *Gallirallus*) from prehistoric sites in the Kingdom of Tonga, including description of a new species. *Proceedings of the Biological Society of Washington*, 118, 465–477.
[http://dx.doi.org/10.2988/0006-324X\(2005\)118\[465:RARGFP\]2.0.CO;2](http://dx.doi.org/10.2988/0006-324X(2005)118[465:RARGFP]2.0.CO;2)
- Kirchman, J.J. & Steadman, D.W. (2006a) Rails (Rallidae *Gallirallus*) from prehistoric archaeological sites in Western Oceania. *Zootaxa*, 1316, 1–31.
- Kirchman, J.J. & Steadman, D.W. (2006b) New species of rails (Aves: Rallidae) from an archaeological site on Huahine, Society Islands. *Pacific Science*, 60, 279–296.
<http://dx.doi.org/10.1353/psc.2006.0007>
- Kirchman, J.J. & Steadman, D.W. (2007) New species of extinct rails (Aves; Rallidae) from archaeological sites in the Marquesas Islands, French Polynesia. *Pacific Science*, 61, 145–163.
<http://dx.doi.org/10.1353/psc.2007.0008>
- Linnaeus, C. (1758) *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species cum characteribus differentiis, synonymis, locis*. Editio Decima, Reformata. Holmiae, Impensis Direct. Laurentii Salvii, 824 pp.
<http://dx.doi.org/10.5962/bhl.title.542>
- Livezey, B.C. (2003) Evolution of Flightlessness in Rails (Gruiformes: Rallidae): phylogenetic, ecomorphological, and ontogenetic perspectives. *Ornithological Monographs*, 53, 1–654.
<http://dx.doi.org/10.2307/40168337>
- Livezey, B.C. & Zusi, R.L. (2006) Phylogeny of Neornithes. *Bulletin of the Carnegie Museum of Natural History*, 37, 1–544.
[http://dx.doi.org/10.2992/0145-9058\(2006\)37\[1:PON\]2.0.CO;2](http://dx.doi.org/10.2992/0145-9058(2006)37[1:PON]2.0.CO;2)
- Lowe, R.T. (1853) *Primitiae et Novitiae Faunae et Florae Maderae et Portus Sancti*. London. [See footnote in App. D, p. XVII, dated 24 Feb 1853 (which refutes 1851 given on the title page as the year of publication); see also Pieper (1985)].
- Manning, P.L., Morris, P.M., McMahon, A., Jones, E., Gize, A., Macquaker, J.H.S., Wolff, G., Thompson, A., Marshall, J., Taylor, K.G., Lyson, T., Gaskell, S., Reamtong, O., Sellers, W.I., van Dongen, B.E., Buckley M. & Wogelius, R.A. (2009) Mineralized soft-tissue structure and chemistry in a mummified hadrosaur from the Hell Creek Formation, North Dakota (USA). *Proceedings of the Royal Society Series B: Biological Sciences*, 276 (1672), 3429–3437.
<http://dx.doi.org/10.1098/rspb.2009.0812>
- Martín, A. & Lorenzo, J.A. (2001) *Aves del Archipiélago Canario*. Lemus Editor, La Laguna, 787 pp.
- McMinn, M., Palmer, M. & Alcover, J.A. (2005) A new species of rail (Aves: Rallidae) from the Upper Pleistocene and Holocene of Eivissa (Pityusic Islands, western Mediterranean). *Ibis*, 147, 4, 706–716.
<http://dx.doi.org/10.1111/j.1474-919X.2005.00442.x>
- Millener, P.R. (1989) The only flightless passerine; the Stephens Island Wren (*Traversia lyalli*: Acanthisittidae). *Notornis*, 36,

- Millener, P.R. & Worthy, T.H. (1991) Contribution to New Zealand's Late Quaternary avifauna. II: *Dendroscansor decurvirostris*, a new genus and species of wren (Aves: Acanthisittidae). *Journal of the Royal Society of New Zealand*, 21, 179–200.
<http://dx.doi.org/10.1080/03036758.1991.10431406>
- Newitt, M. (2005) *A History of Portuguese Overseas Expansion, 1400–1668*. Routledge, London, 300 pp.
- Nunes, J.C., Barcelos, P., Pereira, F., Forjaz, V.H. & Borges, P.A.V. (2004). Monumento Natural Regional do Algar do Carvão (Ilha Terceira) : Biodiversidade e Geodiversidade. *Atlântida*, 49, 279–286.
- Olson, S.L. (1973a) A classification of the Rallidae. *Wilson Bulletin*, 85, 381–416.
- Olson, S.L. (1973b) The evolution of the Rails of the South Atlantic Islands (Aves: Rallidae). *Smithsonian Contributions to Zoology*, 152, 1–153.
<http://dx.doi.org/10.5479/si.00810282.152>
- Olson, S.L. (1975) A review of the extinct rails of the New Zealand region (Aves: Rallidae). *National Museum of New Zealand Records*, 1, 63–79.
- Olson, S.L. (1977) A synopsis of the fossil Rallidae. In: Ripley, S.D., (Ed.), *Rails of the World*, David R. Godine, Boston, pp. 339–373.
- Olson, S.L. & James, H.F. (1991) Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part 1. Non-Passeriformes. *Ornithological Monographs*, 45, 1–88.
<http://dx.doi.org/10.2307/40166794>
- Olson, S.L. & Wingate, D.B. (2000) Two new species of flightless rails (Aves: Rallidae) from the Middle Pleistocene “crane fauna” of Bermuda. *Proceedings of the Biological Society of Washington*, 113, 356–368.
- Olson, S.L. & Wingate, D.B. (2001) A new species of large flightless rail of the *Rallus longirostris/elegans* complex (Aves: Rallidae) from the late Pleistocene of Bermuda. *Proceedings of the Biological Society of Washington*, 114, 509–516.
- Päckert, M., Dietzen, C., Martens, J., Wink, M. & Kvist, L. (2006) Radiation of Atlantic goldcrests *Regulus regulus* spp.: evidence of a new taxon from the Canary Islands. *Journal of Avian Biology*, 37, 364e380.
- PASW Statistic 18 (2011) SPSS 18. Available from: <http://www-01.ibm.com/software/analytics/spss> (Accessed 8 Dec. 2015)
- Pieper, H. (1985) The fossil land birds of Madeira and Porto Santo. *Bocagiana*, 88, 1–6.
- Rando, J.C., López, M. & Seguí, B. (1999) A new species of extinct flightless passerine (Emberizidae: *Emberiza*) from the Canary Islands. *Condor*, 101, 1–13.
<http://dx.doi.org/10.2307/1370440>
- Rando, J.C. & Alcover, J.A. (2008) Evidence for a second western Palearctic seabird extinction during the last millennium: the Lava Shearwater *Puffinus olsoni*. *Ibis*, 150, 188–192.
<http://dx.doi.org/10.1111/j.1474-919X.2007.00741.x>
- Rando, J.C. & Alcover, J.A. (2010) On the extinction of the Dune Shearwater (*Puffinus holeae*) from the Canary Islands. *Journal of Ornithology*, 151, 365–369.
<http://dx.doi.org/10.1007/s10336-009-0463-6>
- Rando, J.C., Alcover, J.A., Navarro, J.F., García-Talavera, F., Hutterer, R. & Michaux, J. (2008) Chronology and causes of the extinction of the Lava Mouse, *Malpaisomys insularis* (Rodentia: Muridae) from the Canary Islands. *Quaternary Research*, 70, 141–148.
<http://dx.doi.org/10.1016/j.yqres.2008.04.012>
- Rando, J.C., Alcover, J.A. & Illera, J.C. (2010) Disentangling ancient interactions: A new extinct passerine provides insights on character displacement among extinct and extant island finches. *PLoS ONE*, 5 (9), e12956.
<http://dx.doi.org/10.1371/journal.pone.0012956>
- Rando, J.C., Pieper, H., Alcover, J.A. & Olson, S.L. (2012a) A new species of extinct fossil scops owl (Aves: Strigiformes: Strigidae: *Otus*) from the Archipelago of Madeira (North Atlantic Ocean). *Zootaxa*, 3182, 29–42.
- Rando, J.C., Alcover, J.A., Michaux, J., Hutterer, R. & Navarro, J.F. (2012b) Late-Holocene asynchronous extinction of endemic mammals on the eastern Canary Islands. *The Holocene*, 22, 801–808.
<http://dx.doi.org/10.1177/0959683611430414>
- Rando, J.C., Alcover, J.A., Olson, S.L. & Pieper, H. (2013). A new species of extinct scops owl (Aves: Strigiformes: Strigidae: *Otus*) from São Miguel Island (Archipelago of Azores, North Atlantic Ocean). *Zootaxa*, 3647 (2), 343–357.
<http://dx.doi.org/10.11646/zootaxa.3647.2.6>
- Rando, J.C., Pieper, H. & Alcover, J.A. (2014). Radiocarbon evidence for house mouse presence on Madeira Island (North Atlantic) one millennium ago. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20133126
<http://dx.doi.org/10.1098/rspb.2013.3126>
- Rijsdijk, K.F., Hengl, T., Norder, S., Otto, R., Emerson, B.C., Avila, S.P., López, H., van Loon, E.E., Tjørve, E. & Fernández-Palacios, J.M. (2014) Quantifying surface-area changes of volcanic islands driven by Pleistocene sea-level cycles: biogeographical implications for the Macaronesian archipelagos. *Journal of Biogeography*, 47, 1242–1254.
<http://dx.doi.org/10.1111/jbi.12336>
- Steadman, D.W. (1991) Extinction of species: past, present, and future. In: Wyman, R.L. (Ed.) *Global Climate Change and Life on Earth*. Routledge, Chapman and Hall. New York, NY, pp. 156–169.
- Steadman, D.W. (1995) Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. *Science*, 267, 1123–

1131.

<http://dx.doi.org/10.1126/science.267.5201.1123>

- Steadman, D.W. (1997) Extinctions of Polynesian birds: reciprocal impacts of birds and people. *In*: Kirch, P.V. & Hunt, T.L. (Eds) *Historical Ecology in the Pacific Islands*, Yale University Press, New Haven/London, pp. 51–80.
- Steadman, D.W. (2006) *Extinction and Biogeography of Tropical Pacific Birds*. Univ. Chicago Press, Chicago.
- Steadman, D.W., Morris, J.R. & Wright, N.A. (2013) A new species of Late Pleistocene rail (Aves: Rallidae) from Abaco, the Bahamas. *Paleontological Journal*, 47, 11, 1355–1364.
<http://dx.doi.org/10.1134/S0031030113110130>
- Vigors, N.A. (1825) Observations on the natural affinities that connect Orders and Families of Birds. *Transactions of the Linnean Society of London*, 14, 395–517.
<http://dx.doi.org/10.1111/j.1095-8339.1823.tb00098.x>
- Worthy, T.H. (2004) The fossil rails (Aves: Rallidae) of Fiji with descriptions of a new genus and species. *Journal of the Royal Society of New Zealand*, 34, 3, 295–314.
<http://dx.doi.org/10.1080/03014223.2004.9517768>
- Worthy, T.H. & Holdaway, R.N. (2002) *The lost world of the moa: prehistoric life of New Zealand*. Indiana, Indiana University Press. xxxiii + 718 pp.