

A new species of rail (Aves: Rallidae) from the Upper Pleistocene and Holocene of Eivissa (Pityusic Islands, western Mediterranean)

M. MCMINN,¹ M. PALMER² & J. A. ALCOVER*

¹Santa Florentina 13, 3^{er}, 07007 Palma de Mallorca.

²Institut Mediterrani d'Estudis Avançats, Cr Miquel Marqués, Esporles

A new species of rail is described from a Pleistocene and Holocene cave deposit on the island of Eivissa, Pityusic Islands (western Mediterranean Sea). *Rallus eivissensis* sp. nov. was an insular relative of the European Water Rail *Rallus aquaticus*. Compared with the extant Water Rail, the new species was smaller and stouter, had shorter and more robust hind limbs and shorter wings, with probably reduced flight ability. The Pityusics were the only Mediterranean islands with a vertebrate Quaternary fauna lacking terrestrial mammals, and this absence is no doubt related to the Eivissan rail evolution. The chronology of the *Rallus eivissensis* sp. nov. extinction overlaps broadly with a period of uncertainty for the arrival of humans at Eivissa, suggesting a relationship between the two events.

Localized endemic insular living rails (Aves: Rallidae, *sensu* Olson 1973) are currently known from a small number of islands in the world (e.g. Galápagos Islands, Guam Island, Okinawa Island, Inaccessible Island, New Zealand, Henderson Island, Lord Howe Island). They are mainly recruited within *Gallirallus*, although other genera (e.g. *Porphyrio*, *Porzana*, *Amaurornis*, *Gallinula*) contain small numbers of insular species, and there are even several insular endemic genera (e.g. *Atlantisia*, *Nesoclopeus*). Nevertheless, the increased palaeontological work of the last two decades has revealed that a huge number of insular endemic rails disappeared after the arrival of the first human settlers on the islands (e.g. Steadman 1991, 1995, 1997). The biogeographical pattern discovered by palaeornithologists shows that rails are prone to evolve on islands originating endemic species or populations, and that the current diversity of insular rails merely represents survivors from the much more diverse family that existed previously. Several rail genera, that currently include no insular endemic species, did so in the past (e.g. *Rallus*, *Fulica*; see Olson 1990, Livezey 2003). Until now, no endemic fossil rails have been described from the Mediterranean islands.

The present paper describes the first insular rail from a Mediterranean island. The material presented here comes from Es Pouàs, a fossiliferous deposit on the island of Eivissa (Ibiza), the larger of the Pityusic Islands (Western Balearics) (541 km²), situated 90 km from the Eastern Iberian Peninsula and about 80 km from Mallorca (see Fig. 1). The Pityusic archipelago contains two main islands (Eivissa and Formentera) surrounded by about 60 small islets (Kuhbier 1984). Their biogeographical history reveals that, during the Upper Pleistocene and the Holocene (until the arrival of humans), these islands were the only ones in the whole Mediterranean area lacking terrestrial mammals (e.g. Florit *et al.* 1989, Alcover *et al.* 1994, 1999, Palmer *et al.* 1999). This faunal anomaly has been analysed by Seguí and Alcover (1999), who considered that the ecology of the pre-human avifauna of Eivissa may parallel that found in some of the Pacific islands, such as the Hawaiian archipelago. The description of the new taxon here erected improves our understanding of the palaeoecology of the island.

MATERIALS AND METHODS

The specimens here presented were collected over 6 years, between 1988 and 1993, during palaeontological fieldwork in the locality of Es Pouàs (St Antoni de Portmany, in the northern part of Eivissa). All the specimens were collected in the vertebrate

*Corresponding author: Institut Mediterrani d'Estudis Avançats, Cta de Valldemossa km 7,5. 07071 Palma de Mallorca.
Email: vieapba@uib.es

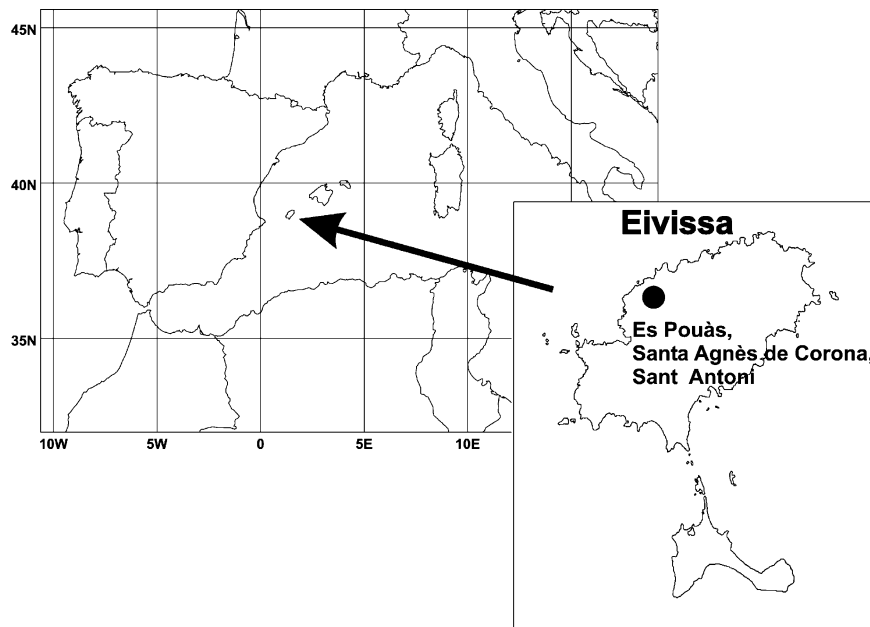


Figure 1. Map of the Western Mediterranean showing the location of Es Pouàs (Eivissa, Pityusic Islands).

collection of the 'Museu de la Naturalesa de les Illes Balears, Palma de Mallorca' (MNIB). Paratypes were selected to include all specimens used for the description or for the measurements, and excluded juvenile bones and broken specimens, except when they were the only available material for an element. Only bones with a sufficiently large sample size were used for the statistical analyses. As a consequence, measurements of the cranium, premaxilla, sternum, coracoid, and synsacrum were excluded from the statistical analyses, and they are only presented in the species description.

The measurements of bones used for statistical comparison are presented in Figure 2. The measurements of the long bones were taken with digital callipers to an accuracy of 0.01 mm, and rounded to the nearest 0.1 mm. All the remaining measurements followed the methodology of von den Driesch (1976).

Separate analyses for size and shape were conducted for each of the six long bones measured, because the fossils were disarticulated. Original data were all natural log-transformed.

Allometry is defined as any change of shape related to size (Slice *et al.* 1996). Static allometry (Klingenberg 1993) results from variations among individuals of the same population and age group, and is commonly observed in birds, because their adults show determinate growth (Boag 1984, Gibson *et al.* 1984). If allometry is ignored, a problem emerges in relation

to between-group comparisons: a simple bias in size can be (erroneously) interpreted as a difference in shapes. The separation of size-related variability from size-free shape differences is a traditional topic in morphometrics. Here we adopted the Burnaby method (Burnaby 1966), as modified by Klingenberg (1993). This assumes that there exists a common vector of size for all the groups studied (i.e. there is a common allometric pattern). Then, a new shape for each specimen can be (statistically) estimated by sliding the original shape on the size vector until the size remains the same for all individuals (i.e. until the shape remains size-invariant). This size vector is a new variable, because it is exactly none of the measured distances, although it is highly correlated with all of them. It is extracted using a special version of Principal Components Analysis (Common Principal Components Analysis, CPCA). The overall strategy implies three steps (after preliminary ln-transformation of the original measures): (1) rigid rotation to the common principal components, (2) setting the scores of the first CPC to zero (i.e. setting the size to be the same for all specimens), and (3) rigid rotation back to the original co-ordinate system (Klingenberg 1993). These three steps were completed using NTSys software (Rohlf 1993).

We analysed the between-group differences in shape using Discriminant Analyses (DA) on CPCA scores omitting the first CPC (i.e. on size-free

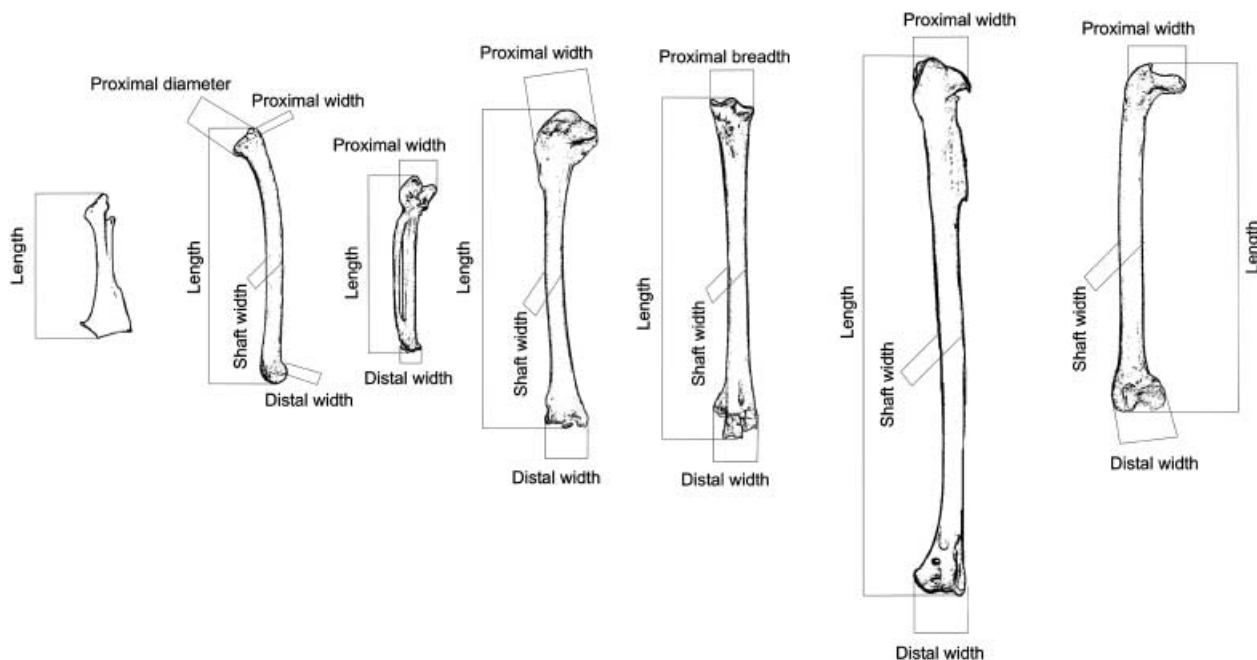


Figure 2. Measurements of the long bones of *Rallus*.

between-group differences). This new set of variables is supposed to be size-invariant, and it can be analysed by standard multivariate methods.

These Discriminant Analyses (separate analyses for each of the six selected bones) focused on testing the multivariate picture of between-group shape differences, but are not easily interpretable in geometric terms. The latter was achieved by performing a set of one-factor (species) ANOVAs on each of the transformed size-free measurements (step 3).

Five chronometric AMS ^{14}C ages from Es Pouàs were obtained through AMS datings performed on the collagen fraction of the bird bones at the R.J. van de Graff Laboratorium, Universiteit Utrecht (Alcover 2003), and all the analytical steps went correctly. The available ^{14}C ages have been calibrated using the Program OxCal ver. 3.5. This program follows the methods of Stuiver *et al.* (1998). To express dates, the general conventions proposed by Kra (1986) and Mook (1986) were followed. All the datings obtained are consistent with the stratigraphy of the deposit. Although no data exist to allow their correction for carbon isotope fractionation, the good condition of the material suggests that there is probably little difference between the measured radiocarbon age and the corrected radiocarbon age. Furthermore, no effects of humic acids or other forms of contamination are expected at this site.

The topography of the cave, the reference grill and the section of square A3 are illustrated in Florit *et al.* (1989), Alcover *et al.* (2001) and Alcover (2003). The stratigraphic column represents a continuous depositional event.

Comparative material examined

Complete or near-complete skeletons of the following species in the collections of the British Museum of Natural History (BMNH) and Museu de la Naturalesa de les Illes Balears (MNIB) were used:

Rallus aquaticus BMNH 1849-11-13-57 (unknown), BMNH 1859-4-7-1 (unknown), BMNH 1909-12-29-1 (unknown), BMNH 1922-3-27-1 (England), BMNH 1930-3-24-49 (unknown), BMNH 1930-3-24-52 (unknown), BMNH S/1953-11-1 (England), BMNH S/1930-24-54 (unknown), BMNH S/1973-32-1 (England), BMNH S/1981-72-6 (England), BMNH S/1982-41-6 (England), BMNH S/1982-51-1 (England), BMNH S/1983-106-1 (England), BMNH S/1984-100-4 (England), BMNH S/1984-33-1 (England), BMNH S/1985-21-1 (England), BMNH S/1985-73-5 (England), BMNH S/1985-95-2 (unknown, captivity), BMNH S/1986-3-4 (England, captivity), BMNH S/1986-3-5 (England, captivity), BMNH S/1986-36-4 (England), BMNH S/1989-9-1

(England), BMNH S/1992-45-1 (Wales), BMNH S/1993-26-1 (Scotland), BMNH unregistered (captivity), MNIB 11945 (Balearic Islands), MNIB 12474 (Iberian Peninsula), MNIB 12569 (Balearic Islands), MNIB 12579 (Balearic Islands), MNIB 20706 (Iberian Peninsula), MNIB 21867 (Balearic Islands), MNIB 21914 (Balearic Islands), MNIB 9946 (Balearic Islands), MNIB 9948 (Balearic Islands), MNIB 9964 (Balearic Islands).

Crex crex: BMNH 1851-7-23-45 (England), BMNH 1890-12-14-2 (England), BMNH 1930-3-24-58 (England), BMNH S/1986-49-3 (England).

Porzana porzana: BMNH S/1952-2-366 (England), BMNH S/1976-47-1 (Oman), MNIB 12568 (Balearic Islands).

Porzana parva: BMNH S/1968-4-1 (Cyprus).

Porzana pusilla: BMNH S/1978-4-1 (Bahrain).

The *Rallus aquaticus* material came from the western Palaearctic (ssp. *aquaticus*), and includes insular (Balearic Islands) and mainland samples.

Systematics

Family Rallidae

Genus *Rallus* Linnaeus 1758

The very long and slender bill of the Eivissan species clearly places it in the genus *Rallus* (Olson 1973). This genus contains no endemic insular living species, although two Pleistocene species have recently been described from Bermuda (Olson & Wingate 2000, 2001) and a new undescribed species has been recorded from Miyakoshima, southern Ryukyu islands (Matsuoka 2000, Table 1), although the latter could perhaps belong to *Gallirallus*. This is the

Table 1. Measurements (in mm) of selected skeletal elements of *Rallus eivissensis* sp. nov. from the Upper Pleistocene and Holocene of Eivissa and *Rallus aquaticus* (several localities). For definition of measurements see Figure 2. Mean, range (max and min), sample size (*n*, in bold the sample size for multivariate comparisons) and standard deviation (sd) are indicated.

	<i>Rallus eivissensis</i>					<i>Rallus aquaticus</i>				
	Mean	min	max	<i>n</i>	sd	Mean	min	max	<i>n</i>	sd
Humerus				17					33	
Length	35.26	32.44	37.94	18	1.58	38.82	34.29	42.10	34	1.89
Proximal width	7.28	5.24	8.24	26	0.59	7.98	7.27	8.68	34	0.41
Shaft width	2.16	1.83	2.39	26	0.14	2.38	1.74	2.82	35	0.19
Distal width	4.85	4.37	5.35	22	0.22	5.29	4.85	5.74	34	0.25
Ulna				14					32	
Length	26.97	24.84	28.62	14	1.23	31.25	24.95	33.93	33	1.83
Proximal width	3.20	2.80	3.55	14	0.22	3.50	3.11	3.89	32	0.21
Proximal diameter	4.20	3.85	4.46	14	0.18	4.58	4.19	4.99	32	0.26
Shaft width	1.58	1.44	1.77	14	0.11	1.70	1.19	1.97	33	0.15
Distal width	3.16	2.94	3.38	14	0.15	3.44	3.15	3.79	32	0.17
Carpometacarpus				10					31	
Length	18.53	15.89	20.85	13	1.66	21.54	19.37	23.31	31	1.02
Proximal width	4.46	4.17	4.86	10	0.23	4.71	4.20	5.12	31	0.23
Distal width	2.53	2.28	3.03	13	0.22	2.68	2.18	3.00	31	0.22
Femur				13					34	
Length	37.23	34.23	40.77	13	2.02	41.50	37.56	44.76	34	1.98
Proximal width	6.29	5.91	6.79	14	0.24	6.59	5.73	7.55	34	0.43
Shaft width	2.69	2.49	2.96	14	0.13	2.74	2.38	3.09	34	0.17
Distal width	5.81	5.2	6.34	13	0.34	6.13	5.42	6.93	34	0.37
Tibiotarsus				10					32	
Length	54.56	49.69	60.3	11	2.96	64.69	57.56	68.49	32	3.07
Medial length	53.05	48.51	58.49	11	2.74	62.74	55.54	69.32	32	3.23
Proximal width	7.60	6.87	9.91	12	0.85	7.92	7	8.71	32	0.46
Shaft width	2.35	2.06	2.56	12	0.15	2.39	2.08	2.76	32	0.18
Distal width	4.88	4.62	5.26	12	0.19	5.09	4.5	5.64	32	0.33
Tarsometatarsus				21					31	
Length	34.31	29.79	37.22	22	2.15	41.39	37.04	45.32	33	2.23
Proximal width	5.15	4.24	5.79	23	0.40	5.32	4.76	5.8	32	0.32
Shaft width	2.56	2.21	2.99	23	0.19	2.46	2.15	2.81	32	0.20
Distal width	5.47	4.42	5.93	21	0.40	5.74	5.18	6.24	32	0.35

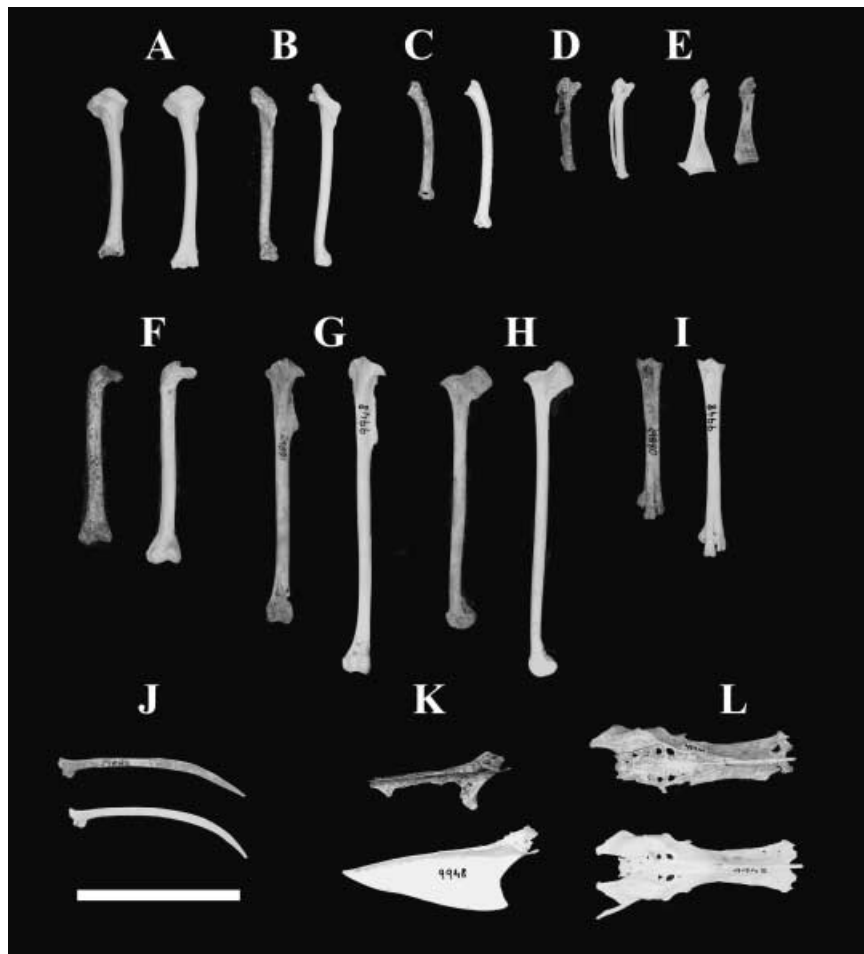


Figure 3. Long bones of *Rallus eivissensis* sp. nov. in comparison with bones of *Rallus aquaticus* (MNIB 9948). (A) Right humerus (MNIB 28624) in caudal view. (B) Right humerus (MNIB 28624) in lateral view. (C) Ulna MNIB 29870. (D) Left carpometacarpus (MNIB 32496) in ventral view. (E) Left coracoid (MNIB 29680) in caudal view. (F) Left femur (MNIB 19818) in caudal view. (G) Left tibiotarsus MNIB 29891 in cranial view. (H) Left tibiotarsus (MNIB 29891) in lateral view. (I) Left tarsometatarsus (holotype, MNIB 29880) in cranial view. (J) Scapula (MNIB 29882) in ventromedial view. (K) Sternum (MNIB 29881) in lateral view. (L) Pelvis (MNIB 19334) in dorsal view. Scale bar = 2 cm.

only western Palaearctic Rallid genus displaying this characteristic type of bill.

***Rallus eivissensis*, sp. nov.**

Holotype

Left tarsometatarsus MNIB 29880. See Figure 3.

Type locality

Es Pouàs, Square A3, level 3, Sant Antoni de Portmany, Eivissa.

Chronology

Late Pleistocene and Holocene. The collagen fraction of a distal fragment of a tibiotarsus belonging

to the new species was dated by AMS ^{14}C (MNIB 19979, square D4, UtC 6222: 6130 ± 80 BP, $5300\text{--}4840$ cal BC 2σ). The lowermost level (square A3, level 7) from where *Rallus eivissensis* bones have been obtained, furnished the dating UtC-6674 obtained on *Corvus corax* collagen: $23\,030 \pm 150$ BP; $21\,400\text{--}20\,750$ cal BC 2σ . The level immediately above this (level 6), furnished the dating UtC-6673 obtained on *Grus grus* collagen: $16\,170 \pm 90$ BP; $18\,000\text{--}16\,700$ cal BC 2σ . Given that the levels were defined as constituted by successive sublevels (i.e. the deposition was continuous and the levels were identified through thin clear discontinuities), and that there is no indication as to which sublevel the dated samples belong, these datings only allow us to

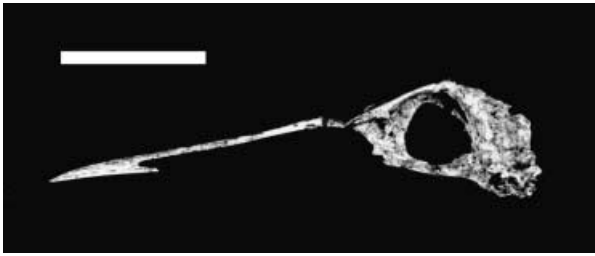


Figure 4. Skull (MNIB 19153) of *Rallus eivissensis* sp. nov. in lateral view. Scale bar is 2 cm.

document with a $P > 95\%$ that the species was living on Eivissa between 5300 and 16 700 cal bc. Although this is the isotopically well-documented known-age range, there is stratigraphical evidence of later material, and we have no doubt of its earlier presence.

Measurements (mm) of the holotype

Length 34.16; proximal width 5.44; shaft width 2.70; distal width 5.43.

Paratypes (all are expressed as MNIB catalogue numbers)

Mandibles (distal fragments) 28585–6, 29863, 29877, 29889. Cranium (fragment) 19153 (see Figure 4). Premaxilla (fragments) 19347, 28577, 28580, 28583, 29562, 29862. Sternum (fragment) 29881. Coracoids 19421, 28052, 28763–4, 28768–9, 29489, 29678–81, 29704, 29871–2, 29874, 29888, 35143. Humeri 19174, 19486, 23092, 23304, 23320, 24902, 28624–7, 28627, 29459, 29849–53, 29864, 29873, 29885, 29893. Ulnae 23240, 29683–9, 29700, 29854–5, 29868–70, 32489–90. Carpometacarpi 19243, 27583–5, 29627, 29682, 29875, 29917, 32494, 32496, 33843. Pelvis 19334, 24167, 29677 (fragments). Femora 19818–20, 23243, 23323, 24308, 27906, 29464, 29477, 29691–2, 29705, 29856, 29876, 29884, 29890. Tibiotarsi 19296–7, 19861–2, 28849, 28851, 29467, 29699, 29858, 29878, 29891, 29910. Tarsometatarsi 19105, 19322–3, 19904, 20203, 23101, 24304, 28878–80, 29476, 29478, 29585, 29695–8, 29701, 29860–1, 29879–80, 29883, 29886.

Measurements (mm) of paratypes

See Table 1 for the measurements of long bones defined as paratypes. Other measurements: cranium total length, 42.15; premaxilla length, 26.6; sternum proximal width, 11.32; coracoid length, 17.58; 17.88; 18.25; 18.72; 18.81; 18.86; 18.90; 19.03;

19.11; 19.18; 19.33; 19.45; 20.03; 21.15; synsacrum length, 29.9; 32.02; 32.88.

Other material attributed to *Rallus eivissensis* sp. nov.

Coracoids (fragments) 19421, 28768–9, 32492. Humeri (fragmented) 24491, 24883, 26449, 28629, 28632, 29486, 29564–5, 29623; (juvenile) 19183, 19487, 23303, 28626, 29703. Pelvis, 2 uncatalogued fragments. Femora (fragmented) 23244, 29857. Tibiotarsi (fragmented) 19303, 19305, 23254; (juvenile), 29468, 29859. Tarsometatarsus (fragmented) 27639.

Etymology

The specific name, *eivissensis*, derives from the Catalan autochthonous toponym of the island, Eivissa.

Diagnosis

A rail slightly smaller than *Rallus aquaticus*, with wings relatively smaller and distal hindlimb elements shorter and slightly more robust, resulting in a shorter and relatively wider body than in *Rallus aquaticus*. In relation to the size of the skull, the bill is slightly shorter than in *Rallus aquaticus*.

Description

On the single skull presently available, the *fonticuli interorbitalis* are larger than in *Rallus aquaticus*. There are no impressions for salt glands on the interorbital bridge, suggesting a lifestyle independent of saline habitats.

The only available sternum of *Rallus eivissensis* is in a fragmentary state, but on the basis of placement of the insertion of the *trabecula lateralis* in the *corpus sterni*, it is slightly shorter and wider than in *Rallus aquaticus*. Its carina height is probably reduced, as the carina edge diverges at a smaller angle with the base of the sternum. The carina reduction does not seem to be of the extent recorded in the Bermudan species *Rallus ibycus* and *Rallus recessus*, the only other described insular endemic species of the genus in the Northern Hemisphere (Olson & Wingate 2000, 2001). Nevertheless, it seems to be indicative for a smaller size of the *musculus supracoracoideus* and *musculus pectoralis*, two muscles involved in flight. All the wing bones are relatively reduced in length, especially the carpometacarpus.

The two available pelvises are relatively more robust, and slightly wider and longer than in *Rallus aquaticus*. The hind limb elements, especially the distal ones, are shorter and more robust.

Measurements of the main long bones of *Rallus eivissensis* sp. nov. are presented in Table 1. To analyse

Table 2. Results for analyses of between-species size and shape differences. Size differences were determined by one-factor (species) ANOVAS of the scores on the first common principal component. Shape differences were determined by multivariate discriminant analyses of the scores obtained from Common Principal Components Analyses, omitting the CPC 1.

	Size			Shape		
	df	F-ratio	<i>P</i>	Wilk's λ	df	<i>P</i>
Carpometacarpus	1, 39	11.78	< 0.01	0.350	2, 38	< 0.001
Femur	1, 45	12.06	< 0.001	0.368	3, 43	< 0.001
Humerus	1, 48	40.76	< 0.001	0.653	3, 46	< 0.001
Tarsometatarsus	1, 50	6.95	< 0.05	0.144	3, 48	< 0.001
Ulna	1, 44	35.36	< 0.001	0.269	4, 41	< 0.001

Table 3. Results of one-factor (species) ANOVAS on the transformed (size-free) measurements. Differences (> or <) are indicated for the cases in which the probability value was under the significance threshold after applying the Bonferroni correction for multiple comparisons. ei: *R. eivissensis* sp. nov. aq: *R. aquaticus*.

	Length	Shaft width	Proximal width	Proximal diameter	Distal width
Carpometacarpus	ei < aq		=		ei > aq
Femur	ei < aq	=	ei < aq		ei > aq
Humerus	ei < aq	=	=		=
Tarsometatarsus	ei < aq	=	ei > aq		ei > aq
Ulna	ei < aq	=	ei > aq	=	=

the between-taxon size differences, a morphometric analysis using CPCA and DA was done. Five of the six measured bones fit the implicit assumptions of a CPCA model. They are the carpometacarpus (CMC), femur (FEM), humerus (HUM), tarsometatarsus (TMT) and ulna (ULN). The tibiotarsus (TBT) did not fit these assumptions.

Assuming that the first common principal component is an unbiased estimate of the general size, significant size differences between species were found for all five bones (one-factor ANOVAS; Table 2).

A multivariate analysis was done to check between-species shape differences on individual elements. The results of between-species Discriminant Analyses of the first five bones are summarized in Table 2. These differences are displayed (Fig. 5) by plotting the scores on the first common principal component of all samples (abscissa; which can be interpreted as a measure of overall size) and the scores of the first axis from the discriminant analysis (ordinate; which can be interpreted as size-free shape differences). The results of one-factor ANOVAS for each of the transformed measurements are summarized in Table 3.

From the analysis of Tables 1–3 and Figure 6 some interesting conclusions arose. Significant differences in size and shape are documented for all bones

analysed. All differences are highly significant (i.e. $P < 0.001$), except for the difference in overall size for the tarsometatarsus ($P < 0.05$). Removing the size effect, *Rallus eivissensis* sp. nov. shows proportionally shorter bones than *Rallus aquaticus* (Table 3). A non-isometric reduction in the bones of *Rallus eivissensis* sp. nov. in comparison with those of *R. aquaticus* is clearly detected. This is due to a greater degree of shortening, rather than of narrowing, of the long bones. The shortening is greater for the distal bones, and more reduced for the proximal ones. As a mean, the humerus length reduction is about 9%, the ulna shortening is about 14% and the carpometacarpus shortening about 17%. The increasing reduction of these bones suggests a shortening of the primary remiges. In the hind limb, the femora length reduction is about 10%, the tibiotarsus shortening is about 15%, while the tarsometatarsus shortening is about 17%. The tarsometatarsus has a wider shaft and greater proximal width in *R. eivissensis* than does *R. aquaticus*. The stouter configuration of the tarsometatarsus caused by its relative shortening gives this bone its most peculiar shape. An artistic reconstruction of the animal is presented in Figure 5. Although body proportions are accurately presented, the coloration is speculative and based on extant relatives.

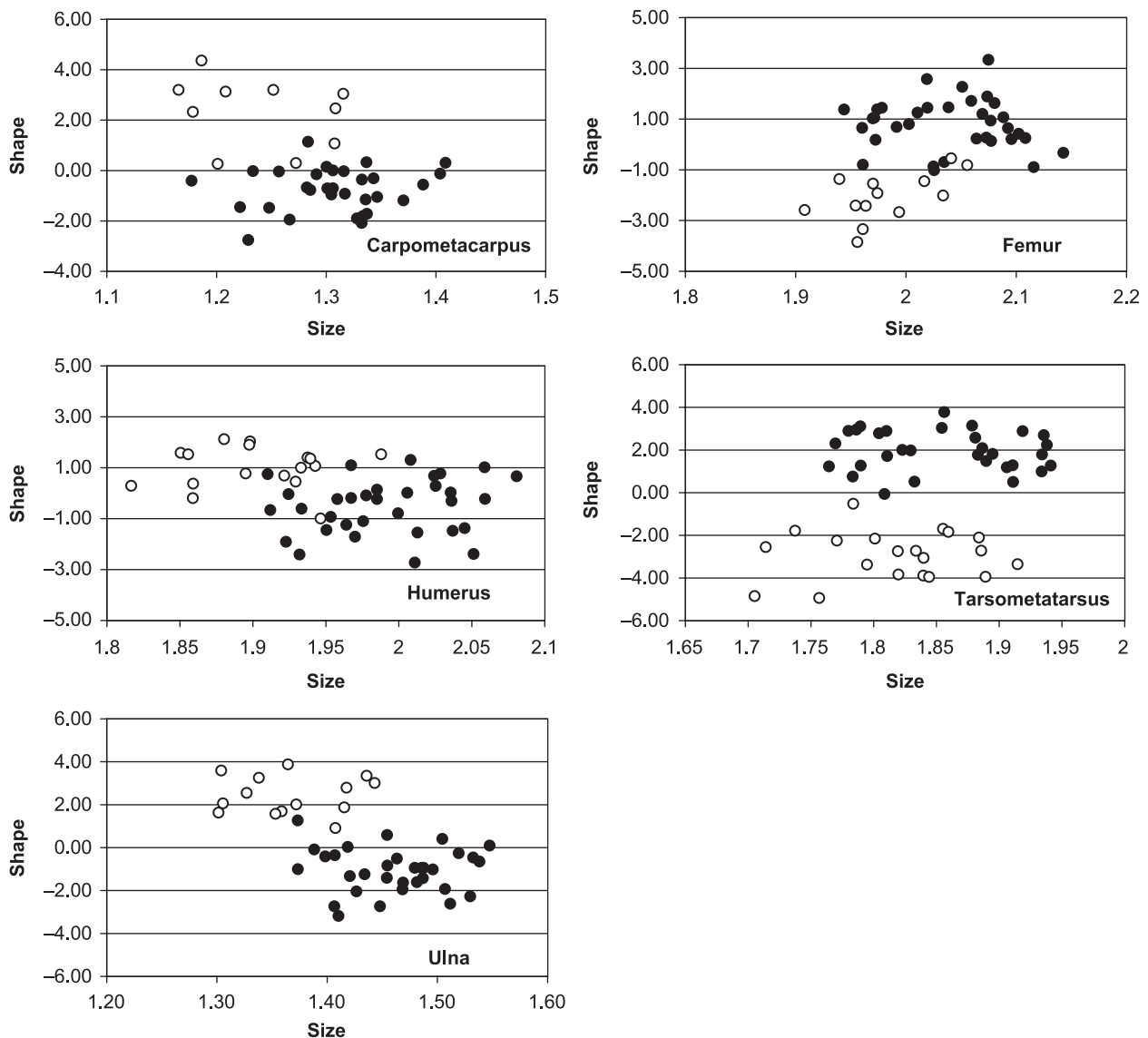


Figure 5. Between-species differences in shape and size. The first common principal component of all samples (abscissa) can be interpreted as a measure of overall size. The scores of the (single) axis from the discriminant analysis (ordinate) can be interpreted as size-free shape differences. Closed circles: *R. aquaticus*. Open circles: *R. eivissensis* sp. nov.

DISCUSSION

Assessment of the relationships of the new species is clear. *Rallus eivissensis* is a close relative of *Rallus aquaticus*, the only species of the genus currently present in the Western Palaearctic region. Both species share not only the long and slender bill, but also a large number of other characteristics. Indeed, they differ only in the characters that can be related to a reduction in flight ability, to the size of hind limb bones and to the proportions of the legs. Given

the presence of *Rallus aquaticus* in the European fossil record (e.g. Tyrberg 1998), and the existing shared characters, it is reasonable to assume that *Rallus eivissensis* is an insular derivative of *Rallus aquaticus*. No comparison has been made with the sub-Saharan species *Rallus caerulescens* and the Malagasian species *Rallus madagascarensis*, the only other two species of *Rallus* from the Old World; but according to the available external measurements both are larger than *R. aquaticus* (Taylor 1996). No direct relationships with these two species are expected.

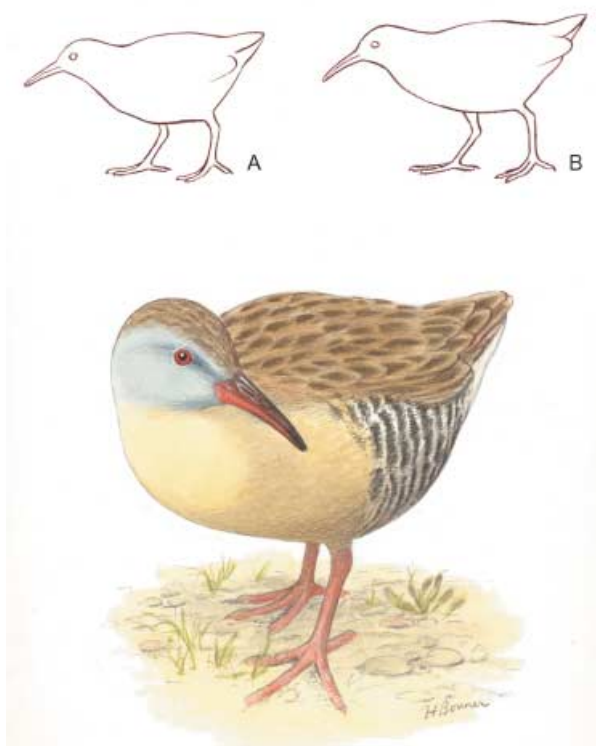


Figure 6. An artistic reconstruction of *Rallus eivissensis* sp. nov. Artist: Aina Bonner (Boston/Palma de Mallorca). A: *Rallus eivissensis* sp. nov. B: *Rallus aquaticus*.

Compared to *Rallus aquaticus*, *Rallus eivissensis* displays different proportions in its legs and body shape. Its morphology suggests some reduction in the development of the flight apparatus, although without achieving a flightless condition.

The studied sample of *Rallus aquaticus* reasonably includes the variational range of the species. No differences between the recent insular sample of Mallorca and the mainland specimens have been detected. Although a study of the variation in this species throughout its distribution range is not available, no great differences are expected between the different Palaearctic populations of this species. The four recognized subspecies of *R. aquaticus* are separated on plumage (Taylor 1996), and no size differences between them have ever been quoted.

No data exist for the timing of the divergence between *R. eivissensis* and its assumed ancestor *R. aquaticus*. The palaeontological record from Eivissa is discontinuous (e.g. Alcover *et al.* 1981, 1994, Agustí & Moyà-Solà 1990). Some Pliocene/Lower Pleistocene (*sensu lato*) deposits have been recorded (e.g. Cova de ca na Reia, Pedrera de can Besora, Cala

Salada). They presented an insular fauna containing rodents (Alcover & Agustí 1985, Alcover *et al.* 2000a, 2000b), a giant tortoise (Bour 1985, Gasser & Ferrer 1997, Filella *et al.* 1999), a lizard (Kotsakis 1981), bats and birds (Alcover 1989), as well as a land molluscan fauna including between 17 and 21 taxa (Gasull & Alcover 1982, Paul 1982, 1984, Paul & Altaba 1992). The Upper Pleistocene and Holocene fauna lacks terrestrial mammals, and tortoises, and contains only six land molluscs. Nevertheless, this fauna contains huge quantities of birds (Florit *et al.* 1989). Between the latter fauna and the former, there is a depositional hiatus that spans hundreds of thousands of years (Alcover *et al.* 1994). The divergence of an insular species of *Rallus* probably started at an indeterminate time within this hiatus. A post-glacial divergence cannot be definitively excluded.

The general body shape of *Rallus eivissensis* sp. nov. differs from that of *Rallus aquaticus* in the same way, but in a smaller degree that *R. recessus* differs from *Rallus elegans*. Its body was slightly wider than that of *R. aquaticus*. The shape of the tarsometatarsus suggests a proportionally heavier body. In life, *Rallus eivissensis* should have had a plumper body, in spite of the sternum carina reduction. Its hind limbs were shorter and more robust, and its wings were relatively shorter. Such a combination of characters suggests a more terrestrial life-style for *Rallus eivissensis* sp. nov., including a reduced flight ability, although there is no evidence for complete flightlessness.

The species bred successfully on Eivissa, as can be deduced from the presence of several juvenile bones in the fossil record (e.g. humeri MNIB 19183, 19487, 23303, 28626, 29703, synsacrum MNIB 29677, tibiotarsi MNIB 29468, 29859). Although *Rallus aquaticus*, its presumed ancestor, is partially migratory, a migratory condition for *Rallus eivissensis* can be ruled out on the basis of its reduced flight ability, and we believe that *Rallus eivissensis* lived exclusively in the Pityusic Islands. The extensive fossil bird deposits on Mallorca and Menorca lack the species. Consequently, its distribution range must have been small, and it was probably limited further to some patches of suitable habitat in the Pityusics. Seven Late Pleistocene bird deposits are known from the Pityusic Islands (Alcover 1990), and at least two of them have a rich fossil record (Cova den Jaume Orat at Eivissa, and Cova des Riuets at Formentera) and one is extraordinarily rich (Es Pouàs). The bones of the Eivissan rail are only known from Es Pouàs. Although its ecology is largely unknown, its reduced potential distribution area and the size of the sample

obtained (161 identified bones among an estimated > 120 000 bird bones obtained in Es Pouàs) suggest that the Pityusics actually supported a small population of *Rallus eivissensis*. Only one other Rallid species, *Crex crex*, is present in the fossil record of Eivissa (Sondaar *et al.* 1995). Fossil rails are also known from the Pliocene deposits of Menorca (unpubl. data). Currently, only a few pairs of *Gallinula chloropus* and *Rallus aquaticus* breed in Eivissa.

Rallus eivissensis represents the first endemic species from the Pityusic Islands that is known to have become extinct in recent times. The more recent evidence for its presence postdates, with a $P > 95\%$, 5300 cal BC. The first evidence of humans on the island predates 1880 cal BC, with a $P > 95\%$. The close timing of the human arrival in the Pityusics (Alcover *et al.* 2001), as well as the vulnerability of insular rails to become extinct after human arrival, strongly suggests that its disappearance can be related to the first human arrival. Its reduced flight ability and its presumed small population size probably facilitated its extinction.

ACKNOWLEDGEMENTS

This paper is included in the Research Project BTE2001-0589 of the Dirección General de Investigación, Ministerio de Ciencia y Tecnología (Madrid). The authors are indebted to Nèstor Torres and Cristòfol Guerau de Arellano for their kindly hospitality during the fieldwork campaigns in Eivissa. We are also indebted to Dr S. L. Olson, Dr T. Worthy and Dr J. Cooper for comments and corrections.

REFERENCES

- Agustí, J. & Moyà-Solà, S. 1990. Neogene-Quaternary Mammalian Faunas of the Balearics. *Atti Convegni Lincei. Accademia Nazionale Dei Lincei* **85**: 459–468.
- Alcover, J.A. 1989. Les aus fòssils de la cova de ca na Reia. *Endins* **14–15**: 95–100.
- Alcover, J.A. 1990. Les aus fòssils de les Balears: estat de la qüestió, estratègia d'estudi, interès i perspectives. *Anuari Ornitològic les Balears* **5**: 9–14.
- Alcover, J.A. 2003. Les rates pinyades (Mammalia: Chiroptera) fòssils del jaciment paleontològic del Pouàs (St. Antoni de Portmany, Eivissa). *Endins* **25**: 141–154.
- Alcover, J.A. & Agustí, J. 1985. *Eliomys (Eivissia) canarriensis* n.sgen., n.sp., nou glírid del Pleistocè de la Cova de Ca Na Reia. *Endins* **10–11**: 51–56.
- Alcover, J.A., McMinn, M. & Altaba, C.R. 1994. Eivissa: a Pleistocene Oceanic-like island in the Mediterranean. *Natl Geographic Res. Exploration* **10**: 236–238.
- Alcover, J.A., Moragues, L.I. & Llabrés, M. (eds) 2000a. Les Balears abans dels humans. Monografia de la Societat d'Història Natural de les Balears **8**: 1–78.
- Alcover, J.A., Moyà-Solà, S. & Bover, P. 2000b. Revisió del suposat bòvid de la cova de ca na Reia (Sta Eulària des Riu, Eivissa). *Bolletí la Societat d'Història Natural les Balears* **43**: 111–115.
- Alcover, J.A., Moyà-Solà, S. & Pons-Moyà, J. 1981. Les quimeres del passat. Els vertebrats fòssils del Plio-Quaternari de les Balears. *Monogr. Científiques, Editorial Moll* **1**: 1–260.
- Alcover, J.A., Ramis, D., Coll, J. & Trias, M. 2001. Bases per al coneixement del contacte entre els primers colonitzadors humans i la naturalesa de les Balears. *Endins* **24**: 1–53.
- Alcover, J.A., Seguí, B. & Bover, P. 1999. Extinction and local disappearances of vertebrates in the western Mediterranean islands. Extinctions in near time. Causes, contexts, and consequences. In MacPhee, R.D.E. & Sues, H.D. (eds) *Advances in Vertebrate Paleobiology*: 165–188. New York: Kluwer Academic/Plenum Publishers.
- Boag, P.T. 1984. Growth and allometry of external morphology in Darwin's finches (*Geospiza*) on Isl Boag, P.T. 1984. Growth and allometry of external morphology in Darwin's finches (*Geospiza*) on Isla Daphne Major, Galapagos. *J. Zool., Lond.* **204**: 413–441.
- Bour, R. 1985. Una nova tortuga terrestre del Pleistocè d'Eivissa: la tortuga de la cova de ca na Reia. *Endins* **10–11**: 57–62.
- Burnaby, T.P. 1966. Growth-invariant discriminant functions and generalized distances. *Biometrics* **22**: 96–110.
- von den Driesch, A. 1976. A guide to the measurement of animal bones from archaeological sites. *Bull. Peabody Mus.* **1**: 1–137.
- Filella, E., Gàsser-Casanova, Z., Garcia-Porta, J. & Ferrer-Ferrer, J.A. 1999. Una puesta fòsil de tortuga terrestre en el Pleistoceno de Formentera (islas Pitiusas, archipiélago Balear). *Treballs del Museu Geologia Barcelona* **8**: 67–84.
- Florit, X., Murer-Chauviré, C. & Alcover, J.A. 1989. Els ocells pleistocènics d'Es Pouàs, Eivissa. Nota Preliminar. *Butlletí la Institució Catalana d'Història Natural* **56**: 35–46.
- Gàsser, Z. & Ferrer, J. 1997. Nous jaciments paleontològics del Miocè i Quaternari de Formentera (Illes Pitiüses, Mediterrani occidental). *Bolletí la Societat d'Història Natural les Balears* **40**: 91–101.
- Gasull, L. & Alcover, J.A. 1982. La Cova de Ca Na Reia: desconcertant estació malacològica del Pleistocè de les Pitiüses. *Endins* **9**: 41–44.
- Gibson, A.R., Baker, A.J. & Moeed, A. 1984. Morphometric variation in introduced populations of the Common Myna (*Acridotheres tristis*): An application of the jackknife to principal components analysis. *Syst. Zool.* **33**: 408–421.
- Klingenberg, C.P. 1993. Multivariate allometry. In Marcus, L.F., Corti, M., Loy, A., Naylor, G.J.P. & Slice, D.E., eds. *Advances in Morphometry*: 23–49. New York: Plenum Press.
- Kotsakis, T. 1981. Le Lucertole (Lacertidae, Squamata) del Pliocene, Pleistocene e Olocene delle Baleari. *Bolletí de la Societat d'Història. Natural les Balears* **25**: 135–150.
- Kra, R. 1986. Standardizing procedures for collecting, submitting, recording, and reporting radiocarbon samples. *Radiocarbon* **28(2A)**: 765–775.
- Kuhbier, H. 1984. Introduction. Biogeography and ecology of the Pityusic Islands. In Kuhbier, H., Alcover, J.A. & Guerau d'Arellano, C. (eds) *Monographiae Biologicae*: **52**: 1–5. The Hague: Dr. Junk.
- Livezey, B.C. 2003. Evolution of flightlessness in rails (Gruiformes: Rallidae): phylogenetic, ecomorphological and ontogenetic perspective. *Ornithol. Monogr.* **53**: 1–654.

- Matsuoka, H.** 2000. The Late Pleistocene fossil birds of the central and southern Ryukyu Islands, and their zoogeographical implications for the recent avifauna of the archipelago. *Tropics* **10**: 165–188.
- Mook, W.G.** 1986. Business meeting: recommendations/resolutions adopted by the twelfth International Radiocarbon Conference. *Radiocarbon* **28**: 799.
- Olson, S.L.** 1973. A classification of the Rallidae. *Wilson Bull.* **85**: 381–416.
- Olson, S.L.** 1990. The prehistoric impact of man on biogeographical patterns of insular birds. *Atti Dei Convegni Lincei* **85**: 45–51.
- Olson, S.L. & Wingate, D.B.** 2000. Two new species of flightless rails (Aves: Rallidae) from the Middle Pleistocene 'crane fauna' of Bermuda. *Proc. Biol. Soc. 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. *Proc. Biol. Soc. Washington* **114**: 509–516.
- Palmer, M., Pons, G.X., Cambefort, Y. & Alcover, J.A.** 1999. Historical processes versus environmental factors as determinants of inter-island differences in endemic faunas: the case of the Balearic Islands. *J. Biogeogr.* **26**: 813–823.
- Paul, C.R.C.** 1982. Pleistocene non-marine molluscs from Cala Salada. *Ibiza. Geol. J.* **17**: 161–184.
- Paul, C.R.C.** 1984. Pleistocene non-marine molluscs from Cova de Ca Na Reia, Eivissa. *J. Conchol.* **31**: 79–86.
- Paul, C.R.C. & Altaba, C.R.** 1992. Els mol·luscs terrestres fòssils de les illes Pitiüses. *Bolletí la Societat d'Història Natural les Balears* **34**: 141–170.
- Rohlf, F.J.** 1993. *NTSYS-pc. Numerical Taxonomy and Multivariate Analysis System*, Version 1.18. Exeter, New York: Setauket.
- Seguí, B. & Alcover, J.A.** 1999. Comparison of palaeoecological patterns in insular bird faunas: a case study from the Western Mediterranean and Hawaii. *Smithsonian Contrib. Paleobiol.* **89**: 67–73.
- Slice, D.E., Bookstein, F.L., Marcus, L.F. & Rohlf, F.J.** 1996. A glossary for Geometric Morphometrics. In Marcus, L.F., Corti, M., Loy, A., Naylor, G.J.P. & Slice, D.E. (eds) *Advances in Morphometrics*: 531–551. New York: Plenum Press.
- Sondaar, P.Y., McMinn, M., Seguí, B. & Alcover, J.A.** 1995. Palaeontological interest of karstic deposits from the Gymnesic and Pityusic islands. *Endins 20/Monogr. la Societat d'Història Natural les Balears* **3**: 155–170.
- Steadman, D.W.** 1991. Extinction of species: past, present, and future. In R.L. Wyman (ed.) *Global Climate Change and Life on Earth*: 156–169. New York, NY: Routledge, Chapman and Hall.
- Steadman, D.W.** 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. *Science* **267**: 1123–1131.
- 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*: 51–80. New Haven/London: Yale University Press.
- Stuiver, M., Reimer, P.J., Bard, E., Beck, J.W., Burr, G.S., Hughen, K.A., Kromer, B., McCormac, G., Van Der Plicht, J. & Spurk, M.** 1998. INTCAL98 radiocarbon age calibration, 24 000–0 cal. BP. *Radiocarbon* **40**: 1041–1083.
- Taylor, P.B.** 1996. Family Rallidae. In del Hoyo, J., Elliot, A. & Sargatal, J. (eds) *Handbook of the Birds of the World*, vol. **3**: 108–209. Barcelona: Lynx Edicions.
- Tyrberg, T.** 1998. Pleistocene birds of the Palearctic: a catalogue. *Publ. Nuttall Ornithol. Club* **27**: 1–720.

Received 26 February 2004; revision accepted 18 March 2005.