A NEW SPECIES OF EXTINCT FLIGHTLESS PASSERINE (EMBERIZIDAE: *EMBERIZA*) FROM THE CANARY ISLANDS[1]

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Abstract. Long-legged Bunting (*Emberiza alcoveri*), a new species of extinct passerine, is described from bones found in Cueva del Viento, a volcanic cave at Tenerife in the Canary Islands. Cranial osteology situates the species at one end of the range of variation of the genus. Its reduced forelimb bones and carina sterni, long hindlimb bones, and estimated wing length, weight, and wing loading, show Long-legged Bunting to be a flightless passerine. The ratio of humerus + ulna + carpometacarpus length/femur length is similar to Stephens Island Wren (*Traversia lyalli*) and Long-billed Wren (*Dendroscansor decurvirostris*), two extinct flightless passerines from New Zealand. The reduction of presumed habitat of Long-legged Bunting, the Laurel forest, and the introduction of terrestrial predators to the island seem to be the reasons for its extinction.

Key words: Canary Islands, Emberiza alcoveri, extinction, flightlessness, Long-legged Bunting, new species, paleontology, Passeriformes.

Resumen. Se describe una nueva especie de paseriforme extinto, el Escribano Patilargo (*Emberiza alcoveri*), a partir de huesos hallados en la Cueva del Viento, un tubo volcánico de Tenerife en las Islas Canarias. La osteología craneal de esta especie la sitúa en uno de los límites de variación del género. El tamaño reducido de los huesos de sus alas y carina sterni, sus largas patas junto a su peso, longitud del ala y carga alar estimada, indican que el Escribano Patilargo era incapaz de volar. La relación longitud del húmero + ulna + carpometacarpo/longitud del fémur es similar a la Isla de Stephens (*Traversia lyalli*) y a la del Chochín de Pico Largo (*Dendroscansor decurvirostris*), dos paseriformes extintos no voladores de Nueva Zelanda. La reducción de su posible hábitat, el bosque de Laurisilva, y la introducción de predadores terrestres en la isla parecen ser las razones de su extinción.

INTRODUCTION

The Canary Islands, in the Macaronesian region of the Atlantic Ocean, are 111 km from the northwest coast of Africa, and situated between 27°37′–29°23′N and 13°20′–18°10′W (Fig. 1). Due to their volcanic origin, the islands contain abundant volcanic caves, some of which are important paleontological sites (Alcover and Florit

1987, McMinn et al. 1990, Jaume et al. 1993). The present paper is based upon bones from Cueva del Viento, a cave (site UTM 28RCS3236) at Tenerife, the largest island of the Archipelago. This volcanic cave is a complex system of galleries originated 0.17–0.13 million years ago (Ancochea et al. 1990).

On the floor of Galería de los Pájaros (Hernández et al. 1995), numerous bones of different species of birds, mammals, and one species of lizard (*Gallotia* sp.) were found (Rando and Ló-
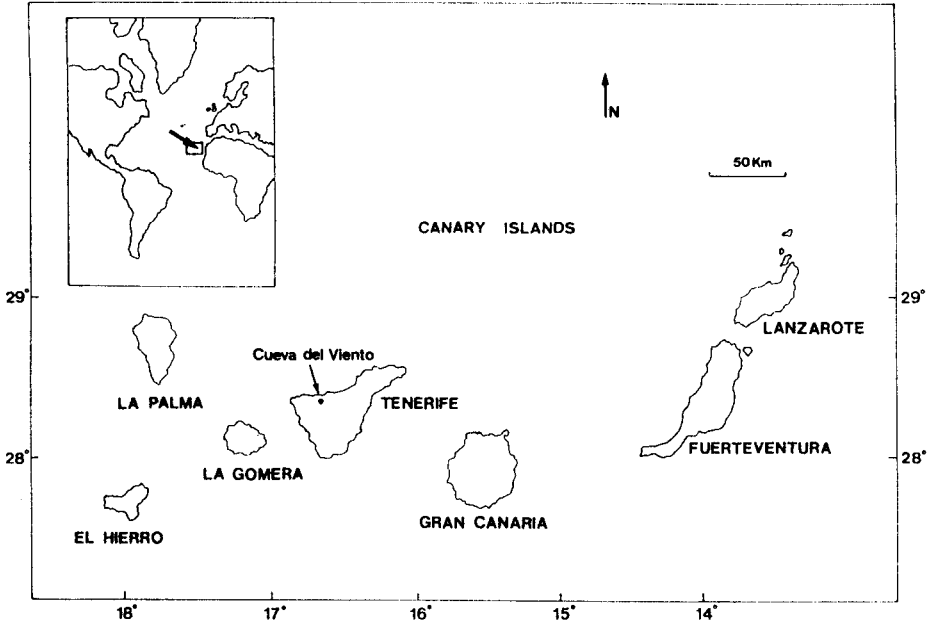
FIGURE 1.   Geographical location of Canary Islands and Cueva del Viento (●) on Tenerife.

pez 1996). The presence of these bones in this remote area of the cave is evidence for the existence of a former entrance, at the bottom of the gallery, now entombed with rocks and sediments. This fact and the small number of visitors in this part of the cave, located more than 1 km south from the entrance and of very difficult access, allowed good preservation of the bones. Some remains were articulated, showing the absence of movement after death. We have identified bones of Houbara Bustard (*Chlamydotis undulata*) (Rando 1995), Buzzard (*Buteo buteo*), Sparrowhawk (*Accipiter nisus*), extinct Canary Islands Quail (*Coturnix gomerae*), Chough (*Pyrrhocorax pyrrhocorax*), pigeon (*Columba* sp.), thrush (*Turdus* sp.), and three more species of passerines (Rando and López 1996).

The purpose of the present paper is to describe one of these species, a new extinct flightless passerine.

METHODS

The bones were collected directly from the cave floor after their locations were plotted on a topographic map of the cave. The fossil material was compared with recent skeletons from Museu de la Naturalesa Ciutat de Mallorca, Palma de Mallorca, Spain (MNCM), United States National Museum (Natural History), Smithsonian Institution, Washington, D.C. (USNM), as well as with specimens loaned by Eulalia Moreno. Anatomical terminology follows Baumel (1993) and Moreno (1985). Measurements were taken to the nearest 0.05 mm, as shown in Figure 2. Comparative material examined is listed in the Appendix.

SYSTEMATIC PALEONTOLOGY

Order Passeriformes
 Family Emberizidae
 Genus *Emberiza* Linnaeus, 1758
 Emberiza alcoveri, new species (Figs. 3–6)

Associated elements of 8 individuals are known.

Holotype. Specimen 1: associated elements including cranium lacking palatal area and jugal bars, complete mandible, right tarsometatarsus (distal part), left tibiotarsus (lacking proximal epiphysis), right tibiotarsus, left ulna (lacking proximal epiphysis), right femur (proximal part), and synsacrum (axial part). Bones numbered individually, CV01–CV08. Collected in August, 1994 by J. C. Rando and M. López.
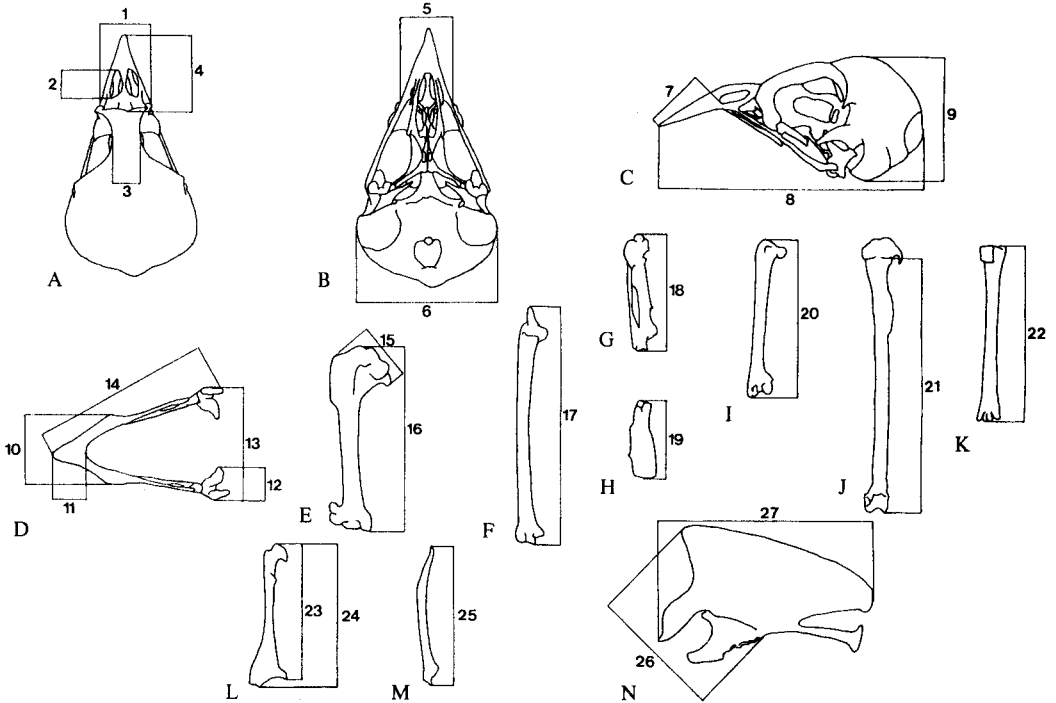
Type locality. Cueva del Viento.

FIGURE 2.   Diagram showing measurements used in this paper (modified from Moreno 1985 and James and Olson 1991). Pictures do not belong to the same species and are not to scale. A: 1, width of nasofrontal hinge; 2, length of narial opening; 3, interorbital width; 4, dorsal length of maxilla. B: 5, width of culmen at jugal articulation; 6, maximum width of braincase. C: 7, length of culmen from anterior edge of narial opening; 8, total length of skull; 9, height of braincase. D: 10, width of mandible at angulus mandibulae; 11, symphysis length; 12, maximum width of articular end; 13, greatest width of mandible; 14, total length of mandible. E: 15, width of proximal epiphysis of humerus; 16, total length of humerus. F: 17, total length of ulna. G: 18, total length of carpometacarpus. H: 19, total length of phalanx proximalis digiti majoris. I: 20, total length of femur. J: 21, length of tibiotarsus excluding crista patellaris. K: 22, total length of tarsometatarsus. L: 23, partial length of coracoid measured from angulus medialis to processus acrocoracoideus; 24, total length of coracoid. M: 25, total length of scapula. N: 26, height of carina sterni measured from apex carina to last incisura intercostalis; 27, total length of sternum.

Distribution. Cueva del Viento. Tenerife, Canary Islands.

Horizon. Upper Pleistocene-Holocene.

Status. Extinct.

Etymology. The specific name is in honor of J. A. Alcover for his contributions to the knowledge of insular vertebrate fossil faunas.

Paratypes. Specimen 2: associated elements including fragmented cranium lacking palatal area, jugal bars, occipital area, and basal braincase, mandible, and right tibiotarsus (CV09–CV11). Specimen 3: associated elements including fragmented braincase, fragmented sternum, fragmented maxilla, left ulna, right humerus, right coracoid, left humerus, right tibiotarsus (lacking proximal epiphysis), right ulna (proximal part), mandible, left tibiotarsus, and femur (medial part) (CV24–CV35). Specimen 4: associated elements of unfused juvenile including left tarsometatarsus, right tibiotarsus, synsacrum (medial part), right ilium and ischium, fragmented left ilium and ischium, left femur (with broken facies articularis acetabularis), right femur (lacking proximal epiphysis), basioccipital fragment, sternum, right humerus, right coracoid, left tibiotarsus (lacking proximal epiphysis), right tibiotarsus (lacking proximal epiphysis), right ulna, left ulna (proximal part), scapula (proximal part), right carpometacarpus, three vertebrae, and a radius (CV36–CV56). Specimen 5: associated elements including right tibiotarsus (lacking proximal epiphysis), left tibiotarsus (lacking proximal epiphysis), left ulna, right ulna, left humerus (lacking proximal epiph-

FIGURE 3. Reconstruction of Long-legged Bunting (*Emberiza alcoveri*), new species, courtesy of A. Bonner.

ysis), left femur (proximal part), right femur (lacking proximal epiphysis), fragmented scapula, synsacrum (axial part), fragmented right tarsometatarsus, fragmented left tarsometatarsus, and two vertebrae (CV58–CV72). Specimen 6: associated elements including three fragments of braincase, fragmented mandible, right humerus, left quadrate, left humerus, left tibiotarsus, left femur, right femur, left ulna, fragmented scapula, left carpometacarpus, and two vertebrae (CV73–CV87). Specimen 7: associated elements including right tibiotarsus, fragment of braincase, frontal area of the cranium with right lacrimal attached, maxilla, right mandible, left mandible (proximal part), left femur, left ulna, right femur, left tibiotarsus, right humerus, left tarsometatarsus, right tarsometatarsus, right carpometacarpus, sternum, synsacrum (axial part), right ilium and ischium, left ilium and ischium, two pedal phalanx, one ungual phalanx, and two ribs (CV88–CV110). Specimen 8: associated elements including right tibiotarsus, left ulna, left tibiotarsus, right femur, left femur (lacking distal epiphysis), right humerus, left humerus, left coracoid, right coracoid, right tarsometatarsus, left ulna, fragmented sternum, right scapula, left carpometacarpus, fragmented mandible, five vertebrae, phalanx 1 of second wing digit, both radii, and one fragmented pterygoid (CV111–VC134).

Institution housing fossil material. Vertebrate Collection of Departamento de Zoología at the Universidad de La Laguna, La Laguna, Tenerife, Spain (DZUL).

Diagnosis. The fossils are attributed to *Emberiza* because of the following combination of characters: the angled premaxilla and maxilla, thin processus postnarialis, ellipsoid narial opening (Moreno 1985), and premaxilla that is not robust and in dorsal view has rapidly converging concave sides. It differs from other known species and is described as a new species larger than any living *Emberiza*, with longer legs and shorter wing elements giving the fossil unique proportions in the genus (Table 1 and Figs. 4–6). The large, globular braincase, has a highly expanded otic area and a strongly developed processus postorbitalis that is more cranially placed. The interorbital bridge is very narrow, with parallel edges. In dorsal view, the caudal margin of the orbit describes a straight angle, with a narrower nasofrontal hinge, a longer and narrower bill that is curved rather than angled, and larger narial openings. The mandibular symphysis is long, height of the ramus mandibulae low, especially at the level of the fenestra mandibulae, with little development of lateral expansions of the angulus mandibulae, the whole bone being slightly built. The foramen orbitonasale is single and elongated (sensu Moreno 1985), and unfused foramen venae occipitalis externae are located on the caudal edge of the foramen magnum.

Postcranial osteological features are rather homogeneous in the genus. In spite of this, some osteological trends can be distinguished in the fossil form, most of them related to the distinct development of forelimb and hindlimb bones. The coracoid has rather weak processus acrocoracoideus, processus lateralis, and facies articularis clavicularis. The humerus has a small proximal epiphysis and weakly developed crista pectoralis. The ulna has unpronounced papillae remigialis caudales. The sternum is broader and shorter, with rostrum and carina sterni weakly developed. The synsacrum is strongly built, with stout antitrochanter and processus terminalis ilii, the later pointing medially. The crista iliaca dorsolateralis is pronounced, with large foramen ilioschiadicum and ossified foramina intertransversaria. The tibiotarsus has a well-developed articular surface, the incisura tibialis being wide and the fossa retrocristalis pronounced, the crista cnemialis lateralis curved and stout.

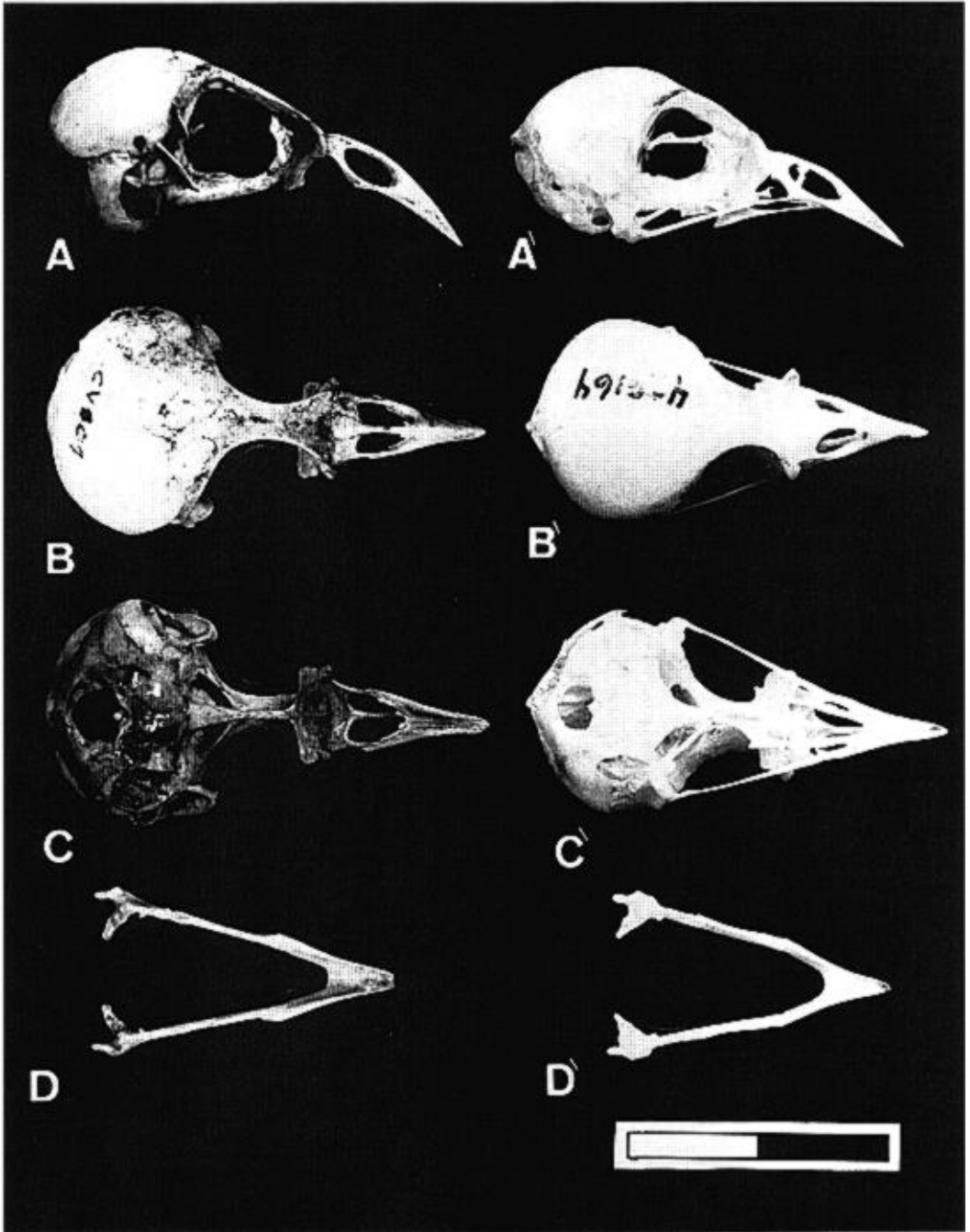*Remarks.* The bill seems rather more curved,

FIGURE 4.   Comparison of cranium and mandible of Long-legged Bunting (*Emberiza alcoveri*), new species, DZUL CV01 Holotype (A–D) with Cabanis's Bunting (*E. cabanisi*), USNM 429164 male (A′–D′). A, B, C and A′, B′, C′ cranium, right lateral, dorsal, and ventral views, respectively. D and D′, mandible, dorsal view. Scale = 2 cm.
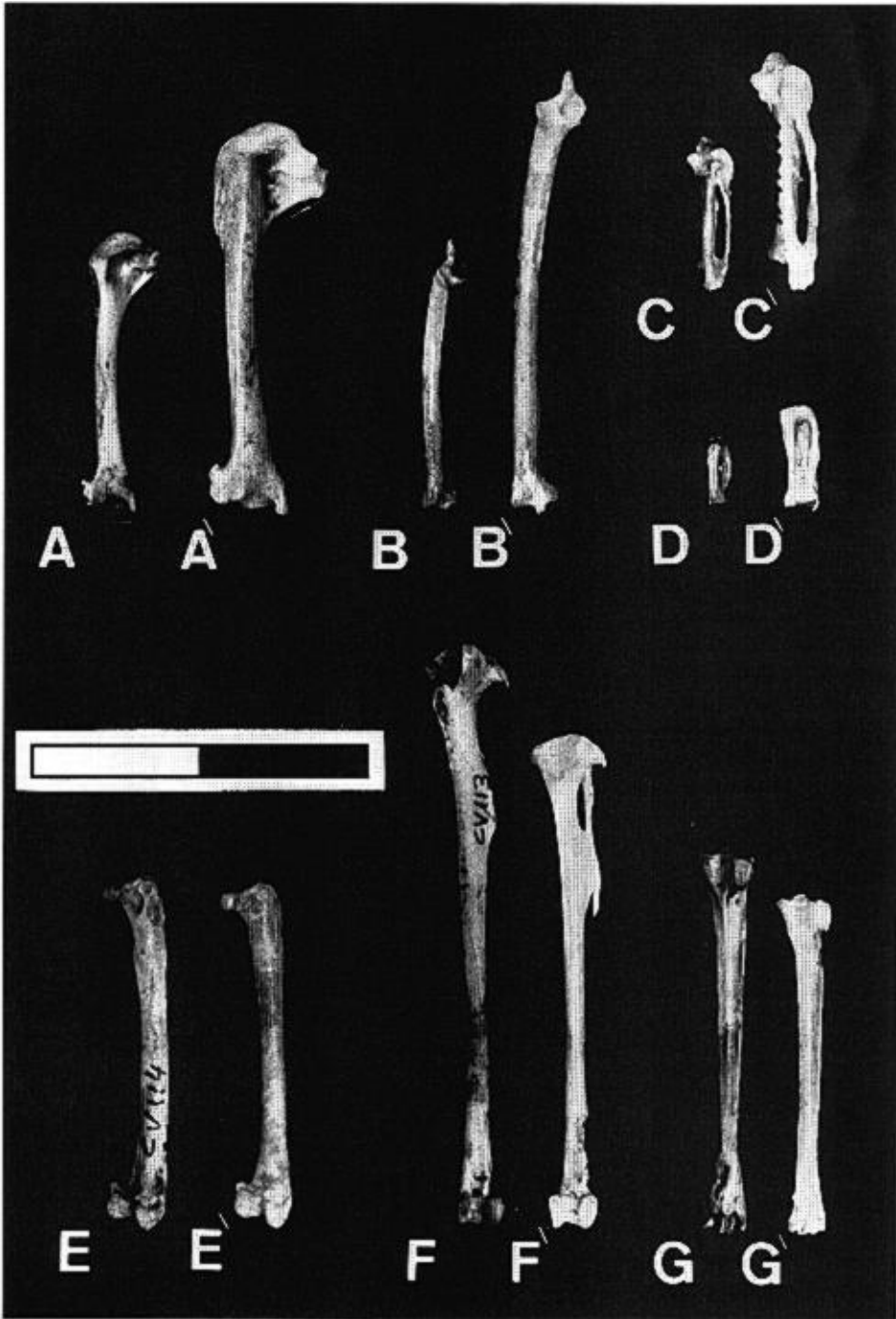
FIGURE 5.   Comparison of wing and leg bones of Long-legged Bunting (*Emberiza alcoveri*), new species, (A–G; several specimens combined) with Cabanis's Bunting (*E. cabanisi*), USNM 429164 male (A′–G′). A, A′ humeri, caudal view; B, B′ ulnae, cranial view; C, C′ carpometacarpi, ventral view; D, D′ phalanx proximalis digiti majoris, dorsal view; E, E′ femora, caudal view; F, F′ tibiotarsi, cranial view; G, G′ tarsometatarsi, plantar view. Scale = 2 cm.
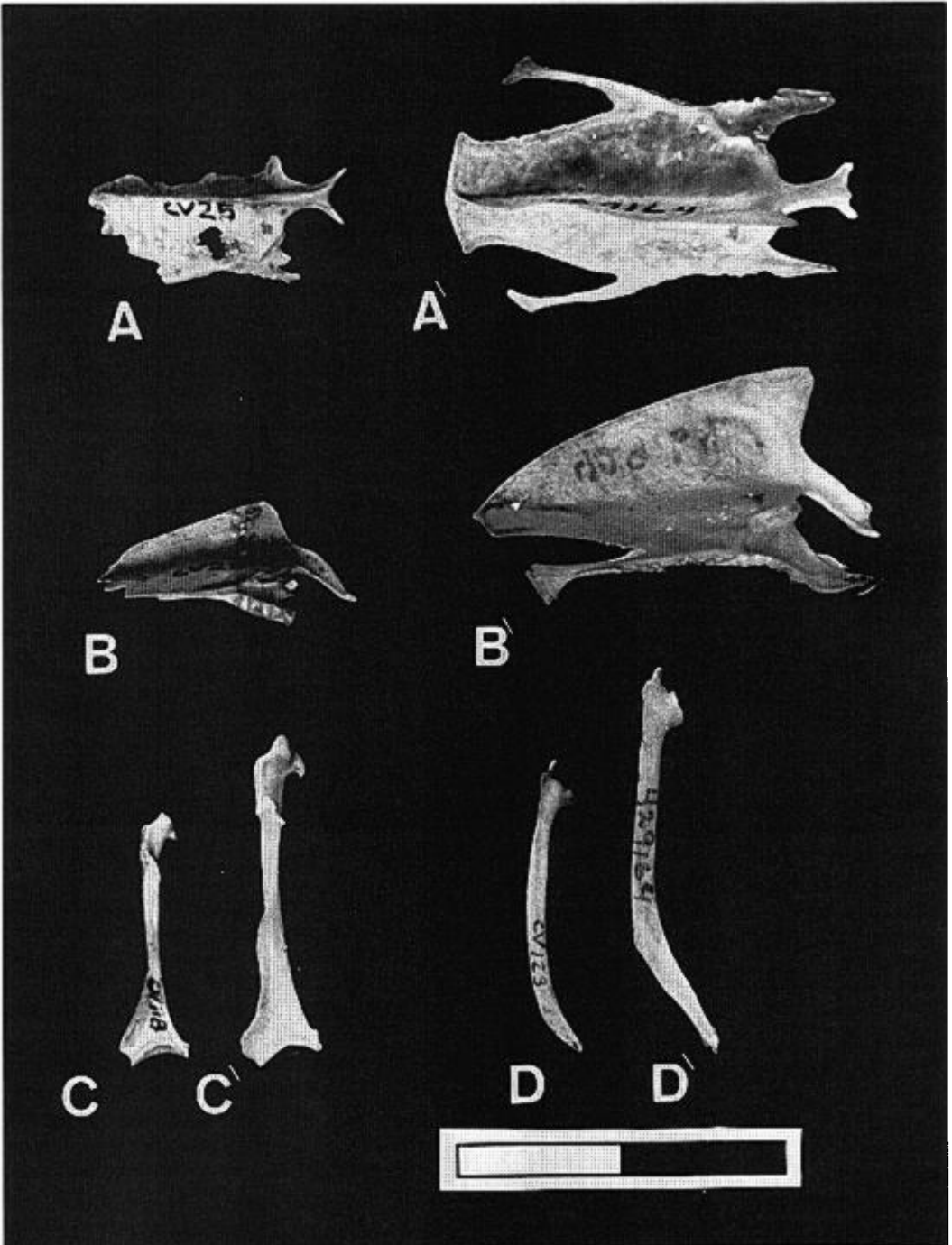
FIGURE 6.   Comparison of skeletal elements of Long-legged Bunting (*Emberiza alcoveri*), new species, (A–D; several specimens combined) with Cabanis's Bunting (*E. cabanisi*), USNM 429164 male (A'–D'). A, B and A', B' sternum, ventral and left lateral views, respectively; C, C' coracoid, dorsal view; D, D' scapulae, medial view. Scale = 2 cm.

TABLE 1. Measurements (mm) of Long-legged Bunting (*E. alcoveri*) and five extant Emberizidae. Just one specimen of Zapata Sparrow (*Zeledonia coronata*) and Cabanis's Bunting (*Emberiza cabanisi*) was available. Means ± SD (*n*) are given. Measurements as in Figure 2.

Measurements	Zapata Sparrow (*Z. coronata*)	African Golden-breasted Bunting (*E. flaviventris*)	Ortolan Bunting (*E. hortulana*)	Cretzschmar's Bunting (*E. caesia*)	Yellowhammer (*E. citrinella*)	Cabanis's Bunting (*E. cabanisi*)	Long-legged Bunting (*E. alcoveri*)
Nasofrontal hinge width	6.15 (1)	4.88 ± 0.19 (6)	4.66 ± 0.19 (7)	4.10 ± 0.23 (6)	4.58 ± 0.13 (3)	5.65 (1)	5.54 ± 0.21 (4)
Narial opening length	4.85 (1)	4.22 ± 0.48 (6)	3.81 ± 0.38 (7)	3.71 ± 0.12 (6)	3.81 ± 0.03 (3)	4.65 (1)	4.51 ± 0.25 (4)
Interorbital width	4.00 (1)	3.13 ± 0.37 (6)	3.25 ± 0.12 (7)	2.90 ± 0.14 (6)	3.55 ± 0.13 (3)	4.00 (1)	3.02 ± 0.32 (4)
Maxilla length	14.19 (1)	12.00 ± 0.74 (6)	12.33 ± 0.69 (7)	11.38 ± 0.40 (6)	11.37 ± 0.26 (3)	14.30 (1)	14.13 ± 0.70 (3)
Culmen							
width	6.20 (1)	4.82 ± 0.27 (6)	4.82 ± 0.23 (7)	4.16 ± 0.27 (6)	4.45 ± 0.13 (3)	5.15 (1)	5.45 ± 0.49 (2)
length	7.60 (1)	5.76 ± 0.46 (6)	5.65 ± 0.46 (7)	5.36 ± 0.17 (6)	5.67 ± 0.15 (3)	6.50 (1)	7.44 ± 0.40 (4)
Cranium							
width	15.80 (1)	13.63 ± 0.26 (6)	14.38 ± 0.26 (7)	14.27 ± 0.36 (6)	15.27 ± 0.28 (3)	15.05 (1)	17.20 ± 0.42 (2)
length	31.40 (1)	27.47 ± 1.16 (6)	28.60 ± 0.56 (7)	27.72 ± 0.65 (6)	28.00 ± 0.58 (3)	31.00 (1)	33.40 (1)
height		11.62 ± 0.23 (6)	11.77 ± 0.20 (7)	13.07 ± 2.61 (6)	11.87 ± 0.54 (3)	12.80 (1)	12.72 ± 0.11 (2)
Mandible							
width	14.00 (1)	11.27 ± 0.57 (4)	11.91 ± 0.53 (6)	11.30 ± 0.18 (6)	12.27 ± 0.21 (3)	12.65 (1)	12.40 ± 0.35 (3)
length	21.55 (1)	18.70 ± 0.32 (5)	20.18 ± 0.80 (7)	18.86 ± 0.80 (6)	19.38 ± 0.21 (3)	22.10 (1)	23.84 ± 0.38 (5)
width at angulus mandibulae	7.15 (1)	6.41 ± 0.18 (5)	7.07 ± 0.21 (6)	5.77 ± 0.45 (6)	7.23 ± 0.03 (3)	6.45 (1)	6.72 ± 0.26 (4)
symphysis length	6.40 (1)	4.14 ± 3.53 (5)	4.40 ± 0.42 (7)	4.04 ± 0.14 (5)	3.40 ± 0.13 (3)	5.10 (1)	5.75 ± 0.16 (5)
articular end width	4.90 (1)	3.53 ± 0.11 (6)	3.68 ± 0.16 (7)	3.64 ± 0.14 (6)	4.10 ± 0.65 (3)	4.15 (1)	4.27 ± 0.16 (6)
Humerus							
length	18.85 (1)	19.46 ± 1.03 (6)	20.24 ± 0.27 (7)	19.49 ± 0.71 (6)	20.53 ± 0.48 (3)	23.10 (1)	16.72 ± 0.24 (5)
proximal epiphysis width	5.40 (1)	5.76 ± 0.21 (6)	6.60 ± 0.11 (7)	6.24 ± 0.34 (6)	6.65 ± 0.26 (3)	6.75 (1)	4.60 ± 0.30 (5)
Ulna length	18.80 (1)	22.57 ± 0.94 (6)	24.69 ± 0.65 (7)	23.48 ± 1.10 (6)	24.32 ± 0.93 (3)	25.90 (1)	16.17 ± 0.54 (6)
Carpometacarpus length	9.85 (1)	12.16 ± 0.54 (6)	14.10 ± 0.40 (7)	13.16 ± 0.68 (6)	14.25 ± 0.35 (3)	14.00 (1)	8.87 ± 0.37 (4)
Phalanx length	4.30 (1)	5.52 ± 0.30 (6)	6.74 ± 0.26 (7)	6.43 ± 0.30 (6)	6.50 ± 0.00 (2)	6.00 (1)	3.95 (1)
Femur length	19.65 (1)	16.99 ± 1.43 (6)	17.73 ± 0.62 (7)	16.85 ± 0.50 (6)	18.28 ± 0.25 (3)	20.20 (1)	19.87 ± 1.79 (4)
Tibiotarsus length	29.75 (1)	25.67 ± 2.14 (6)	28.17 ± 0.70 (7)	26.61 ± 0.71 (6)	29.02 ± 0.88 (3)	27.95 (1)	32.30 ± 1.03 (6)
Tarsometatarsus length	20.95 (1)	18.18 ± 1.23 (6)	19.61 ± 0.46 (7)	18.70 ± 0.71 (6)	20.13 ± 0.49 (3)	20.00 (1)	23.26 ± 0.47 (6)
Coracoid							
total length	17.45 (1)	17.11 ± 0.93 (4)	19.19 ± 0.24 (7)	18.32 ± 0.74 (6)	19.77 ± 0.35 (3)	20.15 (1)	15.25 ± 0.14 (2)
partial length	16.90 (1)	16.52 ± 0.88 (6)	18.19 ± 0.24 (7)	17.46 ± 0.76 (6)	18.63 ± 0.29 (3)	19.20 (1)	14.92 ± 0.24 (3)
Scapula length	19.95 (1)	19.97 ± 0.80 (5)	22.87 ± 0.41 (6)	22.08 ± 0.95 (6)	22.90 ± 0.99 (2)	23.25 (1)	17.90 (1)
Sternum							
length	18.60 (1)	19.94 ± 1.32 (5)	23.84 ± 0.73 (7)	22.20 ± 1.26 (6)	25.62 ± 1.06 (2)	22.20 (1)	11.40 (1)
carina sterni height	10.35 (1)	12.40 ± 0.76 (6)	15.09 ± 0.54 (7)	13.76 ± 1.16 (6)	15.07 ± 0.48 (2)	13.35 (1)	7.73 ± 0.42 (3)

than in other *Emberiza,* because the vertex of the angle, located on the processus dorsonarialis, is ill-defined. The free processus palatinus premaxillaris (Moreno 1985) seems to be noticeable in CV07, but the poorly preserved condition of this feature in all rostral fragments does not allow a strong conclusion about it. Trochlea metatarsi II is stout, flattened, and rotated towards the ventral side of the bone. This is a general feature in all *Emberiza* examined, but with some variation, overlapping in some cases with close taxa such as *Plectrophenax* and *Calcarius.* Expansion of squamosal area is another trend present in most Emberizidae and especially developed in *Emberiza* species (Tordoff 1954, Moreno 1985). In Long-legged Bunting the inflation of squamosals is extreme (Fig. 4).

Cranial osteology suggests that Cabanis's Bunting (*E. cabanisi*), of sub-Saharan distribution, and Yellowhammer (*E. citrinella*), of European distribution, are closer to the endemic Canary Islands species. The similarity with Cabanis's Bunting is mainly due to the rather globose braincase with relatively narrow interorbital bridge and nasofrontal hinge, long, slender, curved rather than angled bill, leading to the elongated condition of the cranium, and a long stylized mandible. Similarity with Yellowhammer is due to the large postorbital processes, a narrow interorbital, very similar shaped narial opening, and a mandible with weak expansion of the cotyla lateralis anteriorly. In spite of these similarities, differences exist largely due to the unique specializations of the fossil species in appendicular and cranial osteology.

The unusual postcranial proportions in Long-legged Bunting can only be explained by means of strong adaptation to ground dwelling. The cranium tends to be of greater dimensions in Long-legged Bunting but the greatest deviation from the general pattern of the genus is the reduced wing elements and the highly developed leg elements. Variation of tarsus length in insular birds was studied by Grant (1966, 1971). Differences in the proportions of the leg bones seem to be related to differences in the type of perches used by some species while foraging. When proportions of these bones change, it is usually the distal ones that change the most. In Long-legged Bunting this pattern is well developed in both wings and legs.

Other osteological features have been proposed in relation to the loss of flight capability.

Millener (1989) pointed out in reference to the sternum of Stephens Island Wren (*Traversia lyalli*), that the bone was broader and shorter, the manubrium sterni absent, the sternocoracoidal area less developed, and the carina sterni highly reduced. In Long-legged Bunting these trends are present but to a smaller degree (holding in mind Cabanis's Bunting as standard), and no loss of structures has occurred. Other features related to flightlessness that also occur in Long-legged Bunting include reduced crista pectoralis in the humerus and inconspicuous papillae remigialis caudales in the ulna (Rich et al. 1975).

DID *EMBERIZA ALCOVERI* FLY?

Evaluating flight capability of a fossil bird is not easy because osteological data may not indicate clearly whether the animal was a weak flyer or flightless (Zusi, pers. comm.). Among Passeriformes, only the Stephens Island Wren and the Long-billed Wren (*Dendroscansor decurvirostris*), two extinct Acanthisittidae from New Zealand, are considered truly flightless (Millener 1989, Millener and Worthy 1991). Millener evaluates reduction of wing elements by comparisons of ratios of combined humerus, ulna, and carpometacarpus length to femur length, the figure being 2.05:1 for Stephens Island Wren, 2.31:1 for Long-billed Wren (from Millener and Worthy 1991, with femur length an estimated value), and 3.26:1 for a fully volant Acanthisittidae. For Long-legged Bunting the figure is 2.10:1 ($n = 4$, considering specimens 4, 6, 7, and 8), 3.33:1 ($n = 7$) for Ortolan Bunting (*E. hortulana*), 3.19:1 ($n = 6$) for African Golden-breasted Bunting (*E. flaviventris*), 3.33:1 ($n = 6$) for Cretzschmar's Bunting (*E. caesia*), 3.23:1 ($n = 3$) for Yellowhammer, 3.12:1 ($n = 1$) for Cabanis's Bunting, and 2.42:1 ($n = 1$) for Zapata Sparrow (*T. inexpectata*) (data from Table 1). In spite of the fact that enlargement of legs tends to decrease this ratio, evolution of hindlimb for ground-dwelling also seems to be associated with flightlessness in Stephens Island Wren ("ran like a mouse," D. Lyall comments, in Millener 1989).

We found for Long-legged Bunting, compared to Cabanis's Bunting (a bird with similar cranial size and characters), a reduction of 81.5% in area of the carina sterni (94.4 mm^2 for Cabanis's Bunting and 17.4 mm^2 for Long-legged Bunting), 29.2% for length of forelimb bones (27.6%, 26.2%, and 36.6% for the humerus,

TABLE 2. Wing areas (from a single wing) and lengths of forelimb bones from six alcohol specimens: four of genus *Emberiza* [one *E. cirlus* 22815 female, one *E. citrinella* 22814 female, and two *Emberiza* sp. 23081 (1) and 22817 (2)], and two *Miliaria calandra* 22507 male (1) and 23074 unsexed (2). All specimens from E. Moreno.

Specimens	Wing area (mm^2)	Forelimb bone length (mm)
Cirl bunting (*Emberiza cirlus*)	5,990	59.7
Yellowhammer (*E. citrinella*)	6,108	56.1
Bunting (*E.* sp.) (1)	5,692	52.5
Bunting (*E.* sp.) (2)	5,840	52.7
Corn Bunting (*Miliaria calandra*) (1)	7,034	69.3
Corn Bunting (*M. calandra*) (2)	7,798	70.7

ulna, and carpometacarpus, respectively), and an increase of 9.7% for length of hindlimb bones (13.5% and 14% for the tibiotarsus and tarsometatarsus, respectively, and a similar size of femur).

In order to estimate the wing loading of Long-legged Bunting, wing areas of six alcohol specimens of genus *Emberiza* were measured. Wing areas were obtained by drawing the shape of the spread wing on millimetric paper. The wing was dissected afterwards and forelimb bones were measured (Table 2). An equation from regression of wing area versus length of forelimb bones was calculated (data from Table 2): $Y = (a + bX)^{-1}$ ($P = 0.002$, $r^2 = 0.92$), with wing area as the dependent variable and length of forelimb bones (X) as the independent variable. According to this equation, wing area was 50.3 cm^2 for Long-legged Bunting and 68.9 cm^2 for Cabanis's Bunting.

Weights of different species of the genus *Emberiza* and Corn Bunting (*Miliaria calandra*) were calculated using the expression $Y = 1.05X^{0.326}$ (Olmos et al. 1996) with tibiotarsus length, the dependent variable, and estimated mass of the bird (X), the independent variable. The real weights of the same species were taken from Cramp and Perrins (1994) (Table 3) to check the validity of this expression. No differences were found between the estimated and real weights (Wilcoxon test, $z = 0.31$, $P = 0.75$).

When applied to the median tibiotarsus length of Long-legged Bunting, this equation indicated a weight of 36.7 g or 35.9% higher than the weight of *E. cabanisi*, which was 23.5 g (mass estimated with the same method).

The ratio body weight/wing area was calculated, and a wing loading of 0.365 g cm^{-2} obtained for Long-legged Bunting. To compare these data, we must use a species of similar body length, because weight varies with the length cubed, whereas the wing area varies with length squared. It follows that the wing loading varies directly with length (Pennycuick 1972). The wing loading of 0.17 g cm^{-2} obtained for *E. cabanisi* is 53% smaller that for Long-legged Bunting.

An equation from regression of forelimb bones versus wing length was calculated (data from Table 3): $Y = e^{3.77+0.01X}$ ($P = 0.002$, $r^2 = 0.860$), considering wing length as the dependent variable and bone lengths (X) as the independent variable. According to this equation, wing length of Cabanis's Bunting (78.3 mm) is 15.8% higher than Long-legged Bunting (65.9 mm).

Change in limb proportions in Long-legged Bunting is higher than in Zapata Sparrow (*Zeledonia coronata*) (a semivolant passerine), and similar to non-volant Stephens Island Wren and Long-billed Wren. The proportions of Long-legged Bunting, its forelimb and hindlimb bones, its very reduced carina and wing length, and

TABLE 3. Median wing length, wing bones length (humerus + ulna + carpometacarpus) (from Moreno 1984 and our data), real weight (from Cramp and Perrins 1994), tibiotarsus length (our data), and weight calculated from regression of seven species of Bunting.

Species	Wing (mm)	Forelimb bone (mm)	Real weight (g)	Tibiotarsus (mm)	Weight calculated from regression (g)
Ortolan Bunting (*Emberiza hortulana*)	85.7	64.0	22.8	28.1	23.9
Cretzschmar's Bunting (*E. caesia*)	82.5	56.1	21.2	26.6	20.2
Rock Bunting (*E. cia*)	79.6	55.1	23.4	27.3	21.9
Cirl Bunting (*E. cirlus*)	79.4	54.5	23.3	27.7	22.9
Yellowhammer (*E. citrinella*)	85.9	57.8	26.7	29.4	27.5
Reed bunting (*E. schoeniclus*)	78.4	50.6	21.1	28.2	24.2
Corn Bunting (*Miliaria calandra*)	97.1	68.3	49.4	34.7	45.7

much higher wing loading, indicate the absence of powered flight.

DISCUSSION

The species of the genus *Emberiza* are omnivorous. Their diet is based mainly on seeds and small invertebrates (Cramp and Perrins 1994). The structure of the bill and mandible of Long-legged Bunting does not show special adaptations for a different diet. However, the strong development of the processes zygomaticus and postorbitalis, which support the muscles adductor mandibulae externus, is significantly different (Fig. 4) and may indicate a diet that included harder seeds than in other species in the genus.

It is difficult to know what the habitat of Long-legged Bunting was. Available data concerning passerines with reduced flight capability and ground-dwelling habits show adaptation to different environments. Stephens Island Wren could have lived in cold, open shrublands (Worthy and Holdaway 1994), and Wren-Thrush (*Zeledonia coronata*), a weak flier of Central America, lives in the dense herb layer of the tropical forest (Hunt 1971). The entrance to the fossil site at Cueva del Viento is situated 700 m above sea level, on cultivated lands, which were an ecotone between Canarian pine (*Pinus canariensis*) forest and Laurel forest (Arco et al. 1990); the latter suffered a drastic reduction, and now is a relict ecosystem. A great variety of seeds (Bramwell and Bramwell 1994) and insects (Oromí et al. 1984) support the idea of Laurel forest or transition forest as a probable habitat for Long-legged Bunting. A dense herb layer would have offered protection from avian predators like Buzzard and Sparrowhawk, which also were present at the fossil site (Rando and López 1996).

The first human population arrived at the Canary Islands over 2,000 years ago (Bravo et al. 1983, Meco 1992). The aborigines introduced goats, sheep, pigs, dogs, cats, and mice on some islands. They cultivated lands and hunted endemic mammals (López and López 1992) and birds (Alcover and Florit 1989, Rando and Perera 1994, Rando et al. 1996, 1997). The second and larger impact was the arrival and colonization by the Europeans in the 15th century. They introduced rats (black rat *Rattus rattus* and Norway rat *R. norvegicus*), and transformed much of the forest into farm land.

Another species that probably lived in a habitat similar to that of Long-legged Bunting, the Tenerife giant rat (*Canariomys bravoi*) (López and López 1987), also is extinct. Bones of the extinct Canary Islands Quail have been found in the cave (Rando and López 1996), but its remains are less numerous than in lowland fossil sites (pers. observ.), where it probably inhabited open woodlands.

Introduced black rats and cats (*Felis catus*) are still present in the forest. The main predator of the White-tailed Laurel Pigeon (*Columba junoniae*), an endemic species that breeds on the ground in Laurel forest, is the black rat (Hernández and Martín 1994); cats also prey on this pigeon (Hernández, pers. comm.).

Long-legged Bunting probably nested in low vegetation or directly on the ground. Its eggs and chicks would have been easily accessible to introduced predators. In the same way, anthropogenic habitat destruction (Santos 1990), leading to reduction of Laurel forests, may have played an important role in extinction of Long-legged Bunting.

Of nearly 100 specimens of birds exhumed in Cueva del Viento, 8% belong to this new species. As mentioned earlier, the other bird species found at this deposit were Buzzard, Sparrowhawk, Chough, extinct Canary Islands Quail, Houbara Bustard, pigeon, *Turdus* sp., and at least two other Passeriformes (Rando and López 1996). The incorporation of these species in the deposit has probably not been random. Rather, the fossil record obtained here must be considered exclusively as a selective sample of the ornithic community from the habitats around the entrance of the cave in the past. Many birds of prey use the hills of the cave for nesting places. Chough also usually nest at the entrance of caves. The presence of these species (Buzzard and Chough) in this deposit is probably related to their "troglophilic" behavior. The birds of prey could have been trapped inside the cave due to their predator activities, whereas ground dwelling species, with weak flying habits, probably were accidentally incorporated into the deposit as a result of their more terrestrial behavior. For such species, the cave served as a selective trap, allowing and, in some way, promoting their entrance into the cave, and hindering their escape. There are many examples of caves that are natural traps for different vertebrates (Alcover 1991).

The finding of a new granivorous passerine of

the genus *Emberiza* in the Canary Islands fits well with the emerging pattern that we have for fossil Canarian birds (Alcover and McMinn 1995). Different authors (Hutterer et al. 1988, Hutterer and Oromí 1993, Alcover and McMinn 1995) consider the fossil vertebrate Canarian fauna to have a strong parallel in the Galápagos Islands. Both archipelagos share striking similarities (for example, small endemic *Tyto*, endemic *Buteo*, lava mice, and large rats). One of the main differences between the two archipelagos, probably related to their different degrees of isolation (100 km to the mainland for Canary Islands versus 1,000 km for Galápagos), is the absence of adaptive radiation in the passerines of the Canary Islands. This contrasts strongly with the Galápagos, where finches display one of the best known examples of adaptive radiation. At the Canary Islands, the different endemic passerine species, Blue Chaffinch (*Fringilla teydea*), Trias's Finch (*Carduelis triasi*), Canary Islands Stone Chat (*Saxicola dacotiae*), and Long-legged Bunting, evolved from different mainland ancestors.

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APPENDIX

Comparative material examined. At least one specimen of all the major genera of Emberizinae was examined. More thorough comparison was done with Old World taxa: *Plectrophenax nivalis* (Snow Bunting) USNM 491667 male, MNCM 20795 1 male and 1 female mixed; *Melophus lathami* (Crested Bunting) USNM 322038 male, USNM 489757 male; *Calcarius laponicus* (Lapland Longspur) USNM 491661 male, USNM 491666 male; *C. pictus* (Smith's Longspur) USNM 489612 female, USNM 489547 male; *Miliaria calandra* (Corn Bunting) USNM 603362 female, USNM 603354 female, MNCM 12137 unsexed, MNCM 9973 unsexed, MNCM 12138 unsexed, MNCM 12040 unsexed, MNCM 12165 unsexed, MNCM 20567 unsexed, MNCM 12537 unsexed, MNCM 20917 unsexed, MNCM 21915 unsexed; *Emberiza citrinella* (Yellowhammer) USNM 226847 male, MNCM 12041 male, MNCM 12039 male, CEMM A-8408124 female; *E. cirlus* (Cirl Bunting) USNM 561903 male, MNCM 12561 female, MNCM 11197 female, MNCM 21964 male, MNCM 20915 unsexed, CEMM A-79117 male; *E. cia* (Rock Bunting) USNM 226792 female, CEMM A-8210095 male, MNCM 12197 unsexed; *E. cioides* (Meadow Bunting) USNM 318358 female; *E. hortulana* (Ortolan Bunting) USNM 604931 unsexed, USNM 603367 male, USNM 603370 female, USNM 604924 male, USNM 604927 female, USNM 603368 male, USNM 604920 female; *E. caesia* (Cretzschmar's Bunting) USNM 603336 male, USNM 603346 female, USNM 603348 female, USNM 603339 unsexed, USNM 603344 male, USNM 604907 male; *E. impetuani* (Lark-like Bunting) USNM 321548 unsexed; *E. tahapisi* (Cinnamon-breasted Bunting) USNM 430677 female; *E. cabanisi* (Cabanis's Bunting) USNM 429164 male; *E. flaviventris* (African Golden-breasted Bunting) USNM 430416, USNM 430655 male, USNM 430679 female, USNM 430678 female, USNM 318632 male, USNM 429162 male; *E. melanocephala* (Black-headed Bunting) USNM 553027 male; *E. schoeniclus* (Reed Bunting) USNM 226793 male, MNCM 6095 unsexed, MNCM 13505 unsexed, MNCM 6069 unsexed, MNCM 12525 unsexed, MNCM 20678 female, MNCM 9952 unsexed; *E. capensis* (Cape Bunting) MNCM (collection number not available); *E. tristrami* (Tristram's Bunting) USNM 318759 unsexed; *E. rutila* (Chestnut Bunting) USNM 344036 unsexed; *E. aureola* (Yellow-breasted Bunting) USNM 557523 male, USNM 318472, USNM 557524 female; *E. fucata* (Chestnut-eared Bunting) USNM 322041 male; USNM 318354 male; *E. pusilla* (Little Bunting) USNM 292852 male, USNM 318587 male, USNM 318588 female, MNCM 20900 unsexed; *E. elegans* (Yellow-throated Bunting) USNM 319392 unsexed, USNM 289936 unsexed, USNM 321877 male, USNM 311878 male; *E. rustica* (Rustic Bunting) USNM 344899 male; *E. spodocephala* (Black-faced Bunting) USNM 200319 male, USNM 500138 female, USNM 500120 female, and USNM 319181 male.