

close to the ground, and in one instance pecked to death by adults from neighboring groups during territorial fights. A mean of 1.60 ± 1.19 young per year survived to adulthood in each group (range 0–3, $n = 13$; Sherman 1995a), which is similar to data from French Guiana. Our estimate of 0.57 ± 0.53 young per year can be low if the three groups watched in 1995 had laid a replacement clutch at the end of the rainy season. Dominant White-winged Trumpeter females can lay up to two consecutive replacement clutches (Sherman 1995a).

We thank all our Nouragues colleagues who reported trumpeter groups and participated in capture operations, Bruno Bellaton and Catherine Julliot who provided two sightings of chicks, Dragan Crnobrnja who brought back a dead chick found at Saint Eugène field station, and Peter T. Sherman who kindly sent us his articles before publication. Peter T. Sherman, Walter D. Koenig, and two anonymous reviewers greatly improved the manuscript. This study was partly financed by a grant from the Office National de la Chasse (91-45) to Marc Théry, and by CNRS URA 1183.

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The Condor 101:909–915
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A LATE TERTIARY WOODCOCK FROM MENORCA, BALEARIC ISLANDS, WESTERN MEDITERRANEAN¹

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Abstract. *Scolopax carmesinae* n. sp. is described from late Tertiary coastal outcrops of Punta Nati (NW Menorca, Balearic Islands). The species is known from one proximal fragment and one complete humerus. Estimated size is 10–20% smaller than living Eurasian Woodcock *S. rusticola*. Although osteological features in the humerus are not as specialized as in modern woodcocks, resembling in some aspects Gallinaginae, the general Scolopacinae conformation is fully recognizable. Differentiation of these two subfamilies must have taken place before the end of the Tertiary.

Scolopax carmesinae n. sp. might have been the ancestor of *S. rusticola*. Except for the recent Nearctic form *S. minor* and the fossil *S. hutchensi*, remaining living and fossil species of *Scolopax*, which are all insular endemic forms, probably originated from sedentary, insular populations of *S. rusticola*.

Key words: biogeography, Late Tertiary, Menorca, paleontology, *Scolopax carmesinae*, Western Mediterranean, woodcock.

Resumen. Se describe *Scolopax carmesinae* n. sp. a partir de un fragmento proximal de húmero y de un húmero completo, extraídos de brechas fosilíferas del Terciario tardío de Punta Nati (NO de Menorca, Islas

¹ Received 11 August 1998. Accepted 8 April 1999.

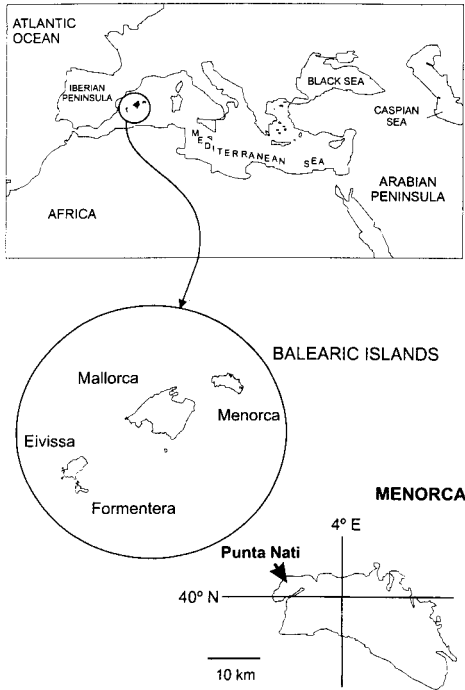


FIGURE 1. Geographic location of Menorca and the fossiliferous outcrops of Punta Nati.

Baleares). Se estima que la especie era entre un 10% y un 20% menor que la actual *S. rusticola*. Las características osteológicas del húmero no son tan especializadas como en las becadas modernas, presentando algunos aspectos en común con la subfamilia Gallinagininae. La conformación general del hueso permite, no obstante, reconocer la morfología propia de las Scolopacinae, de manera que la separación de ambas subfamilias debió ser previa al final del Terciario. *Scolopax carmesinae* n. sp. se sitúa posiblemente en la línea filética que dió origen a *S. rusticola*. A excepción de la especie neártica actual *S. minor* y la fósil *S. hutchensi*, el resto de becadas conocidas, la totalidad de las cuales son formas endémicas insulares, se originaron probablemente por neoevolución a partir de poblaciones insulares sedentarias de *S. rusticola*.

The fossiliferous karstic infillings that outcrop in Punta Nati (NW Menorca, Balearic Islands; Fig. 1) are small, scattered breccia outcrops that are not easily datable, and are thought to cover a wide span of time, probably from the Upper Miocene to the Pleistocene (Bate 1914b, Pons-Moyà et al. 1981, Quintana 1998). Three of these sites (3, 6, and 16) have been considered of Upper Miocene to Pliocene age (Agustí et al. 1982, Agustí and Moyà-Solà 1990, Alcover et al. 1999). Their fauna includes a Testudinidae (*Cheirogaster gymnesica*; Bate 1914a), a Gliridae (*Muscardinus cyclopeus*; Agustí et al. 1982), a Leporidae (genus and species undetermined), a recently known, highly diverse Procariidae avifauna, as well as additional

mammalian and avian remains. Among them is a small species of *Scolopax*.

METHODS

The materials were collected by J. Quintana and S. Moyà-Solà in August 1995. Fossil remains were obtained by treating the breccia matrix with acetic acid and then consolidated with Paraloid. The bones are catalogued in the collection of the Institut de Paleontologia de Sabadell (IPS; Sabadell, Spain). Their study involved comparison with specimens from the vertebrate collection of the Museu de la Naturalesa de les Illes Balears (Ciutat de Mallorca) (MNCM; Palma de Mallorca, Spain), the Département des Sciences de la Terre of the Université Claude Bernard Lyon 1 (DSTL; Lyon, France), and the United States National Museum (Natural History), Smithsonian Institution (USNM; Washington, D.C.).

Measurements were taken as follows: (1) maximum length of the humerus, (2) width of proximal epiphysis, from the outer edge of tuberculum dorsale to the outer edge of crista bicipitalis, (3) maximum width of distal epiphysis, (4) dorsoventral width of the diaphysis measured in the middle of the shaft, (5) craniocaudal width of the diaphysis measured at the same point, and (6) distance from the apex of processus supracondylaris dorsalis to the distal edge of condylus dorsalis. All measurements were taken using a caliper graduated up to 0.05 mm.

The anatomical terminology follows Howard (1929) and Baumel (1993); orientation of the bones is in accordance with the latter author. Classification follows del Hoyo et al. (1996).

SYSTEMATIC PALEONTOLOGY

Order Charadriiformes (Huxley)
 Family Scolopacidae Vigors
 Subfamily Scolopacinae (Vigors)
 Genus *Scolopax* Linnaeus 1758
Scolopax carmesinae n. sp.

Holotype. Right humerus with proximal epiphysis crushed, IPS 11823 (Fig. 2C, F). Collected in August 1995 by Josep Quintana and Salvador Moyà-Solà.

Type locality. Point 6, Punta Nati, Menorca, Gymnesic Islands (Balearic Archipelago).

Age. A pre-Messinian age was first assigned (Agustí et al. 1982, Agustí and Moyà-Solà 1990). Nevertheless, Alcover et al. (1999) proposed a Lower or Middle Pliocene age for the deposits of Punta Nati containing the Leporidae.

Etymology. From Carmesina, the princess of the "Greek Empire" in the XVth century Catalan novel *Tirant lo Blanc*. But "carmesina" can also mean in Catalan a reddish color, similar to that of the clay that entombed the bones of this woodcock through time. The specific name is used here in the genitive case.

Paratypes. Proximal half of right humerus, IPS 0194 (Fig. 2B, E). Collected in August 1995 by Josep Quintana and Salvador Moyà-Solà.

Additional material. A badly preserved proximal fragment of a right carpometacarpus, MNCM 47362, is tentatively referred to the species. As its ascription is not sure, it is not advisable to include it in the type series.

Measurements. Table 1.

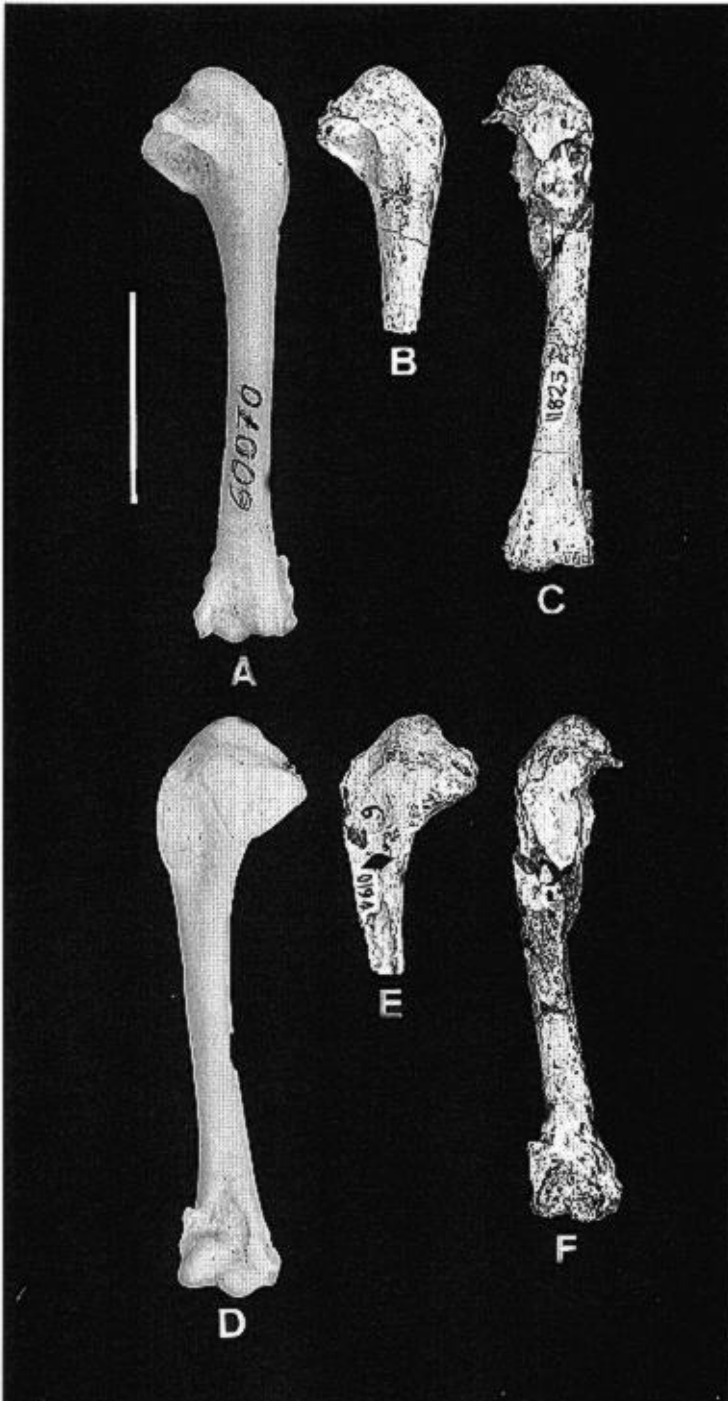


FIGURE 2. Caudal view of right humerus of: (A) *Scolopax rusticola* MNM 60070; (B) *S. carmesinae* n. sp. IPS 0194 paratype, and (C), IPS 11825 holotype. (D–F), same in cranial view. Scale = 2 cm.

TABLE 1. Measurements of the humerus of *Scolopax carmesinae* n. sp. and *S. rusticola*. Mean \pm SD, range, and sample size are given for recent samples of *S. rusticola*. Numbers at left hand column refer to measurements taken as specified in Methods. See Olson (1976) for measurements of the humerus of *S. anthonyi* and *S. minor*, and Emslie (1998) for measurements of *S. hutchensi*. P = paratype, all others holotype.

	<i>S. carmesinae</i> n. sp.	<i>S. rusticola</i>
1	48.0	54.6 \pm 2.2 52.4–60.0 n = 9
2	11.7 ^P	13.5 \pm 0.4 13.2–14.5 n = 9
3	9.1	9.9 \pm 0.3 9.5–10.3 n = 9
4	4.2	4.3 \pm 0.1 4.2–4.6 n = 9
5	3.4	3.8 \pm 0.1 3.6–4.1 n = 9
6	7.4	8.1 \pm 0.2 8.0–8.4 n = 9

Comparison material examined. A preliminary comparison was completed with almost all genera of Western Palearctic Charadriiformes. A more detailed examination of Scolopacinae and Gallinaginae was undertaken: *Limnodromus griseus* DSTL 177.1; *Lymnocryptes minimus* DSTL 160.2, MNM 21736, MNM 39430, MNM 39423, MNM 39426, and one unnumbered specimen in MNM; *Gallinago gallinago* DSTL 158.1, 158.2, 158.4, 158.5, 158.6, 158.7, three unnumbered specimens in MNM; *Scolopax rusticola*, DSTL 161.1, 161.2, 161.3, 161.4, MNM 3823, 6025, 9958, 9968, and one unnumbered specimen in MNM; *S. minor*, seven specimens were examined in USNM (collection numbers not available).

Diagnosis. Humerus (IPS 11823, 0194) intermediate in size between *Scolopax minor* and *S. rusticola*, 10 to 20% smaller than the latter in length. Proximal margo caudalis as in *Scolopax*, but not in Gallinaginae, without a well developed proximodistal ridge. Crista bicipitalis not as expanded as in *S. rusticola* (Fig. 2A, D) (despite it being somewhat abraded in the fossil). Excavation under caput humeri not as well defined, despite this feature being somewhat variable.

Processus supracondylaris dorsalis pointing proximally as in Scolopacinae and Gallinaginae, not caudally as in other subfamilies. Well developed, as in *Scolopax rusticola*, not reduced to a round tuberculum, as in *S. minor*; not as distally placed as in *S. rusticola* resembling somewhat the tendency shown by Gallinaginae. Fossa m. brachialis deeper, more ventrally expanded, tuberculum supracondylare ventrale more ventrally placed, not as cranial as in *S. rusticola*. Processus flexorius not as distally developed nor ventrally

protruded, the whole distal epiphysis not as expanded as in *S. rusticola*.

Remarks. Among the Scolopacidae, the Scolopacinae and Gallinaginae share a number of features that caused them to be grouped previously in the Scolopacinae. In the distal humerus, the shape of the processus supracondylaris dorsalis separates them from other subfamilies. Nevertheless, *Scolopax* differs from the Gallinaginae by unique characters such as the absence of the external tricipital groove, the more distally placed processus supracondylaris dorsalis, the more expanded distal epiphysis, with a wide, shallow olecranal fossa, and the more distally and ventrally developed processus flexorius. It also is in some of these features where differences among *S. rusticola* and *S. carmesinae* n. sp. are to be found. In *S. carmesinae* n. sp. we recognize a modern woodcock, but with osteological trends in the humerus not so developed as in *S. rusticola* or *S. minor*. It is obvious that both chronologically and morphologically, the fossil form is closer to the point of divergence of *Scolopax* and Gallinaginae.

A fragmentary proximal carpometacarpus, MNM 47362, could also belong to *Scolopax carmesinae* n. sp. Its size is coincident with that of the species, assuming the same body proportions as in recent *S. rusticola*. Morphologically, the fossil also seems to be intermediate between *Scolopax* and Gallinaginae. It resembles *Gallinago gallinago* and differs from *S. rusticola* in the absence of a tuberculum on the ventral edge of the os metacarpale minus, where the bone joins the os metacarpale majus. In *Lymnocryptes minimus* the feature is present but rather undeveloped. As in *S. rusticola* and *L. minimus*, versus *G. gallinago*, the os metacarpale minus is not ventrally expanded in its proximal insertion. The fossil differs from *S. rusticola* and to a lesser degree from *G. gallinago* and *L. minimus* in the absence of a protruded area between fossa infratrochlearis and the processus pisiformis, in the shorter symphysis between os metacarpale minus and majus and in the relative position of both bones, the os metacarpale minus being more ventral in the fossil, and parallel to os metacarpale majus in the insertion area, not angled and divergent towards the distal epiphysis. Some of these differences point to a similarity with other Scolopacidae such as *Philomachus* or *Tringa*, and combined with the poor preservation of the bone, it cannot be certainly ascribed to *S. carmesinae* n. sp.

Apart from the six recognized, living species of *Scolopax* (*S. rusticola*, *S. mira*, *S. saturata*, *S. celebensis*, *S. rochussenii*, and *S. minor*) and a possible new species from the Philippines (del Hoyo et al. 1996), there are just two fossil forms assigned to the genus: *S. anthonyi* (Wetmore 1920), from the late Pleistocene or even more recent (Olson 1976) of Puerto Rico, and *S. hutchensi*, from the late Pliocene and Pleistocene of Florida (Emslie 1998). *Scolopax anthonyi* was first described in *Gallinago*, but was moved to *Scolopax* by Olson (1976). Its size is intermediate between *S. minor* and *S. rusticola*. *Scolopax hutchensi* is a small woodcock, with the humerus of similar length but seemingly more slender than *S. carmesinae* n. sp. (see Emslie 1998). It is known from several skel-

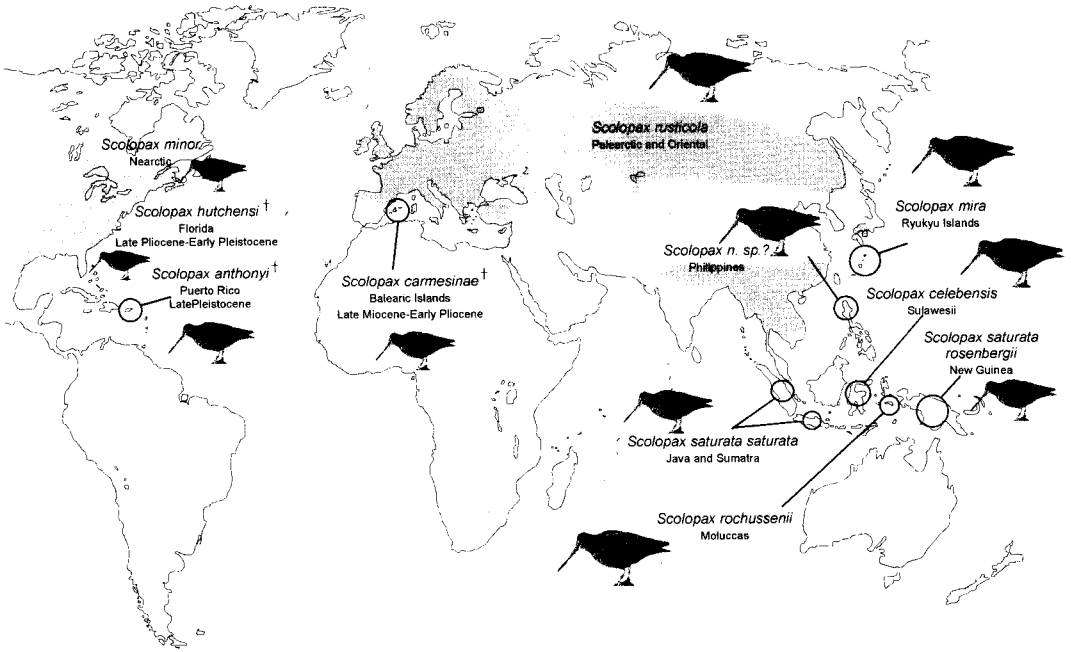


FIGURE 3. Geographical distribution of fossil and living species of the genus *Scolopax*.

etal elements and its osteology is most similar to *S. minor*, despite proportions that do not seem to be identical to this species (Emslie 1998).

Scolopax ghardalamensis (Fischer and Stephan 1974), from the Pleistocene of Malta, was revised by Olson (1976), who found the species to be invalid. *Scolopax baranensis* (Jännösy 1979), from the Lower Pliocene of Hungary, is a *nomen nudum* (Mlikovsky 1992). This species was described based on a proximal fragment of the right carpometacarpus, that according to the diagnosis, was of similar size to *S. rusticola* but of more slender proportions. Measurements given are difficult to standardize: proximal width of the bone is 3.2 mm, and thickness of the diaphysis measured immediately distally from the processus metacarpalis I is 2.5 mm. Dorsoventral and craniocaudal width of the proximal epiphysis of the carpometacarpus MNM 47362, tentatively referred to *S. carmesinae* n. sp., and dorsoventral and craniocaudal thickness of the diaphysis are respectively 3.05, 7.25, 2.35, and 3.35 mm. In accordance with the description and with the insignificance of the proximal carpometacarpus among Scolopacidae (see above), it is improbable that the material from Menorca and from Hungary belong to the same bird.

Specimens of just two of the living species have been examined, because comparison material of *Scolopax mira*, *S. saturata*, *S. celebensis*, and *S. rochussenii* was not available. *Scolopax mira* (Fig. 3) inhabits the central Ryukyu Islands, and sometimes has been considered as conspecific with *S. rusticola*. *Scolopax saturata* lives in montane habitats of Sumatra, Java, and New Guinea, and is somewhat smaller than *S. rusticola*—mean tarsus length of 10 skins in the British

Museum of Natural History is 35.16 mm, compared with 35.7 and 36.2 for two samples of the latter species in Cramp and Simmons (1983). *Scolopax celebensis* and *S. rochussenii* inhabit respectively central and north-east Sulawesi and the north Moluccan Islands, and are considered to form a superspecific group in the genus (del Hoyo et al. 1996). It is unlikely that any of these woodcocks represent the same taxon as *S. carmesinae* n. sp., owing to size and geographic distribution.

DISCUSSION

In the light of present data, there are two possible hypotheses to explain present and fossil configuration of the genus *Scolopax*. *Scolopax carmesinae* n. sp. could be considered as an ancestor of *S. rusticola* lineage. There is no conclusive evidence for the existence of pre-Pleistocene palearctic forms of *Scolopax*, and transition between these two forms could certainly have been accomplished by an increasing size combined with specialization of the skeleton. *Scolopax rusticola* is discontinuously but widely distributed through the Palearctic, the Oriental region, and the northern islands of the Australasian realm (Fig. 3). All other living or fossil species in the genus are islanders except *S. minor* and *S. hutchensi*. At least four forms of *Scolopax* evolved in no less than six islands in the Oriental and north Australian region: the two subspecies of *S. saturata*, *S. s. saturata*, and *S. s. rosenbergii*, and the related *S. celebensis* and *S. rochussenii*. *S. mira* also is an insular endemic form in the easternmost Palearctic. On the island of Mindanao (Philippines), another species of *Scolopax* seems to have evolved, possibly new to science, distinct from the *S. rusticola* known

to winter there (del Hoyo et al. 1996). All these species, far from the general condition of *S. rusticola*, are sedentary. There also is strong evidence of sedentary populations of *S. rusticola* in the Azores, and Madeira and Canary Islands (Cramp and Simmons 1983, Hayman et al. 1988). This fact suggests a pattern of sedentation in certain insular environments in *S. rusticola* lineage that could have given rise to the other mentioned species by insular evolution. *Scolopax anthonyi*, the fossil form from Puerto Rico, also would fit in this pattern, and such an origin has already been postulated, derived from a *rusticola*-like stock that colonized North America (Olson 1976).

Scolopax minor is unique in the genus due to its high degree of specialization in the postcranial skeleton (Olson 1976) and skull morphology (R. L. Zusi, in Olson 1976), leading ornithologists to assign it its own genus, *Philohela*, for many years. Like *S. rusticola*, *S. minor* is monotypic and mainly migratory over a wide continental range. Nevertheless, an origin from *S. rusticola* also has been postulated for the species (Olson 1976) as mentioned previously. The specialized condition would have been attained after colonization of the New World. The endemic species from Puerto Rico, *S. anthonyi*, also could have evolved from a *rusticola*-like colonizer that reached the Antilles from North America before *S. minor* attained the morphological characteristics that separate it from *S. rusticola* (Olson 1976). It is uncertain why in the period of time in which *S. minor* developed specialization, *S. anthonyi* remained rather unmodified, being more similar, in its osteology, to *S. rusticola* than to *S. minor*.

An alternative hypothesis is a transatlantic origin of *Scolopax anthonyi*, probably in a more recent arrival of Old World woodcocks to the New World. This hypothesis is supported by the existence of sedentary populations of *S. rusticola* on Atlantic islands, as far west as the Azores. That no other species of *Scolopax* is known from the Antilles also supports this alternative. If the origin was Nearctic, insular radiation would be expected as happened in the Oriental and Australian regions. Puerto Rico is the only island known to have been colonized by a woodcock, and is the easternmost of the Greater Antilles. The other nearctic *Scolopax* species, *S. hutchensi*, is known only from sites on the mainland, and it appears to have had relatively longer wings in reference to leg bones if compared to *S. minor* (Emslie 1998). This pattern fits with a continental, fully volant form rather than with an insular sedentary species. As stated by Emslie (1998), morphological characters of the species are close to those of *S. minor*, and the age is older than that of *S. anthonyi*.

Scolopax anthonyi would fit in the modern assemblage of *rusticola*-derived species, originated by colonization and sedentation on extralimital islands, in the same way in which populations became sedentary in the southern limit and in the areas of Atlantic and East Indian influence of the present-day distribution range. *Scolopax minor* and *S. hutchensi* might have originated via other evolutionary pathways, not necessarily so recent.

It is difficult to ascertain whether *Scolopax carmesinae* n. sp. was a migratory, probably widespread woodcock, similar to living *S. rusticola* or *S. minor*,

or whether it was rather an endemic, sedentary species in Menorca. The first possibility fits well in the evolutionary pattern described for the group, whereas in the second case, some nesoevolutive speciation would be expected. In *S. anthonyi*, for example, the carpometacarpus was proportionately shorter than in modern *S. rusticola*. This fact was understood as a reduction in flight requirements, a consequence of sedentation in an insular environment (Olson 1976). No complete carpometacarpus of *S. carmesinae* n. sp. is known, but fragment MNCM 47362, if certainly referable to the species, may provide some light. The relation of the width of the proximal epiphysis of the carpometacarpus to the length of the humerus is only 1–2% smaller than in the case of recent *S. rusticola* (four specimens in MNCM). The relation of carpometacarpus length to humerus length is 6–8% smaller in *S. anthonyi* than in *S. rusticola* (data from Olson 1976). If the fragmented carpometacarpus really represents *S. carmesinae* n. sp., proportions of the species probably would not be different from those of *S. rusticola*.

Menorca is at present in the migratory route of *Scolopax rusticola*. Partially sedentary populations are recognized in north Mediterranean coasts (Cramp and Simmons 1983). Nevertheless, no sedentary population is known to exist on any Mediterranean island today. These islands are probably not suitable environments for woodcocks to settle in, if geographic position in reference to the migratory routes and phyto-geographic affinities of the islands in which sedentary populations and endemic species of *Scolopax* exist or have existed are considered.

I thank Salvador Moyà-Solà and Josep Quintana for facilities in studying the materials they collected in Menorca. I also thank Cécile Mourer-Chauviré, Storrs L. Olson, Josep A. Alcover, and Joan J. Fornós for a critical review of the manuscript. Cécile Mourer-Chauviré kindly helped me during my stay in the Université Claude Bernard (Lyon), and subsequently sent some additional measurements. Joanne Cooper also provided me with some useful measurements. Antoni Ginard assisted me with scientific nomenclature. I appreciate the improvements in English usage made by W. Belton through the Association of Field Ornithologists' program of editorial assistance, and Charles D. Duncan's kind help during the process. I thank S. D. Emslie and an anonymous reviewer for their comments on the manuscript. This work has been funded by a Ministerio de Educación y Cultura (Spanish Government) doctoral grant and by the DGICYT project PB94-1175.

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