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► **To cite this version:**

Monica Gala, Arnaud Lenoble. Evidence of the former existence of an endemic macaw in Guadeloupe, Lesser Antilles. *Journal für Ornithologie = Journal of Ornithology*, 2015, 156 (4), pp.1061-1066. 10.1007/s10336-015-1221-6 . halshs-01393267

HAL Id: halshs-01393267

<https://shs.hal.science/halshs-01393267v1>

Submitted on 7 Mar 2023

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Evidence of the former existence of an endemic macaw in Guadeloupe, Lesser Antilles

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ABSTRACT — The discovery of a bone referred to the genus *Ara* Lacépède, 1799 from a Pleistocene fossil-bearing deposit on Marie-Galante demonstrates macaws to have been present in Guadeloupe before any Amerindian settlement. This directly contradicts the hypothesis that macaws described in historical records concerning the Lesser Antilles were introduced by native peoples from South America. The fossil bone is a terminal phalanx similar in size to a large macaw. Based on its size and geographic arguments, the fossil bone found on Marie-Galante can be attributed to an endemic large macaw (Lesser Antillean Macaw, *Ara guadeloupeensis* Clark in Auk 22:266–273, 1905) presumed to have inhabited the Guadeloupe Islands. This discovery currently provides the strongest evidence supporting the former existence of this now-extinct macaw.

Received 27 October 2014; Reviser 12 January 2015; Accepted 7 April 2015.

Key words — *Ara guadeloupeensis*; Extinct birds; Guadeloupe; Marie-Galante; Macaw; Pleistocene; fossil-bearing deposit.

Introduction

Only a limited number of macaw bones are currently known from the Lesser Antilles. All documented instances of macaw bones have been recovered from archaeological contexts and, consequently, it is impossible to exclude these examples representing birds introduced to the islands as pets or for commerce by Amerindians (Olson and López 2008; Wiley and Kirwan 2013). Moreover, only two Psittacidae are known from the Guadeloupe islands: an Amazon parrot bone (*Amazona* sp.) from the Amerindian site of Petite-Rivière, La Désirade (Grouard 2001) and an ulna found by Barbotin during his excavations at Folle-Anse, Marie-Galante. This latter specimen, initially thought to belong to the Lesser Antilles Macaw *Ara guadeloupensis* (Williams and Steadman 2001), was recently reassigned to the extinct *Amazona violacea* by Olson and López (2008).

As it stands, the sparse archaeological record does not support the existence of an endemic macaw formerly inhabiting Guadeloupe. Establishing such a presence would require new material providing evidence for a distinct species, as exemplified by the *Ara autochtones* described on Hispaniola and Puerto Rico (Wetmore 1937; Olson and López 2008), or the documentation of a specimen from a pre-colonization context.

Here, we report a terminal Psittacidae phalanx found in a late Pleistocene fossil deposit from Marie-Galante, whose size and morphology support it representing a member of the genus *Ara*. This find provides credible evidence for the existence of a now-extinct endemic macaw in Guadeloupe.

Materials and methods

The Psittacidae bone from Blanchard Cave was compared to specimens from the comparative zoology collection held by the PACEA laboratory (PACEA), the Bivaag research project (BIVAAG), both housed in the Bordeaux University, and the Natural History Museum of Paris (MNHN). Samples for radiocarbon dating were pretreated by the Radiocarbon Dating Center in Lyon, France (lab code: Lyon), while isotopic ratio were measured by the mass accelerator Artemis housed at Saclay, France (lab code: SacA).

Blanchard Cave is a fossil-bearing site in south-western Marie-Galante (Lenoble et al. 2009), one of the islands forming the Guadeloupe archipelago (Fig. 1). Lying 200 m from the current shoreline, the site comprises a single 30-m-long chamber opening onto the coastal plain. Excavations conducted in the spring of 2013 and 2014 revealed a 4-m-deep deposit overlain by a pre-Columbian layer (Goetz et al. 2014). The avian assemblage recovered from the non-anthropogenic deposits consists of 341 bones, primarily Passeriformes (54 %) and Procellariiformes (6 %), with a single bone (GB2013-I32c-d23) referred to a Psittacidae.

Twelve layers, containing the remains of frogs, lizards, snakes, birds and bats in variable proportions, have been identified, with the Psittacidae bone recovered from a depth of 1 m in the 15-cm-thick layer 5. This layer is preserved at the base of the rearwall of the cave and overlain by a thick rubble layer, which excludes any potential disturbance by crab burrows or Amerindian postholes. This

layer, as well as the main portion of the deposit, is a soft organic silt composed of microscopic fragments of vegetal tissues indicative of a fossil guano produced by frugivorous bats (Lenoble et al. 2009). Authigenic phosphates minerals are also abundant, suggesting that others animals, such as insectivorous bats or birds of prey, contributed to the layer's formation (Bos 2012). A radiocarbon date obtained on a sample of the organic fraction from the layer 5 sediment produced an age of $10,690 \pm 70$ years uncal BP (Lyon-6976_SacA 19445). Good agreement with the dating of the overlying rubble layer (layer 3, 9740 ± 50 years uncal BP, Lyon-5726_SacA-14261) and underlying layer 6 ($14,010 \pm 80$ years, Lyon-6977_SacA 19446) indicates that the formation of layer 5 can be securely placed to the latest Pleistocene.

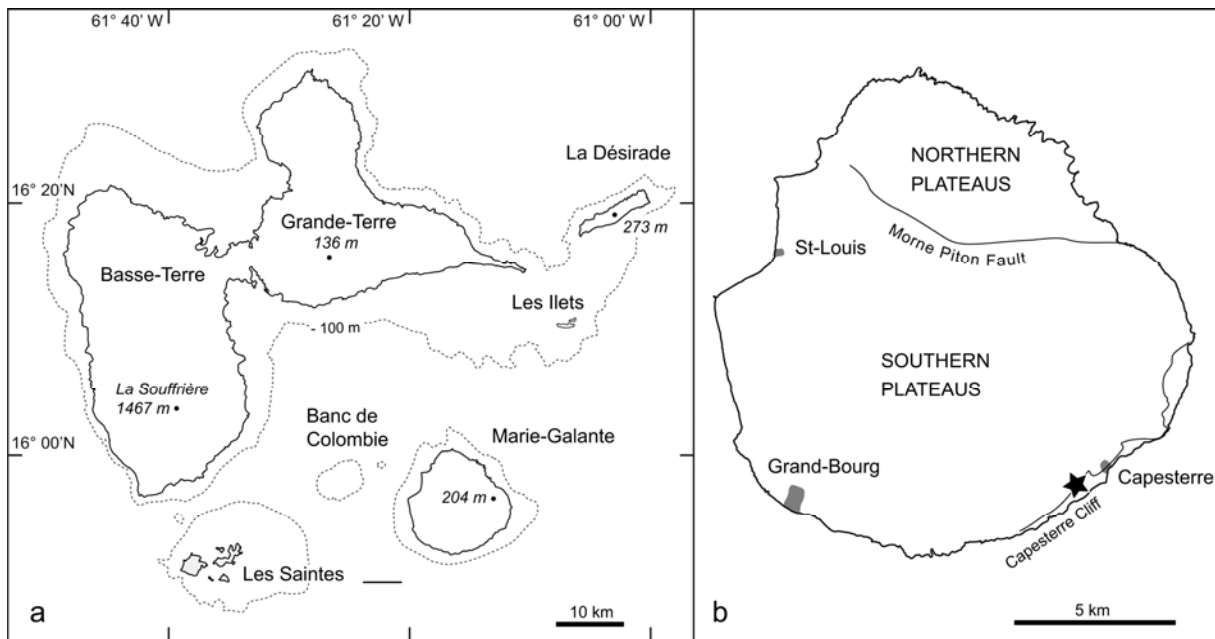


Figure 1. Site location. a Guadeloupe Islands with isobaths (-100 m) indicating lowered sea levels during the Last Glacial (bathymetric data from the IGN-SHOM). b Marie-Galante Island with location of the site (black star).

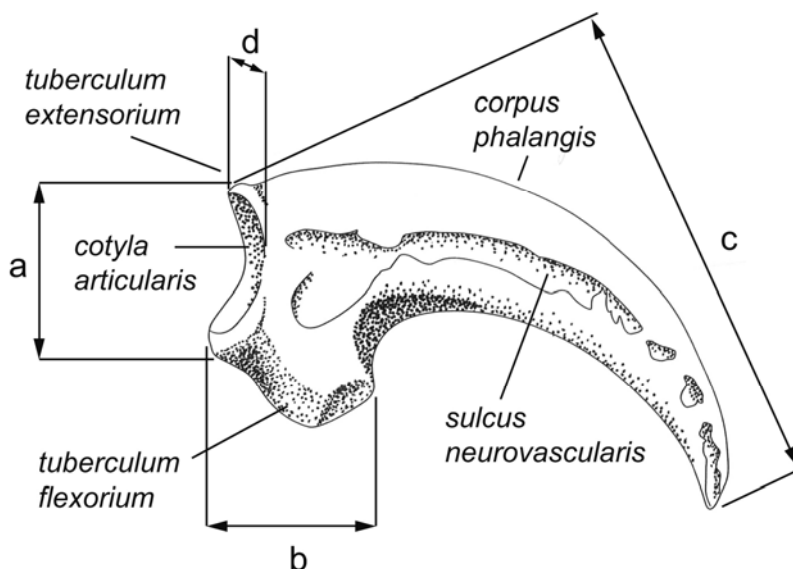


Figure 2. *Psittacidae* unguis bone with indication of measurements taken (following Boev 2001); a length of facies articularis, b distance between the base and ventral edge of the facies articularis, c overall length, d maximum width of facies articularis.

The layer 5 faunal assemblage differs from those recovered from the other layers given its richness and substantial diversity of species, which includes an important proportion of variously-sized birds. Fossil owl pellets in the form of 2–4 cm long agglomerates of imbricated bones indicate Barn Owls (*Tyto*) to be the dominant accumulation agent responsible for the bones collected from this layer.

The following specimens were used for osteological comparison: *Ara macao* (BIVAAG-200913 B—female; PACEA-O-609; MNHN 1995-262—adult male); *Ara ararauna* (MNHN 1995-233—young male); *Ara chloroptera* (PACEA-O-667, young); *Ara rubrogenys* (PACEA-O-670—adult female); *Amazona vinacea* (PACEA-O-666—young); *Amazona oratrix* (BIVAAG-200913 A, adult male). Anatomical description follows the terminology of Livezey and Zusi (2006) with metric analyses based on the method described by Boev (2001), both shown in Fig. 2.

Results

Class Aves Linnaeus, 1758

Order Psittaciformes Wagler, 1830

Family Psittacidae Illiger, 1811

Subfamily Psittacinae (Illiger, 1811)

Tribe Arini Gray, 1840

Genus *Ara* Lacépède, 1799

The curvature, robustness, conical shape, the presence of a developed, but not prominent *tuberculum extensorium*, and a distinct *sulcus neurovascularis* indicate the fossil to be a terminal phalanx from a zygodactyle bird (Ostrom 1974; Feduccia 1993). The curvature of the Blanchard specimen is similar to ungual bones of the second or third digit of an *Ara* (Fig. 3). As large macaws from both the *Ara* and *Amazona* genera display no size dimorphism (Guedes et al. 2001), size represents a reliable diagnostic criteria. Comparison of the Blanchard specimen to modern comparative material shows the closest analog to be *A. macao* (Table 1). The fossil phalanx is also similar to modern *Ara* specimens as the *sulcus neurovascularis* originates from the margin of *cotyla articularis* (Fig. 4), even if the *sulcus* in fossil specimens extends almost across the entire *corpus phalangis* compared with the partially extending *sulcus neurovascularis* of the examined modern *Ara*.

The oval *cotyla articularis* of the Blanchard specimen is slightly larger than that of the second digit of *A. macao*, but thinner and less circular than that of the third. Similarly, the *tuberculum extensorium* is slightly larger than that of the second digit of *A. macao* in the comparative sample. In proximal view, the *tuberculum flexorium* is oval-shaped and flattened, making the Blanchard specimen similar to the ungula bone of the third digit of the *A. macao*, while, at the same time, differing from the second digit of the distal phalanx, which is more circular.

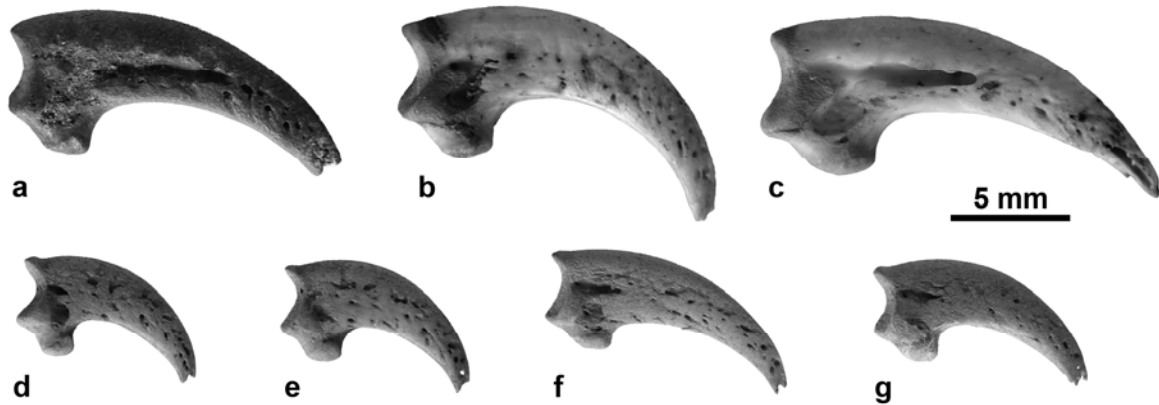


Figure 3. Right *Psittacidea* ungula bones (lateral view). **a** Blanchard specimen. **b** *A. macao* (BIVAAG-200913B), digit II. **c** *A. macao* (PACEA-O-609), digit III. **d–g** *A. vinacea* (PACEA-O-666), digits I, II, III and IV.

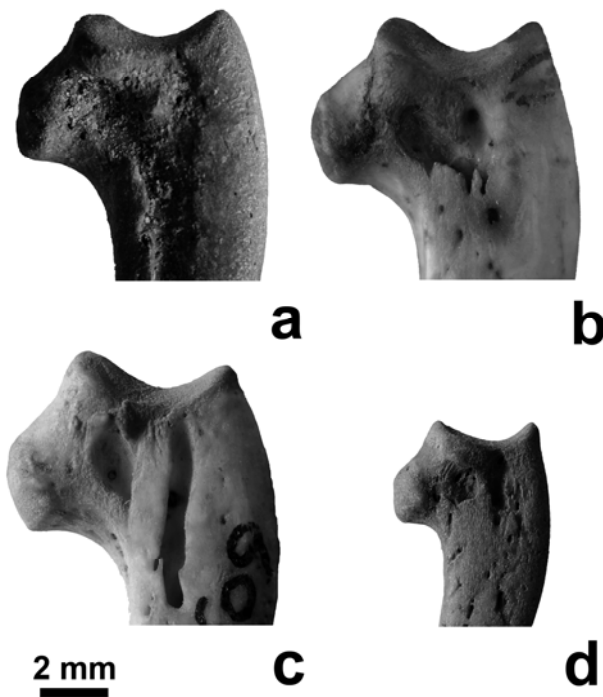


Figure 4. Proximal extremities (lateral view). **a** Blanchard specimen. **b** *A. macao* (BIVAAG-200913B), digit II. **c** *A. macao* (PACEA-O-609), digit III. **d** *A. vinacea* (PACEA-O-666), digit III.

The Blanchard specimen is larger than the examined *Amazona* unguis. More importantly, the *Amazona* distal phalanxes have a circular *tuberculum flexorium* separated from the *processus neurovascularis* by a more or less pronounced concavity depending on the digit. Both of these characters are absent in the Blanchard specimen. Overall, the size and morphology combined with osteological characteristics show the Blanchard specimen to be directly comparable with the distal phalanx of the second or third digit of a member of the genus *Ara*.

The fossil bone is longer than specimens assigned to *A. vinacea* and *A. oratrix* from our reference collection, although both taxa are smaller species of the *Amazona* genus. The largest extant Amazon

parrots are the Lesser Antilles species *Amazona guildingui*, *A. versicolor* and *A. imperialis*. Quantitative comparison with these taxa is precluded by the fact that no specimens were identified in the zoological collections we consulted nor are they available in any publication concerning phalanx. However, while the largest species of their genus, these birds are nevertheless significantly smaller than large macaws such as *A. macao* (Collar 1997). Moreover, osteological differences with our comparison material are significant enough to exclude the fossil bone representing a member of the *Amazona* genus.

	a	b	c	d
Blanchard specimen	4.6	3.9	15.3	3.5
<i>Ara macao</i> BIVAAG -200913B				
Digit I	4.5	3.6	13.5	2.9
Digit II	4.6	4.2	15.1	3.2
Digit III	4.7	4.4	16.1	3.6
Digit IV	4.9	4.6	17.8	4.0
<i>Ara macao</i> PACEA O-609				
Digit I	4.2	4.1	13.6	3.1
Digit II	4.5	4.8	13.7	3.2
Digit III	4.9	5	17.6	3.6
Digit IV	4.7	4.4	16.5	3.3
<i>Ara macao</i> MNHN 1995-262				
Digit I	4.5	3.9	13.0	3.0
Digit II	4.4	4.3	14.7	3.3
Digit III	4.6	4.5	16.4	3.9
Digit IV	4.7	4.5	18.1	3.8
<i>Ara arauna</i> MNHN 1995-233				
Digit I	4.9	4.2	14.3	3.2
Digit II	5.2	4.7	16.1	3.5
Digit III	5.2	5.1	17.7	3.9
Digit IV	5.4	5.1	19.5	4.1
<i>Ara chloroptera</i> PACEA-O-667				
Digit I	4.0	3.5	13.0	2.8
Digit II	4.5	4.3	14.4	3.0
Digit III	4.5	4.5	16.7	3.6
Digit IV	4.5	4.2	15.0	3.2
<i>Ara rubrogenys</i> PACEA-O-670				
Digit I	3.1	2.8	10.3	2.2
Digit II	3.1	3.1	11.2	2.6
Digit III	3.1	3.6	14.6	2.8
Digit IV	3.2	3.1	13.0	2.5
<i>Amazona vinacea</i> PACEA-O-666				
Digit I	3.7	2.8	8.7	2.5
Digit II	3.3	3.0	9.4	2.3
Digit III	3.5	3.2	11.2	2.8
Digit IV	3.3	3.0	10.3	2.7
<i>Amazona oratrix</i> BIVAAG-200913A				
<i>Digitus pedis</i>	3.7	3.5	10.9	2.8
<i>Digitus pedis</i>	3.7	3.6	10.6	2.7
<i>Digitus pedis</i>	4.0	3.9	12.3	2.9

Table 1.
Measurements of
Psittacidea distal
phalanx in mm (Digiti
pedis, phalanx
ungualis).

Several minor details do differ, such as the prominent *sulcus neurovascularis* in the fossil specimen or the ratio between bone length and a more developed *facies articularis* compared to modern *A. macao*. However, the limited number of modern specimens included in this study does not obviate these differences reflecting intra-species variability. Similarly, the modern specimen shows the development of the *sulcus neurovascularis* to present significant inter- if not intra-specimen variability. These small osteological differences are therefore insufficient for referring the Blanchard specimen to a species other than *A. macao*. A detailed osteological examination of the fossil shows its closest analog to be digit III of *A. macao*, while its size makes it most comparable to the ungual bone of digit II from the same species. This could suggest that the fossil bone corresponds to a slightly smaller bird than the *A. macao* specimens we examined.

Discussion

The likelihood that the Blanchard specimen represents a slightly smaller macaw than *A. macao* fits with the hypothesis of an extinct macaw species having once inhabited Guadeloupe. While two endemic macaws, the Lesser Antilles Macaw (*A. guadeloupensis* Clark 1905) and the Violet Macaw (*Anodorynchus purpurascens* Rothschild 1905), are mentioned in historical documents, it has recently been demonstrated that Rothschild (1905) incorrectly based his description of the second on the Guadeloupe Amazon *A. violacea* (Lenoble 2015). Therefore, Guadeloupe would have been home to only a single species of large macaw, the *A. guadeloupensis*. Size information available in Father Du Tertre writings (Du Tertre 1667) led Clark (1905) to conclude that the Lesser Antilles Macaw would have been slightly smaller than *A. macao*.

Referring the Blanchard specimen to *A. guadeloupensis* is further supported by the Pleistocene geography of the Guadeloupe archipelago. The emersion of Les Saintes and Colombie Bank due to lower Pleistocene sea-levels significantly reduced the distance between Marie-Galante and Guadeloupe, which today stands at 26 km (Münch et al. 2013). Moreover, the geography of the archipelago during the Last Glacial lowstand (~20 ky, Jouzel et al. 2002) reveals Marie-Galante to have been separated from Guadeloupe by a succession of three channels, the largest being less than 6 km wide (Fig. 1). Such short distances would not have presented a significant obstacle for flying vertebrates, most likely rendering the Guadeloupe Islands a single geographical unit during the Pleistocene.

No comparative sample is available for the fossil ungula bone from Blanchard as specimens attributable to the Lesser Antilles Macaw are currently unknown from museum collections. As such, the Blanchard specimen can only tentatively be assigned to the extinct macaw of Guadeloupe (*Ara* cf. *guadeloupensis*). The short distances separating Marie-Galante from Guadeloupe during the Pleistocene as well as the good size agreement between the Blanchard specimen and Clark's (1905) description of the Lesser Antilles Macaw nevertheless makes this hypothesis the most parsimonious.

Current archaeological evidence for the earliest Amerindian occupation of the Lesser Antilles comes from the Pre-ceramic occupation dated to 5.3 ky cal BP at Etang Rouge on Saint-Martin (Martias

2005; Bonnissent 2008) and a pollen core drilled in the marshes of the Vieux Fort River on Marie-Galante, which produced evidence for the human-induced modification of the landscape and accumulation of micro-charcoals at around 5 kyr cal BP (Siegel et al. 2008). The date of 10.7 ky BP (12 ky cal BP) for layer 5 of Blanchard Cave containing the terminal phalanx referred to *Ara* cf. *guadeloupensis* securely predates the initial Amerindian colonization of the Lesser Antilles.

In their review of West Indies parrots, Williams and Steadman (2001) assume that 50–60 species of Psittacidae, including 10–12 species of large macaws, would have inhabited the Lesser and Greater Antilles in the absence of prehistoric and historic human impact, instead of the 12 extant species of Amazon parrots and parakeets. However, this conclusion has been challenged by Olson and López (2008), who consider the Lesser Antilles land mass insufficient for sustaining indigenous or even endemic species of *Ara*. Moreover, the variety of West Indies parrots and macaws deduced from historical accounts could also result from misinterpretations of sketchy descriptions (Wiley and Kirwan 2013), as was demonstrated for a macaw presumed to have once occupied Hispaniola (Olson 2005). Moreover, because Amerindians kept and transported animals between islands, it cannot be excluded that macaws described in historical sources were in fact introduced from South America (Greenway 1967; Snyder et al. 1987; Olson and López 2008). The question remains whether the Lesser Antilles species identified in historical sources, the Martinique Macaw (*Ara martinica* Rothschild 1905), Dominican Green-and-yellow Macaw (*A. atwoodi* Clark 1908) and the Lesser Antilles Macaw (*A. guadeloupensis*), were endemic species (Hume and Walters 2012). Wiley and Kirwan's (2013) review of available historical evidence led them to conclude that the Lesser Antilles Macaw is the most credible of all the Lesser Antilles hypothetical species of indigenous *Ara*. The discovery of an ungual bone in a pre-Amerindian deposit from Blanchard Cave indicates that a large macaw similar in size to the hypothetical Lesser Antilles Macaw was present in the Guadeloupe archipelago before any human settlement. This discovery therefore lends robust support to the hypothesis of the Lesser Antilles Macaw's former existence.

Acknowledgements

This study was conducted as a part of the BIVAAG Program established by the Centre National de la Recherche Scientifique (CNRS), with support from a European POFEDER grant 2007–2013 n°2/2.4/-33456, the Guadeloupe Regional Council, the Direction de l'Environnement et de l'Aménagement du Territoire (DEAL) of Guadeloupe, and the Direction des Affaires Culturelles (DAC) of Guadeloupe. We are very grateful to Veronique Laroulandie for her valuable help and suggestions. We would like to thank Christine Lefevre for access to the bird bone collections of the Laboratoire d'Anatomie Comparée of the Muséum Nationale d'Histoire Naturelle of Paris, Cécile Mourer-Chauviré for helpful comments, Frédéric Fronteneau and Laurent Delavis for donating modern specimens that augmented the Université de Bordeaux osteological collection, and also Maxime Pelletier and Émilie Campmas for preparing the anatomical reference material. Monica Gala thanks Mathieu Langlais, Éric Pubert, Alain Queffelec, Ivana Fiore and Antonio Tagliacozzo for their help.

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