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"Small Size" in the Philippine Human Fossil Record: Is It Meaningful for a Better Understanding of the Evolutionary History of the Negritos?

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Abstract

"Pygmy populations" are recognized in several places over the world, especially in Western Africa and in Southeast Asia (Philippine "negritos," for instance). Broadly defined as "small-bodied *Homo sapiens*" (compared with neighboring populations), their origins and the nature of the processes involved in the maintenance of their phenotype over time are highly debated. Major results have been recently obtained from population genetics on present-day negrito populations, but their evolutionary history remains largely unresolved. We present and discuss the Upper Pleistocene human remains recovered from Tabon Cave and Callao Cave in the Philippines, which are potentially highly relevant to these research questions. Human fossils have been recovered in large numbers from Tabon Cave (Palawan Island) but mainly from reworked and mixed sediments from several archaeological layers. We review and synthesize the long and meticulous collaborative work done on the archives left from the 1960s excavations and on the field. The results demonstrate the long history of human occupations in the cave, since at least ~30,000 BP. The examination of the Tabon human remains shows a large variability: large and robust for one part of the sample, and small and gracile for the other part. The latter would fit quite comfortably within the range of variation of Philippine negritos. Farther north, on Luzon Island, the human third metatarsal recently recovered from Callao Cave and dated to ~66,000 BP is now the oldest direct evidence of human presence in the Philippines. Previous data show that, compared with H. sapiens (including Philippine negritos), this bone presents a very small size and several unusual morphological characteristics. We present a new analytical approach using three-dimensional geometric morphometrics for comparing the Callao fossil to a wide array of extant Asian mammals, including nonhuman primates and *H. sapiens*. The results demonstrate that the shape of the Callao metatarsal is definitely closer to humans than to any other groups. The fossil clearly belongs to the genus *Homo*; however, it remains at the margin of the variation range of *H. sapiens*. Because of its great antiquity and the presence of another diminutive species of the genus *Homo* in the Wallace area during this time period (*H. floresiensis*), we discuss here in detail the affinities and potential relatedness of the Callao fossil with negritos that are found today on Luzon Island.

Keywords

Philippines, Tabon Cave, Callao Cave, Homo Sapiens, Upper Pleistocene, Small Body-Size

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1. Introduction: Who Are the "Negritos"?

Since the second half of the fourteenth century, several human groups living in Southeast Asia until the present have been called *pygmies* or, more often, *negritos* (see, e.g., Quatrefages 1887). They were generally recognized as such because of their phenotypic attributes, considered to be different from their neighbors from the same geographical areas. Such features include a short stature, curly hair, and dark skin color. Such groups have been described in the Andaman Islands, Malay Peninsula, Papua New Guinea, and Philippines, and in 1862 Armand de Quatrefages, then professor of anthropology and ethnography at the Muséum national d'Histoire naturelle in Paris, most likely was the source of the idea to extend the appellation *negritos* to all those different Asian groups (Quatrefages 1887: 27–28; see also Flower 1880; Hamy 1876: 114–115). Quatrefages eventually extended the geographical distribution of the negritos from Sumatra to Japan by including several other groups based on their physical attributes, but Meyer (1899; see also Barrows 1910: 365–363) restricted it to Philippines, Andaman, and Malay Peninsula. The idea to group the negritos living in various regions of Asia and Melanesia was more or less directly related to the commonly accepted hypothesis at this time that they were the descendants of an ancient and widely distributed population that had been progressively constrained and restricted geographically to more remote areas by successive arrivals of newcomers (see, e.g., Pickering 1850: 180; Montano 1886: 67; Blumentritt 1900: 13).

Those human groups have been the subjects of a considerable number of studies in the many disciplines of anthropology for more than a century now. The particular fascination of early physical anthropologists for Philippine negritos in their attempts to classify races and for some of them to better understand the (pre)history of humans all over the world is probably well illustrated, among others, by the publications of Bean (see esp. Bean 1910a, 1910b). In addition to a very special interest in ear shape variation and its supposed usefulness in racial classifications, Bean is also famous among paleoanthropologists for proposing the species *Homo philippinensis* (Bean 1910a). Although this species was, of course, never recognized as a valid taxon (Bean created this new species to accommodate in his classifications one particular living individual he observed and "studied";

see Bean 1910a: 227–236), it is nevertheless still quite famous nowadays in the collective knowledge of Philippine people (even if it is most of the time associated or confused with "*Homo erectus philippinensis*"; see below).

If the fascination with the so-called negritos of early physical anthropologists working on the characteristics and delimitations of human races—or even species (Kneeland 1883; Bean 1910a; Pycraft 1925)—is now part of the history of the discipline, it is nevertheless obvious that those groups continue to crystallize the attention of many anthropologists, linguists, archaeologists, geneticists, and so forth.

It is now accepted that the phenotypic resemblances of African pygmies and Asian negritos are not due to a common and exclusive origin but rather result from recent convergences whose causes in terms of involved evolutionary mechanisms are nevertheless still debated (see, e.g., Migliano et al. 2007, 2011; Perry and Dominy 2009; Becker et al. 2010, 2011). Nowadays, the term *pygmy* is generally used for Western Africans only, whereas *negrito* is most commonly restricted to the groups found in Southeast Asia and, even more precisely, to the Agta (or Aeta, Ayta, Ata, or Ati) inhabiting northeastern and west central Luzon Island in the Philippines. While such generic appellations are sometimes considered convenient, they can lead to misunderstandings and misconceptions because they are frequently understood as recovering a true meaning in terms of common origins or actually shared biological affinities for all considered groups (see Bahuchet 1993). However, the hypothesis of a shared origin for the many Asian negrito groups is still under discussion. Indeed, two main hypotheses are currently proposed to explain the presence of negritos in several distant geographical zones in Southeast Asia. The first is directly linked with the traditional hypothesis formulated by nineteenth-century researchers mentioned above, proposing that all extant negrito groups represent relicts of what was once a widely distributed population of "negrito-like" *Homo sapiens*, that is, an "ancestral population" corresponding eventually to the first arrivals of our species in the area. The second hypothesis considers, rather than a shared origin for their phenotypic resemblances, a kind of convergent evolution in different negrito populations living under equivalent environmental conditions (for review and discussion of those hypotheses, see, e.g., Migliano et al. 2007; Perry and Dominy 2009; Scholes et al. 2011).

A significant number of genetic studies have been conducted recently on the different groups of Asian negritos. The results are numerous and appear sometimes contradictory, that is, difficult to synthesize and accommodate easily in a single model of migrations and population history of Southeast Asian human groups (see, e.g., Stoneking and Delfin 2010). Some results indicate negrito groups show distinctive mitochondrial DNA and Y-chromosome lineages, which could be explained by their long isolation from neighboring populations (Thangaraj et al. 2003, 2006; Hill et al. 2006; Delfin et al. 2011). At the same time, strong genetic similarities have been found between Southeast Asian negritos and "non-negritos," suggesting either a common migration event for the origin of all Southeast Asian groups (Abdulla et al. 2009) or—at least in the Philippines—a distinct and more

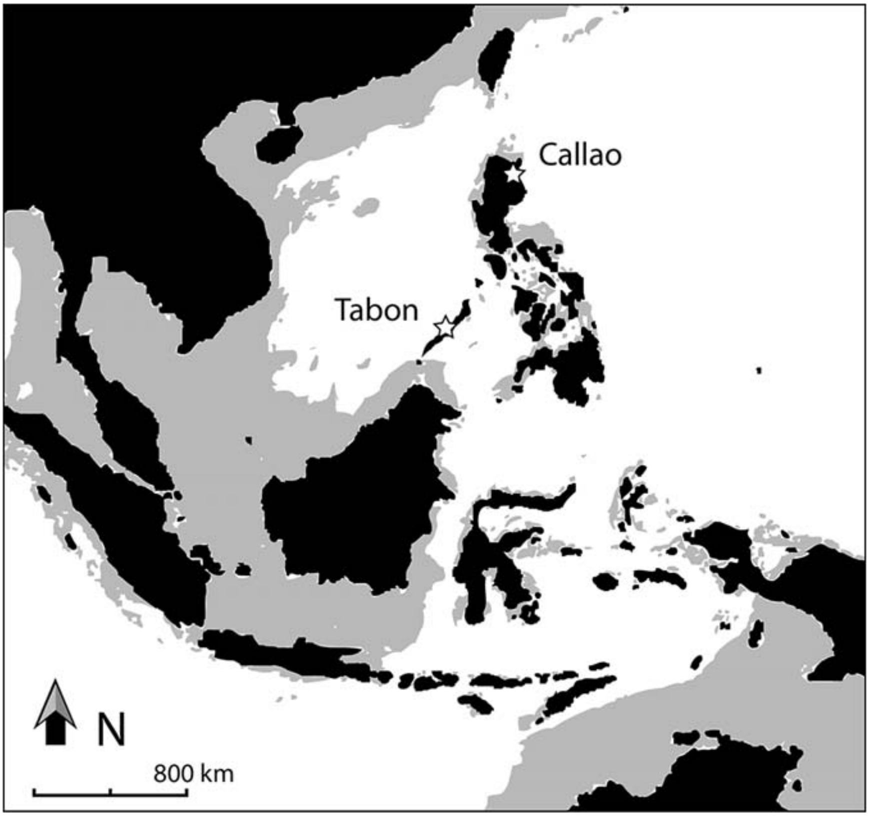


Figure 1. Location of Tabon Cave (Palawan, Philippines) and Callao Cave (Cagayan Province, Luzon, Philippines). Approximated paleoshorelines of the lowest sea levels in the Quaternary are shown in gray.

ancient origin of negritos (eventually related to Australian aborigines) and recent admixture with non-negritos (Delfin et al. 2011; Gunnarsdóttir et al. 2011; Scholes et al. 2011).

To progress in the understanding of the "negrito phenomenon," it would be crucial to know when negritos arrived in each area where they are documented today–in other words, to know the age of the appearance of the "negrito phenotype" in each region. Archaeology, through paleoanthropology, would be the discipline from which such data are expected. However, archaeological researches on ancient Southeast Asian Upper Pleistocene sites (i.e., potentially related with early migrations of our species) still need significant developments. In the Philippines, for instance, the last decades have seen a tremendous development of archaeological researches on the migrations and cultural dynamics of the "Austronesian-speaking people" (Bellwood and Dizon 2005; Mijares 2006; Hung et al. 2007, 2011; Bellwood 2011); at the same time, few—but very significant—efforts (as we aim to show in this article) have been made on earlier archaeology in the archipelago.

In this article, we focus exclusively on Philippine negritos through examination of currently available Upper Pleistocene archaeological and paleoanthropological evidence from Palawan and Luzon Islands. Upper Pleistocene human fossils are still very scarce in the Philippine archaeological record, but excavations in Tabon Cave in Palawan and Callao Cave in Luzon have given the oldest human remains known so far from the Philippines (Dizon et al. 2002; Détroit et al. 2004; Mijares et al. 2010). The geographical location of those two archaeological sites (Figure 1) is important because Palawan and Luzon Islands are still inhabited by negrito groups. Indeed, the Batak from the northern part of Palawan are described as negrito-like hunter-gatherers (Eder 1977), and the Agta (the "true negritos") are still occupying northeastern Luzon, and especially the Cagayan region where Callao Cave is located (Griffin and Estioko-Griffin 1985). We examine and discuss those two Upper Pleistocene archaeological human bones assemblages, since we have shown in previous studies that they could attest to an ancient presence of *Homo sapiens* of rather small body size in those geographical areas (Détroit et al. 2004; Mijares et al. 2010). To test this observation more thoroughly, this article focuses specifically on (1) the first up-to-date synthetic review of the new researches conducted on Tabon Cave, augmented with previously unpublished observations on the human remains, and (2) the presentation and discussion of the results obtained from a new three-dimensional (3D) geometric morphometric analysis of the fossil human third metatarsal found in Callao Cave compared with extant Asian *H. sapiens* and nonhuman catharrines and ursids.

Upper Pleistocene Human Remains from Tabon and Callao Caves and Their Potential Relatedness with the Philippine Negritos

Tabon Cave (Quezon, Palawan)

From 1962 to 2012: A short history of excavations and research projects on Tabon Cave. The cave of Tabon is located on the Lipuun Point, a small karstic massif situated on the municipality of Quezon (western coast of Palawan; Figure 1). The Lipuun Point was "discovered" and intensively surveyed during the 1960s by the National Museum of the Philippines, under the direction of Robert B. Fox (1962). More than two hundred caves were identified at this time, and several of them were excavated, uncovering a part of the incredible archaeological richness of this small massif of limestone (Fox 1970). Many of the caves were used as burial places during late Neolithic and metal-age cultural periods, including the small rock shelter where the Manunggul jar—one of the "national treasures"—was found. However the excavation of Tabon Cave, whose floor was also partly covered by large fragments of burial jars at the time of its discovery by archaeologists, revealed evidences

Figure 2. The human frontal bone recovered from Tabon Cave (no. P-XIII-T-288).

of much more ancient human occupations. Several archaeological assemblages characterized by abundant lithic artifacts and the absence of pottery were identified, and several ^{14}C dates older than 15,000 BP were obtained (Fox 1970). Tabon Cave is thus an emblematic site for the early archaeology of the Philippines. It is particularly famous for the discovery of the "Tabon Man skullcap" (which is in fact an almost complete human frontal bone; Figure 2), reportedly found in a disturbed stratigraphical context but most probably associated to the Upper Pleistocene archaeological layers and considered for many years the earliest human fossil known in the Philippines. However, the huge amount of work on the site during the 1960s was only partly published in a synthetic monograph (Fox 1970), which not only covers Tabon Cave but also presents all the preliminary results obtained from the study of all the caves discovered in the Lipuun Point. Accordingly, this publication lacks many details, and it is sometimes confusing in the presentation of the complex archaeostratigraphy of Tabon Cave, which is disturbed by several sedimentary reworked areas where most of the human fossils were found. (Fox explained those sedimentary disturbances by the digging activity of the birds known as "Tabon Megapodes" for their nests.) The archaeological material (including pottery, lithics, and human fossils) is also very preliminarily presented, and unfortunately, the detailed studies and publications that were scheduled at this time and mentioned repeatedly in Fox (1970) never materialized. After the death of Robert Fox, most of the material—including the human fossils—recovered during the excavations remained untouched for almost three decades.

In the late 1990s, the National Museum of the Philippines made a particular effort to reinvestigate the site and its archaeology, with several field campaigns undertaken from 1999 to 2001. A new collaborative research project with the Muséum national d'Histoire naturelle, based primarily on the study and dating of the human fossils, was established and subsequently developed. A synthetic publication of the results of the new studies and analyses undertaken in this frame is currently under way. However, several significant results have already been obtained and published: the description and direct dating of several of the human fossils (Dizon et al. 2002; Détroit et al. 2004; Corny 2008), the analysis of parts of the lithic assemblages (Jago-on 2007; Schmidt 2008; Xhauflair and Pawlik 2010), and the 3D reconstruction of the spatial distribution of all the archaeological material found during the excavations undertaken in the 1960s (Corny and Détroit 2010). Significant contributions on Tabon Cave were also published recently on lithics (Patole-Edoumba 2009; Patole-Edoumba et al. 2012) and sedimentology and dating by Lewis (2007; Lewis et al. 2008a).

Age and morphological characteristics of the human fossils from Tabon Cave. The study of the human fossils from Tabon Cave was undertaken in two steps, and some of the work is still in progress. The three human remains selected for their potential ancestry by Fox (1970: 40), including the famous Tabon frontal bone, were described in detail for the first time, and two of them were directly dated (Dizon et al. 2002). The second step included the analysis of 11 new human bone fragments found during the excavations undertaken by the National Museum from 1999 to 2001, including a direct date obtained for one of the specimens (Détroit et al. 2004). The direct dates obtained with the U-series method gave the results of 16,500 ± 2,000 BP for the frontal bone (no. P-XIII-T-288), 31,000 +8,000/–7,000 BP for one of the two fragments of mandible (no. P-XIII-T-436-Sq19), and 47,000 +11,000/–10,000 BP for a fragment of tibial shaft found in 2000 (no. IV-2000-T-197). Because of the methodological constraints of direct U-series dating techniques applied on bones (note the large error ranges associated to each date), those dates should certainly be considered indications of the age of the fossils rather than their absolute age. In this respect, those results nevertheless confirm the great antiquity of several human bones discovered in Tabon Cave and are in agreement with Fox's (1970: 40) hypothesis that the "fossil human bones were associated with Flake Assemblage III" and thus "may be dated from 22,000 to 24,000 years ago," based on the radiocarbon dates obtained for this archaeological assemblage.

As far as the morphology of the fossils is concerned, one of the most striking results obtained from the anthropological analyses and comparisons is the very large variability in size and robustness in the assemblage of human remains (Dizon et al. 2002; Détroit et al. 2004). This is particularly evident if we take into account the three fossils selected by Fox and the 11 bones discovered more recently. If the majority of the specimens (including the frontal bone, no. P-XIII-T-288, and the fragment of mandible, no. P-XIII-T-436-Sq19) exhibit rather small dimensions, the other fragment of mandible (no inventory number; see Dizon et al. 2002) shows very large dimensions and a very robust morphology of its mandibular corpus. Metrical comparisons undertaken for this particular specimen show that its dimensions exceed those of the very large mandible of the *Homo sapiens* Wajak 2 and are equivalent to the dimensions of several *Homo erectus* specimens (Dizon et al. 2002: 664–665). The study of this particularly large and robust specimen included also comparisons with several specimens of *Pongo pygmaeus*. Because of a certain confusion that arose after this publication (see, e.g., Curnoe et al. 2012: 2, which also includes an incorrect quotation regarding the concerned specimens), we insist here that the hypothesis that this fragment of mandible could belong to an orangutan was clearly discarded on morphological grounds (Dizon et al. 2002: 663–664). Apart from this large individual, several fossil specimens recovered from Tabon Cave could potentially correspond to the range of variation of morphology and especially size of the Philippine negrito. However, more detailed comparisons with series of recent negritos are needed to test this hypothesis further. This work is scheduled in the near future and will include the whole series of human bones recovered from Tabon Cave. Indeed, the new collaborative and multidisciplinary work undertaken on the whole collections and archives from Tabon Cave preserved at the National Museum of the Philippines revealed the considerable amount of archaeological specimens and data collected during the excavations in the 1960s. To date, more than two hundred bones and fragments of bones found in Tabon Cave have been identified as human in the collections (Corny 2008). Those large quantities of human bones—not mentioned in Fox (1970)—certainly correspond to a mix of actually ancient fossils and fragmentary skeletal remains derived from the Neolithic/metal-age burial jars that were present on the surface of the cave when it was discovered. The archives include a substantial number of field documents, notes, sketches, maps, and the complete and systematic inventory record of all the individual discoveries made during the excavations. Most of those documents contain precious primary information and data (never before published), which allowed us to completely reconstruct the 3D spatial distribution of all the objects recovered from the cave (Corny and Détroit 2010). This ongoing work, cross-validated by several field campaigns since 2006, has already confirmed the presence of at least two in situ lithic assemblages (without pottery) located below the layers containing mixed lithics and potsherds. Fieldwork focusing on the study of the long stratigraphic sequence and new samples obtained from various layers, including charcoals from a fireplace still preserved in a small remnant of one of the two ancient archaeological layers, should give a more comprehensive and definite picture of all the layers deposited in the cave. This work on spatial distribution was also useful to assess the original location of the human bones in the stratigraphy, and it has already been possible to verify the exact provenience of the frontal bone (no. P-XIII-T-288), which was indeed derived, as most of the total series of human bones, from an area where the deposits were highly disturbed and reworked. As shown by the dates obtained on two of the fossils, the disturbed zones actually contain Upper Pleistocene human remains, and we are presently working on the whole collection of human bones to distinguish those which are potentially old based on their state of preservation and mineralization. Preliminary results of the anthropological analysis of the whole collection tend to confirm the presence of two morphotypes, one small and gracile and one large and robust, which seems to be difficult to explain by sexual dimorphism in a single population only. To complete this work and to test this hypothesis, we need more solid chronological data on the deposits, as well as on the fossil specimens.

Callao Cave (Peñablanca, Cagayan Region, Luzon)

Callao Cave in the context of the prehistory of the Cagayan region. Callao Cave is located in the Callao limestone formation in the municipality of Peñablanca, northeastern Luzon (Cagayan Province; see Figure 1). The Cagayan region is famous for its richness in prehistoric sites: caves in the limestone formations and open air sites in the Cagayan Valley. As early as 1947, several open-air sites of the Cagayan Valley delivered fossils of large mammals now extinct on Luzon (Rhinoceros, Elephas, Stegodon, etc.) and tentatively attributed to the Middle Pleistocene (Beyer 1947; von Koenigswald 1956). By the end of the 1950s, stone tools—described as the "Cabalwanian pebble tool complex"—as well as tektites were found on the surface of the same sites (von Koenigswald 1958). Though no conclusive evidences of the actual association of the lithic tools with the old fauna were found, the hypothesis of the presence of Homo erectus on Luzon Island (the famous hypothetical Homo erectus philippinensis) started to be taken very seriously among prehistorians and paleontologists. At the end of the first six years of the Lipuun Point project in Palawan, Fox realized, with the discoveries made in Tabon Cave, that the presence of humans in the Philippines was indeed ancient (Fox 1970). In 1971, Fox and the National Museum decided to launch a new research project in the Cagayan Valley, with the ambition to find new sites and clues of the actual association of the stone tools and the extinct faunas (Fox 1971). Numerous sites were found, and large assemblages of fossil remains and lithic tools were collected, with in fact a majority of flakes rather than pebble tools (Fox 1973; Fox and Peralta 1974). Despite numerous efforts made in the 1970s and more recently on the excavation of the major open-air sites of the Cagayan Valley (Espinosa Ranch and Madrigal Ranch, e.g.) and the development of several geological projects (Lopez 1972; Vondra and Mathisen 1978; Mathisen and Vondra

1983; Bautista and de Vos 2000; de Vos and Bautista 2003), no solid evidence has been found until now for the Middle Pleistocene age of the lithic tools, that is, the presence of humans at this time period in the Philippines (Pawlik and Ronquillo 2003; Dizon and Pawlik 2010; Patole-Edoumba et al. 2012).

In 1976, the National Museum extended the Cagayan project to the exploration of the caves of the Callao limestone formation, expecting to find old archaeological layers better preserved than in open-air sites (Ronquillo and Santiago 1977). Numerous caves and rock shelters have been excavated since the late 1970s, and a rich archaeological record has been obtained for the late Upper Pleistocene and the Holocene (see, e.g., Ronquillo 1981, 2000; Mijares 2005, 2007). While tested in 1979 and 1980 for its archaeological content, new excavations were started in Callao Cave in 2003 under the direction of Armand S. Mijares. During this first new field campaign, an archaeological layer containing flake tools and charcoals was radiocarbon dated to 25,968 ± 373 BP, which was the most ancient date obtained for an in situ human occupation layer in Northern Luzon (Mijares 2005). In 2007, a breccia layer containing a dense assemblage of animal teeth, bones, and bone fragments was found in square 2, at a depth of ~270–295 cm below the cave surface (Mijares et al. 2010). Two cervid teeth from the breccia layer gave U-series ages of 52,000 ± 1,400 and 54,300 ± 1,900 years ago, with a combined ESR/U-series result of 66,000 +11,000/–9,000 years ago for the first one (and no result for the second one). Not a single lithic tool was found in this breccia layer, but cut marks were securely identified on the surface of at least seven animal bones (Mijares et al. 2010; Manalo 2011). Among the animal bones, a human right third metatarsal (MT3; Figure 3) was identified that gave a direct U-series age of 66,700 ± 1,000 (Mijares et al. 2010). Observations made on the state of preservation of the faunal remains indicate that the breccia layer probably corresponds to an accumulation of bones and teeth redeposited after water transport (Mijares et al. 2010). While additional fieldwork and sedimentological analyses are needed to clarify the exact timing and process of deposits corresponding to the breccia layer, such reworking could explain the discrepant ESR/U-series results (Mijares et al. 2010).

Size and shape affinities of the Callao third metatarsal. While showing a clear "human-like" morphology, the overall size of the MT3 is obviously small. It is almost complete, but its distal part is damaged. Micro-computed tomographic images do not show the presence of a metaphyseal surface. The internal morphology of the distal part would thus better correspond to an adult metatarsal whose head was broken postmortem. The first series of morphological and metrical comparisons showed that the characteristics of the Callao MT3 are definitely closer to *Homo sapiens* than to other primates presently found on Luzon Island (*Macaca fascicularis*) or on relatively close islands (*Pongo* and *Hylobates* which are present in Borneo). The main distinctive morphological traits of the Callao MT3 are that the dorsal surface of the shaft is straight, the medial and lateral borders of the shaft are slightly and regularly convergent from posterior to anterior, and the proximal articular facet for the lateral cuneiform shows an elongated triangular

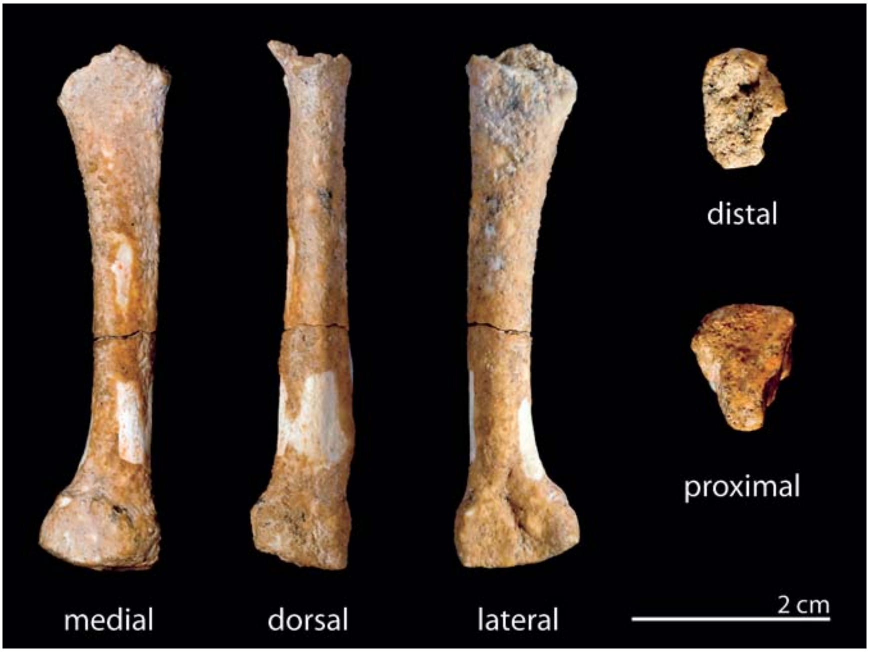


Figure 3. The human right third metatarsal recovered from Callao Cave.

outline (Mijares et al. 2010). Those features are not found on *Macaca*, *Hylobates*, and *Pongo*, and the overall size of the Callao MT3 is clearly larger than those of *Macaca* and *Hylobates*, and really smaller than *Pongo*. In Mijares et al. (2010), metrical comparisons with two small samples of Philippine negrito (males and females) showed that the Callao MT3 enters the range of variability of the negritos for the total length, while the majority of the other dimensions are smaller in the Callao MT3 (especially the dimensions of the proximal articular facet).

Because the Callao MT3 shows peculiar characteristics in terms of size and shape, we are currently developing a new comparative analysis of the fossil based on 3D geometric morphometric methods (Procrustes analysis), for which we present here the first preliminary results. The Procrustes method allows rigorous statistical analyses of size and shape differences, and it is now applied frequently in taxonomically oriented paleoanthropological studies (see, e.g., Harvati 2003; Harvati et al. 2004; Slice 2005; Terhune et al. 2007; Baab 2008; Bouée and Détroit 2008, 2010; Zeitoun et al. 2010). The first step of this study is to test the analytical approach on a large comparative sample of third metatarsals, including *H. sapiens* and several Asian mammals for which the morphology and size of the MT3 is relatively close to human. The second step consists in the assessment of the morphometric affinities of the Callao MT3 and to test the results obtained previously in Mijares et al. (2010). The total sample includes 138 third metatarsals of recent adult *H. sapiens*

Figure 4. Location of the 20 landmarks registered on each individual 3D model (from left to right: proximal, dorsal, and medial views).

(Philippine negritos and other Asian *H. sapiens*), *Pongo*, cercopithecids (*Macaca* and *Nasalis*), hylobatids (*Hylobates* and *Nomascus*), ursids (*Helarctos* and *Ursus*), and *Ailurus*. This sample covers a large spectrum of Asian genera in order to check for all potential confusions in the attribution of the Callao MT3; however, note that only two of them are present on Luzon Island (*Homo* and *Macaca*). All the third metatarsals were digitized with a Nextengine surface scanner, and the 3D Cartesian coordinates of a total of 20 landmarks (Figure 4) were registered for each individual 3D model using Landmark (IDAV visualization and Graphics Research Group 2007). All Procrustes superimpositions and associated statistics were performed with R (R Development Core Team 2011), with the package "shapes" (Dryden 2012) and several functions written by Claude (2008).

The first analysis includes the 20 landmarks for all the specimens, except the Callao MT3, which is incomplete in its distal part. Results of the principal components analysis (PCA) show a clear pattern in the repartition of the specimens on principal component 1 (PC1) and PC2, which accounts for more than 55% of the total variation (Figure 5). Shape differences are clearly related to locomotor behaviors and substrate preferences. PC1 distinguishes arboreal individuals (nonhuman primates and *Ailurus*), which plot on the negative side of the axis, from terrestrial individuals (*H. sapiens* and ursids), which plot on the positive side. Along PC2, terrestrial plantigrades are separated into quadrupeds (ursids, negative values for PC2) and bipeds (*H. sapiens*, positive values for PC2). From this first analysis, it is clear that shape variations of the third metatarsal are good indicators of locomotor behaviors and thus clearly distinguish human bipeds from other mammals.

The second analysis aims at including the Callao MT3 in the study to assess its shape affinities. Because of the incomplete state of the Callao MT3, the second analysis was made only on the 15 landmarks of the proximal part of the third

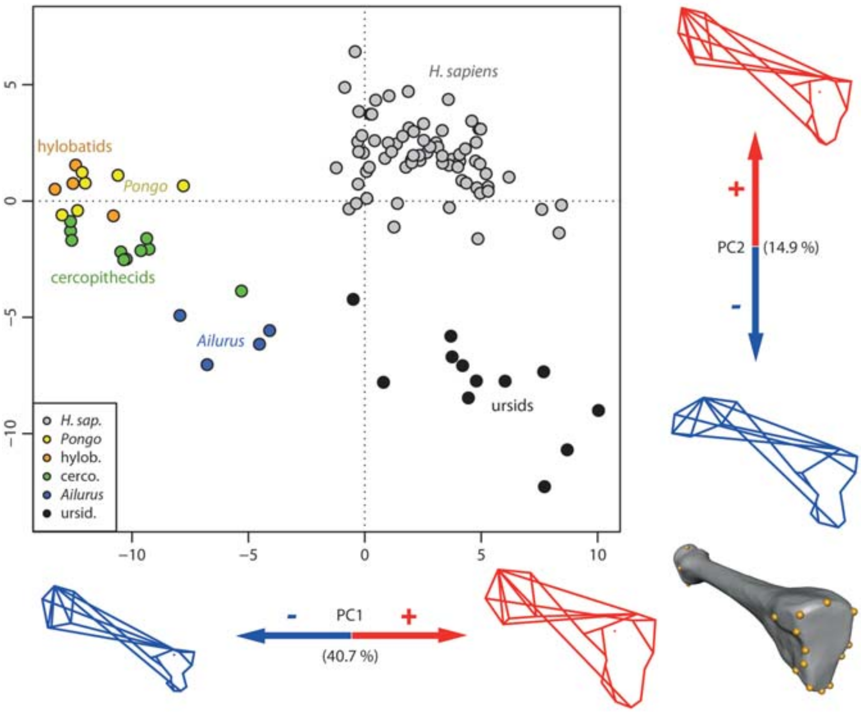
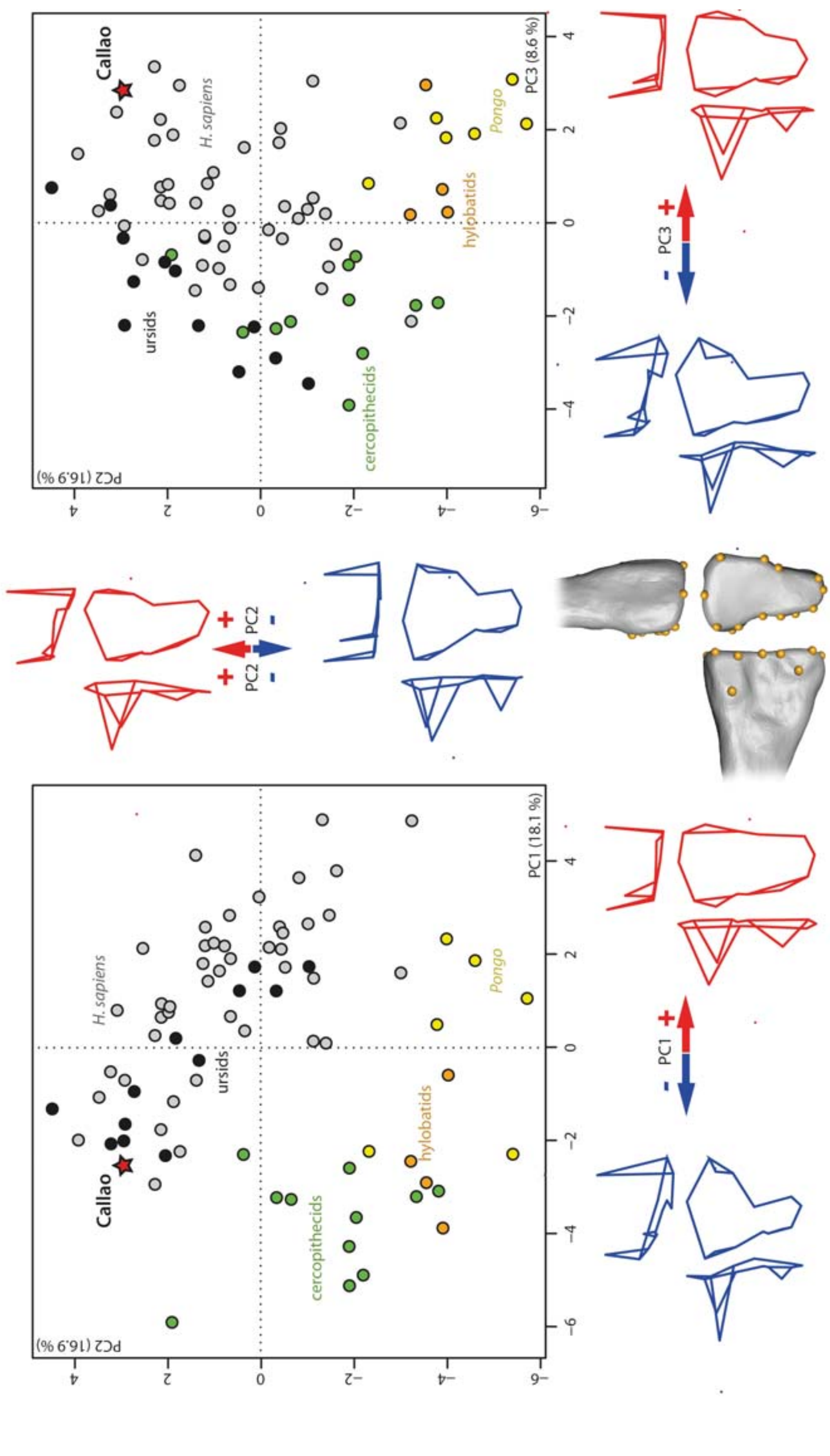


Figure 5. Procrustes analysis of 20 landmarks on complete right third metatarsals: scatter plot of PC1 versus PC2, and visualization of shape changes along PC1 and PC2.

metatarsals. The results of the PCA are more subtle than in the previous analysis, but the position of the specimens on PC1-PC2-PC3 (Figure 6), which explains more than 43% of the total variation, is still strongly related with locomotor behaviors and substrate preferences of the different taxonomic groups. In this analysis, the Callao MT3 plots clearly closer to *H. sapiens* than to any other group. The shape of the Callao MT3 definitely corresponds to a bipedal individual, but it is obviously at the margin of the distribution of the *H. sapiens* sample included in this analysis.

Those preliminary results, combined with the results obtained previously, confirm that the Callao MT3 belongs to a bipedal individual (i.e., to the genus *Homo*). The small dimensions of the Callao MT3 would align it more firmly with the Philippine negritos, but it remains obvious that this fossil presents a series of peculiar morphological features. This study needs to be continued to ascertain the affinities of the Callao fossil. Some of the comparative samples need to be enlarged, and fossil specimens of the genus *Homo* should be included. Even though third metatarsals are scarce in the hominin fossil record, including the Liang Bua specimens (Jungers et al. 2009a; Jungers et al. 2009b) appears to be particularly


Callao
H. sapiens
ursids
cercopithecids
hylobatids
Pongo
PC1 (18.1 %)
PC2 (16.9 %)
PC3 (8.6 %)
PC1
PC2
PC3

recommended since common characteristics are shared by the sites of Callao and Liang Bua: the age of the fossils, and the positions of Flores and Luzon Islands across the Wallace line and thus the highly endemic faunas of the two islands (Heaney 1998; van den Bergh 1999; de Vos et al. 2007; van den Bergh et al. 2009; Heaney et al. 2011).

Discussion and Concluding Remarks

The human fossils found in Tabon and Callao Caves are very significant discoveries since they are the oldest human remains known so far from the Philippines and from Island Southeast Asia as a whole, together with the fossils from Niah Cave in Sarawak, Borneo Island (Harrisson 1959; Barker 2005; Gilbertson et al. 2005; Barker et al. 2007). The earliest securely dated archaeological evidence indicates a human presence in Australia at around 40–45 kya (O'Connell and Allen 2004), but very few Australian fossils of this antiquity were known until now (Thorne et al. 1999; Brown 2000; Gillespie and Roberts 2000; Bowler et al. 2003). The Tabon and Callao fossils are thus particularly relevant to discussions regarding the timing and process of the first arrivals of *Homo sapiens* in Australasia and the potential contemporaneity of our species with other hominin species (late *H. erectus* in Java, and *H. floresiensis* in Flores; see, e.g., Brown et al. 2004; Zeitoun et al. 2010).

The results of the anthropological studies of the human fossils from Tabon and Callao presented in this article point out several interesting characteristics of their morphology. In particular, some of the fossil specimens from both sites are small and gracile, showing to some extent affinities with Philippine negritos. The Callao metatarsal is small and definitely closer to Philippine negritos than to Philippine non-negritos, while the human fossil assemblage from Tabon Cave is mosaic, including eventually two different morphological groups. However, if the Tabon fossils clearly enter the variation range known for Asian *H. sapiens*, it is not exactly the case until now for the Callao fossil. Even though our results are still preliminary and need further developments of the analyses to be confirmed, it remains possible to hypothesize on plausible explanations for our observations taking into account the particular biogeographical settings of Palawan and Luzon.

Borneo, where the early *H. sapiens* remains of Niah were found, is part of Sundaland and was thus attached to the mainland during Quaternary low sea levels. It was most probably not the case for Palawan Island, and certainly not for Luzon Island (see, e.g., Voris 2000). The presence of Upper Pleistocene human fossils on those Philippine islands clearly indicate sea crossing capabilities for the human groups that settled in the area. It also probably implies a quite strong isolation of those pioneer groups, and it is possible that a certain amount of insular endemism

Figure 6 (*opposite*). Procrustes analysis of 15 landmarks on the proximal part of right third metatarsals: scatter plot of PC1 versus PC2 and PC3 versus PC2, and visualization of shape changes along PC1, PC2, and PC3.

could have played an important role in the makeup of those early human populations. A closer look at biogeographical settings shows contrasted situations for the two islands: Palawan is geographically very close to Borneo and their respective faunas are very similar, while Luzon is more remote and presents a highly endemic ("impoverished") fauna (Heaney 1998; Heaney et al. 2011). According to the results of the analyses made on the Callao fossil, and taking into account its age in excess of 60 kya, we are considering seriously the possibility that it could belong to a particular—endemic—type of *Homo* (mimicking *H. floresiensis*?). However, we are fully aware that a single bone is clearly not sufficient to support such a hypothesis. For the time being, it is thus reasonable to keep the main hypothesis that it belongs to *H. sapiens*, particularly negritos. Further excavations and research in Callao Cave are promising, and new findings are expected to help test those hypotheses more thoroughly. As far as Tabon Cave is concerned, it is necessary to continue the anthropological analysis of the whole assemblage of human bones and to pursue the work on the chronology of human occupations in the cave. With present results, it seems plausible that two morphologically different human populations were living in the Lipuun Point during the Upper Pleistocene time period. While still conditional and depending on the exact age of the two morphotypes, this observation could be accommodated in one of the two models for the origin of the Philippine negritos: either distinct origins for negritos and non-negritos (corresponding to two different migrations into Palawan), or a common origin followed by divergent evolutions. While often described as probably belonging to a subadult individual, the Deep Skull from Niah Cave on Borneo Island is small in size and presents a gracile morphology (Brothwell 1960; Kennedy 1977; Barker et al. 2007). This fossil specimen dated to 45,000–39,000 cal BP (Barker et al. 2007) presents striking similarities with the gracile morphotype observed in Tabon Cave. Accordingly, the almost contemporaneous human remains recovered from Niah and Tabon probably indicate the presence of a human population of small body size during part of the Upper Pleistocene time period in "central" Island Southeast Asia (i.e., Borneo and Palawan Island).

As a concluding remark on the question of the origin of Philippine negritos, striking observations can be made from the paleoanthropological and archaeological record of the Philippines. However, the amount of currently available fossils and associated archaeological data is still obviously to meager for pretending to decipher such a complex question as the population (pre)history of the Philippines. The fossils from Tabon and Callao document some of the earliest arrivals of the genus *Homo* in the Philippine archipelago, but late Upper Pleistocene and early Holocene human remains are almost absent from the Philippine fossil record. Until now, the cremated human remains recovered from Ille Cave (Palawan) and directly dated to ~9,000–9,500 cal BP are the only exception (Lewis et al. 2008b). This finding documents the earliest intentional cremation from Southeast Asia, with a series of complex mortuary gestures before and after the cremation of the human bones (Lewis et al. 2008b). The bones represent a female individual with a short stature (Lewis et al. 2008b), and it is expected that future detailed morphological descriptions and comparisons could provide valuable insights on its biological affinities. The evolution of the morphology of the inhabitants of the Philippines through time until the present-day picture thus remains largely unknown. However, future research efforts, combining paleoanthropology, linguistics, and genetics, are expected to bring new results and arguments in the discussion. Anthropological and genetic work on "recent archaeological" individuals (pre-Hispanic period) found in recent excavations or already present in the collections could probably help to fill in a part of the gap between very ancient fossils and extant populations.

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