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Another interpretation of *Homo antecessor*

Francesc Ribot Trafí[1], Mario García Bartual[2], Eulalia García-Nos[3], Alfredo José Altamirano Enciso[4], Alexander J. Nevgloski[5] & Qian Wang[6]

1) *Museo Municipal de Prehistoria y Paleontología Josep Gibert, Calle Las Tiendas, sn, 18858 Orce, Granada, Spain*
e-mail: fribottrafi@hotmail.es

2) *Museo Paleontológico de Elche and Fundación CIDARIS, Plaza de San Juan, 03203 Elche, Alicante, Spain*
e-mail: mgbartual@yahoo.es

3) *Laboratorio de Estudios Paleolíticos, Universidad Nacional de Educación a Distancia (UNED), Calle Senda del Rey, 7, Madrid, Spain*
e-mail: olayagarcia.nos@gmail.com

4) *Universidad Nacional Mayor de San Marcos, Escuela de Estudios Generales, Calle Germán Amézaga 375, Lima 15081, Peru*
e-mail: zooarqueologo@gmail.com

5) *75 Greenridge St. Johnson City, NY 13790, USA*
e-mail: ajn1968@hotmail.com

6) *Department of Biomedical Sciences, Texas A&M University College of Dentistry, 3302 Gaston Ave, Dallas, TX 75246, US*
e-mail: qian.wang@tamu.edu

We have carefully read the article by Bermúdez de Castro & Martinón-Torres (2019) titled "What does *Homo antecessor* tell us about the origin of the 'emergent humanity' that gave rise to *Homo sapiens?*". The authors update their thoughts on the human remains of the TD6.2 level of Gran Dolina de Atapuerca (Burgos, Spain), and then support their research with previous work by members of the Atapuerca team. This work includes: *a)* the validity of the *Homo antecessor* taxon; *b)* the phylogenetic relationships between this taxon and the line that leads to *H. sapiens* and *H. neanderthalensis;* and *c)* the geographic area of the origin of *H. antecessor.* The first two points pivot, fundamentally, on the midfacial morphology of the subadult individual ATD6-69 (Hominid 3), a specimen that is said to exhibit modern type facial morphology (e.g., Bermúdez de Castro *et al.,* 1997, 2017; Arsuaga *et al.,* 1999; Rosas, 2000). This modern morphology is defined by the presence of a flexed midface (i.e. canine fossa, arched or horizontal straight zygomaticoalveolar crest, and maxillary inflection), the relationship of the modern type nasal ridges, and the curved upper border of the temporal squama. This morphology has been proposed to be a derived feature of *H. sapiens* and led to the positioning of *H. antecessor* as the last common ancestor (LCA) of *H. sapiens* and *H. neanderthalensis* (e.g., Bermúdez de Castro *et al.,* 1997, 2004; Arsuaga *et al.,* 1999; Rosas, 2000; Bermúdez de Castro & Arsuaga, 2001-2002; Lacruz *et al.,* 2019). However, since 2013 the researchers of the Atapuerca team changed this point of view, and in different works they argue that *H. antecessor* represents a lateral branch, without descent, from the line that would later originate the LCA (Gómez-Robles *et al.,* 2013; Bermúdez de Castro *et al.,* 2017; Bermúdez de Castro & Martinón-Torres, 2013, 2014, 2019; Welker *et al.,* 2020). However, this conclusion is not taken into account in the work of Lacruz *et al.* (2019), in which *H. antecessor* is again proposed as the most likely LCA of *H. sapiens* and *H. neanderthalensis.*

Regarding the midfacial morphology in ATD6-69, in two of our articles published in 2018 (Ribot *et al.,* 2018a,b), we reviewed all the characteristics considered as derived in this hominin and concluded that all of them can be found in *H. erectus* of China and, therefore, the human remains from TD6 should be reclassified as *H. erectus* (Ribot *et al.,* 2018a,b; also Wang, 1998; Wang & Tobias, 2000). Among these characteristics, the canine fossa is the hallmark and shows strongly correlation between *H. antecessor* to *H. sapiens.* However, a more thorough review of facial morphology leads us to the conclusion that in *H. erectus* of Atapuerca (= *H. antecessor*), the depression of the zygomatic process of the maxilla of ATD6-69 is not homologous to the true canine fossa found in most hominins including modern humans (Nevgloski, 2000; Ribot *et al.,* 2020). The definition of canine fossa most widely accepted by anatomists and paleoanthropologists describes it as a boney depression located just below the infraorbital foramen (e.g., Testut, 1899; Mellinger, 1940; Weidenreich, 1943; Goss, 1966; Tobias, 1967; Orts Llorca, 1970; Gray *et al.,* 1970; Anderson, 1978; Aiello & Dean, 1990; McMinn *et al.,* 1993; Wolpoff, 1999; Nevgloski, 2000; Lieberman, 2011; Wood, 2011; White *et al.,* 2012; Jeon *et al.,* 2017; Ribot *et al.,* 2020), while in ATD6-69 the maxillary depression is located lateral, not below, to the infraorbital foramen and affects much of the maxillary process of the zygomatic (Arsuaga *et al.,* 1999; Nevgloski, 2000; Ribot *et al.,* 2020). In ATD6-69 the region inferior to the infraorbital foramen is flat or even slightly convex, a morphology very different from that of *H. sapiens.* Nevgloski (2000) found that the canine fossa is located below the infraorbital foramen in a total of 140 modern human skulls with 71 of which being subadults; to this sample are added 42 more skulls from the Laboratory of Paleopathology and Paleoanthropology of the National Museum of Archeology of Catalonia in Barcelona, from the Universidad Nacional Mayor de San Marcos, School of General Studies in Perú, and from the Department of Biomedical Sciences, Texas A&M University College of Dentistry, and in all specimens the canine fossa is located below the infraorbital foramen. Therefore, while there is variability in morphology, in size and depth, the canine fossa is conservative with respect to its situation in the maxilla (Nevgloski, 2000).

In ATD6-69, the lateral position of the depression relative to the infraorbital foramen is similar to what Oschinsky defined as the zygomaxillary fossa (Oschinsky, 1962; Rak, 1983) - also called Oschinsky's fossa. This fossa, initially is a superolateral extension of the canine fossa (Fig. 1). It develops because of an extreme anterior projection of the zygomaxillary tuberosity that leads to the presence of two distinct fossae in two distinct areas of the maxillary zygomatic process: the canine fossa (inferior to the infraorbital foramen) and the Oschinsky‘s fossa (lateral to the infraorbital foramen and more located in the maxillary process of the zygomatic) (Oschinsky, 1962; Rak, 1983; Oettlé *et al.,* 2017) (Fig. 2). Oschinsky‘s fossa has been observed by Oschinsky in recent Eskimos (Oschinsky, 1962) (see Fig. 1) and by others in some hominin fossils (Rak, 1983; de Ruiter *et al.,* 2018; Ribot *et al.,* 2020) (Fig. 3). Examples of Oschinsk‘y fossa found in conjunction with a canine fossa include AL 333-1 (*Australopithecus afarensis* - Rak, 1983; also described in Kimbel *et al.,* 1982), MH1 (*Australopithecus sediba* - de Ruiter *et al.,* 2018), KNM-ER 1813 (*Homo habilis* - Ribot *et al.,* 2020), while in ATD6-69 *(H. erectus),* and SH 5 (pre-Neanderthal) there is an Oschinsky's fossa but the canine fossa is missing. In ATD6-69*,* Oschinsky‘s fossa is more widespread and deep, but during ontogeny it would be reduced in depth by the anterior expansion of the maxillary sinus, which would partially fill the area of the canine fossa. The same is true with ATD6-58, a left adult zygomaxillary fragment, in which an Oschinsky‘s fossa is located in the same place as that of ATD6-69, but reduced in depth (Bermúdez de Castro *et al.,* 1997, 2004; Rightmire, 1998; Bermúdez de Castro & Arsuaga, 2001-2002).

Thus, we believe that specimens of *H. erectus* at Atapuerca do not exhibit a modern canine fossa. Though there is a fossa lateral to the infraorbital foramen, this depression is better defined as Oschinsky's fossa. This indicates that the canine fossa has been obliterated and that the flat morphology of the maxilla under the infraorbital foramen would be similar to European *(H. heidelbergensis)* and African (*H. rhodesiensis* or *H. heidelbergensis*) hominins of the middle Pleistocene, and not like that seen in *H. sapiens.*

However, Lacruz *et al.* (2019) take up the idea that *H. ancestor* is the LCA of *H. sapiens* and *H. neanderthalensis,* mainly based on the cupping of the infraorbital area, which has been called the canine fossa. Thus, the face of *H. antecessor* would be retained in *H. sapiens* (symplesiomorphic) and would be modified in *H. neanderthalensis* (derived: parasagittal orientation of the infraorbital plane with obliteration of the canine fossa). Accordingly, *H. heidelbergensis* and *H. rhodesiensis* would be excluded as LCA, since their facial morphology is more similar to that of Neanderthals (parasagittal orientation of the infraorbital plane, although less than in *H. neanderthalensis* - Maddux, 2011 - and absence of a canine fossa - Rak, 1986); so they place *H. heidelbergensis* at the base of *H. neanderthalensis.*

In the work of Lacruz *et al.* (2019), the consideration of the ATD6-69 face as modern would be based on two premises, in the mid-facial morphology and in the bone remodeling pattern. However, as we have been repeating in this work, the midface of ATD6-69 does not show a canine fossa and its region inferior to the infraorbital foramen is flat/slightly convex. This indicates that the infraorbital morphology of ATD6-69 is closer to that of *H. heidelbergensis* than to that of *H. sapiens.* According to Lacruz *et al.* (2019), the modern appearance of ATD6-69 would also be corroborated by analyzing the bone remodeling pattern, which identified resorption in the nasoalveolar clivus and in the maxilla (orthognathic face) similar to those found in the *H. sapiens* subadult (Lacruz *et al.,* 2013). However, Kurihara *et al.* (1980) and McCollum (2008), with samples of modern children and subadult faces, find a 26% and 55%, respectively, of a mostly depositional pattern in the anterior lower face (see McCollum [2008] for the great variability also in children and subadult chimpanzees). On the other hand, the face of MH1 (subadult of *A. sediba*) has a resorptive pattern very similar to that of most *H. sapiens* (Lacruz *et al.,* 2015), although

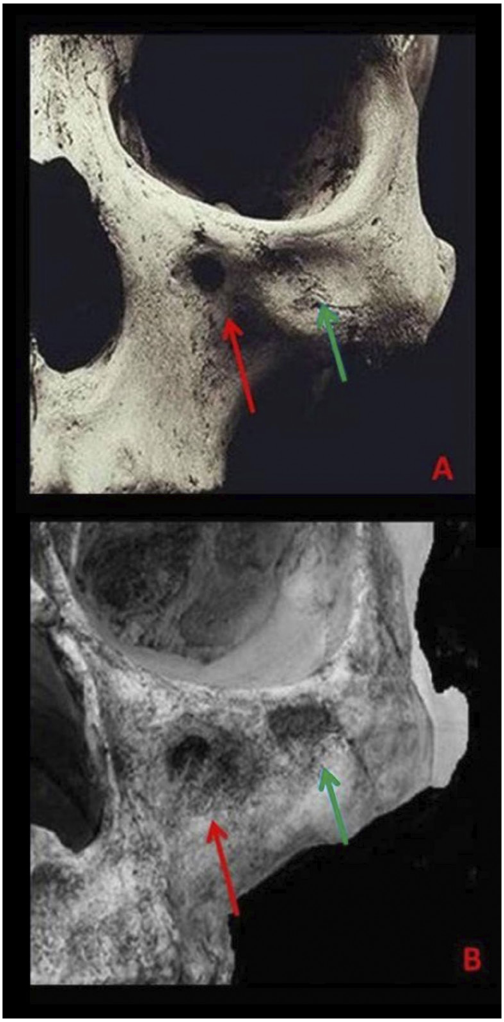

Fig. 1 - Infraorbital morphology of a current Eskimo skull (A), and the Kennewick man skull (B). The Oschinsky's fossa (green arrow) is located lateral to the infraorbital foramen; the canine fossa (red arrow) is located below the infraorbital foramen. Note that in B the canine fossa is greatly reduced. A) Modified from a Photograph by Aleš Hrdlička, ca. 1910. Credit Wellcome Collection. Attribution 4.0 International (CC BY 4.0). B) Cast. The colour version of this figure is available at the JASs website.

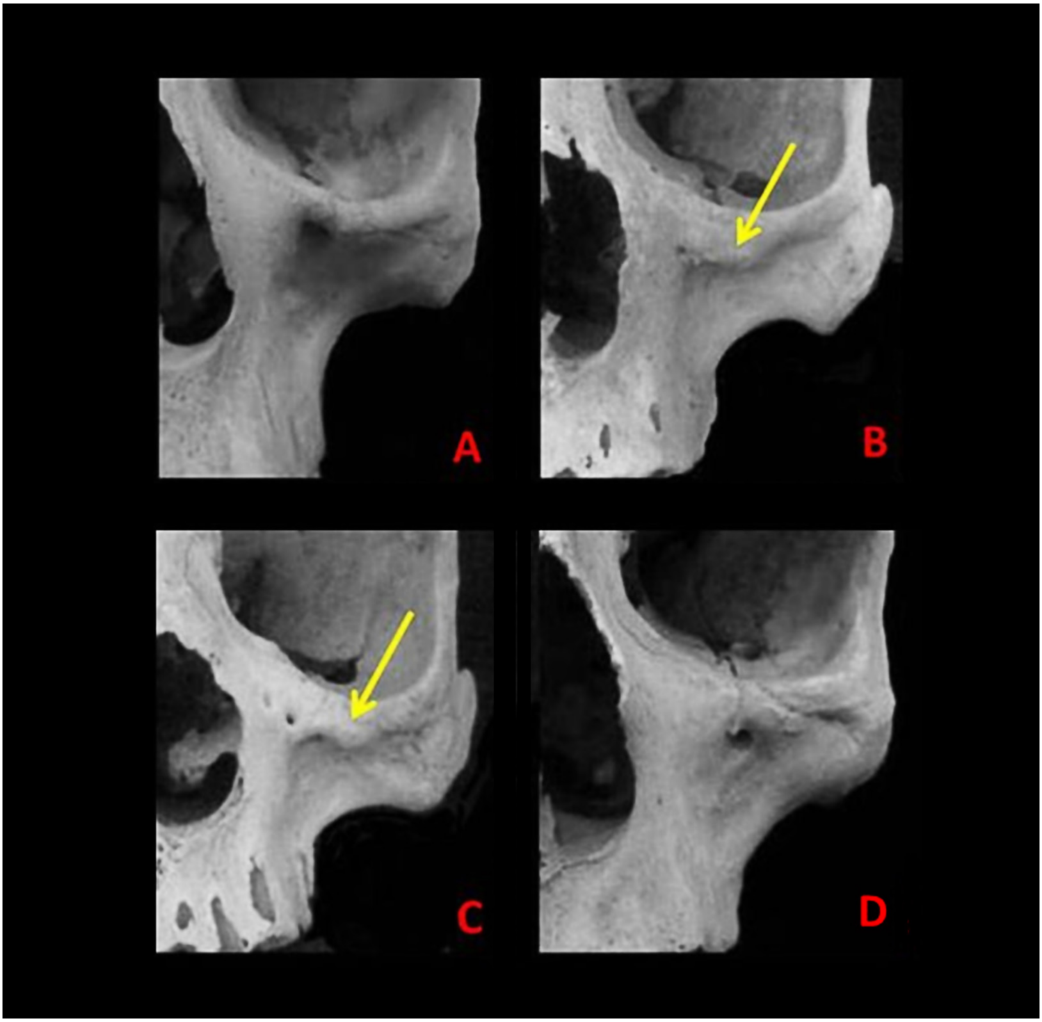

Fig. 2 - Oschinsky's fossa formation process in 4 different skulls of current* Homo sapiens. *A) Canine fossa with lateral extension (LPPMANC collection - photo F.R.T.); B) Superolateral narrowing of the canine fossa, due to the projection of the zygomaxillary tuberosity (yellow arrow); C) Great projection of the zygomaxillary tuberosity (yellow arrow), which begins the formation of the Oschinsky's fossa (Sonhuayo, Peru, SON 05.01.08 - photo A.J.A.E.); D) Oschinsky's fossa completely separated from the canine fossa (LPPMANC collection - photo F.R.T.). Note in the 4 skulls that the canine fossa is always located below the infraorbital foramen. LPPMAN: Paleoanthropology and Paleopathology Laboratory of the National Museum of Archeology of Catalonia. The colour version of this figure is available at the JASs website.

it has a more prognathic (mesognatic) face than ATD6-69 and *H. sapiens.* All this indicates that, as the sample is increased, there is a strong intraspecific variability in the remodeling patterns, both in orthognathic and prognathic faces; in this case it has only been observed in a single specimen, ATD6-69. Likewise, the presence of a resorptive pattern in MH1, ATD6-69 and *H. sapiens* could indicate the emergence of this model at different times in human evolution. This assertion would be in accordance with the proposal of Freidline *et al.* (2013), according to which modern-like facial morphology occurred independently in Africa, Asia and Europe at different times during the early and middle Pleistocene. However, in their principal component analysis (PCA), Freidline and colleagues (op. cit.) interpret lateral depression to the infraorbital foramen as a true canine fossa, so it is argued that modern-like facial morphology occurred independently in Africa and Asia, with Europe being a "cul-de-sac". The same reasoning behind the interpretation of the infraorbital depression also occurs in Lacruz *et al.* (2013, 2019), though Lacruz et al.'s arguments to locate them as LCA are not sufficiently relevant in this sense, and therefore we reaffirm that surely the so-called *H. antecessor* is at the base of the line that led to *H. heidelbergensis,* but not to *H. sapiens.*

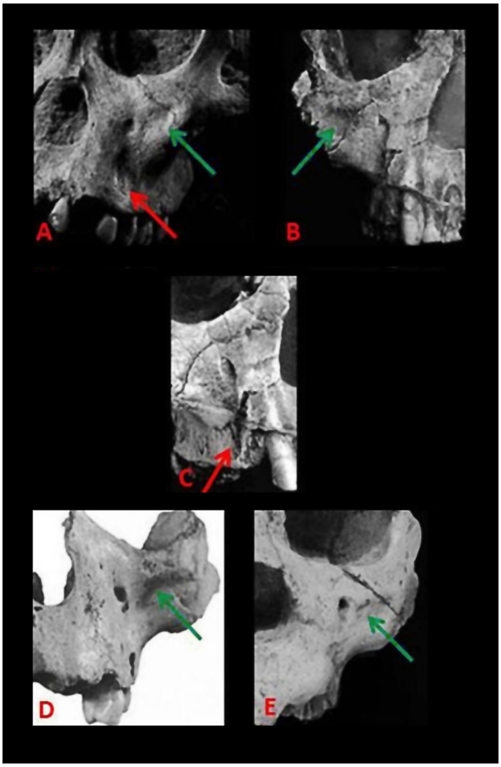

Fig. 3 - Examples of the presence of Oschinsky's fossa (indicated by a green arrow - the canine fossa is indicated with red arrows -) in fossil hominins. A) MH1 (**Australopithecus sediba*****) - modified from de Ruiter et al., 2018; B and C) KNM-ER 1813 (*****Homo habilis*****) - cast; D) ATD6-69 (*****Homo erectus*****) - image adapted from FAQ at the talk.origins Archive; E) SH 5 (*****Homo heidelbergensis*** ***or pre-Neanderthal) - cast. Note that the region inferior to the infraorbital foramen in ATD6-69 is flat or somewhat convex, morphology different from*** **Homo sapiens.** ***Images not scaled. The colour version of this figure is available at the JASs website.***

Finally, the authors of the paper (Bermúdez de Castro & Martinón-Torres, 2019) support the hypothesis that Southwest Asia, with special emphasis on the Levantine Corridor, was a favorable area for the establishment of hominin groups. They postulate that around the 900 kya this area would be the possible center of the origin of *H. antecessor.* From this point of view, *H. antecessor* would have to follow a circummediterranean route in order to populate Europe from Southwest Asia. This center of origin and dispersion in Southwest Asia would be supported by the work of Almogi-Labin (2011), which suggests that the changes in the climate in the northern area of the Negev desert was much more moderate than that of North Africa. At the end of the lower Pleistocene and early middle Pleistocene aridity increased dramatically, with a strong climatic deterioration between 0.9 and 0.7 Ma (Almogi-Labin, 2011). However, in the context of the discussion on the dispersion of *H. erectus* to Europe, these data are not transcendental since, despite great aridity in North Africa, there is a large number of sites with human presence lasting around one million years, including the upper levels of the Algerian sites of Ain Hanech (Raynal *et al.,* 2001; Sahnouni *et al.,* 2004) and Tighennif (Ternifine) (Geraads *et al.,* 1986, 2002; Geraads, 2016; Vrba, 1997; Sahnouni & van der Made, 2009). The Thomas Quarry I site in Morocco is similarly aged (Raynal *et al.,* 1995, 2001, 2004). These populations were able to move to Europe through the Straits of Gibraltar and/or the Alboran Sea area (Gibert, 1999; Gibert *et al.,* 2003; 2008, Gibert Beotas *et*

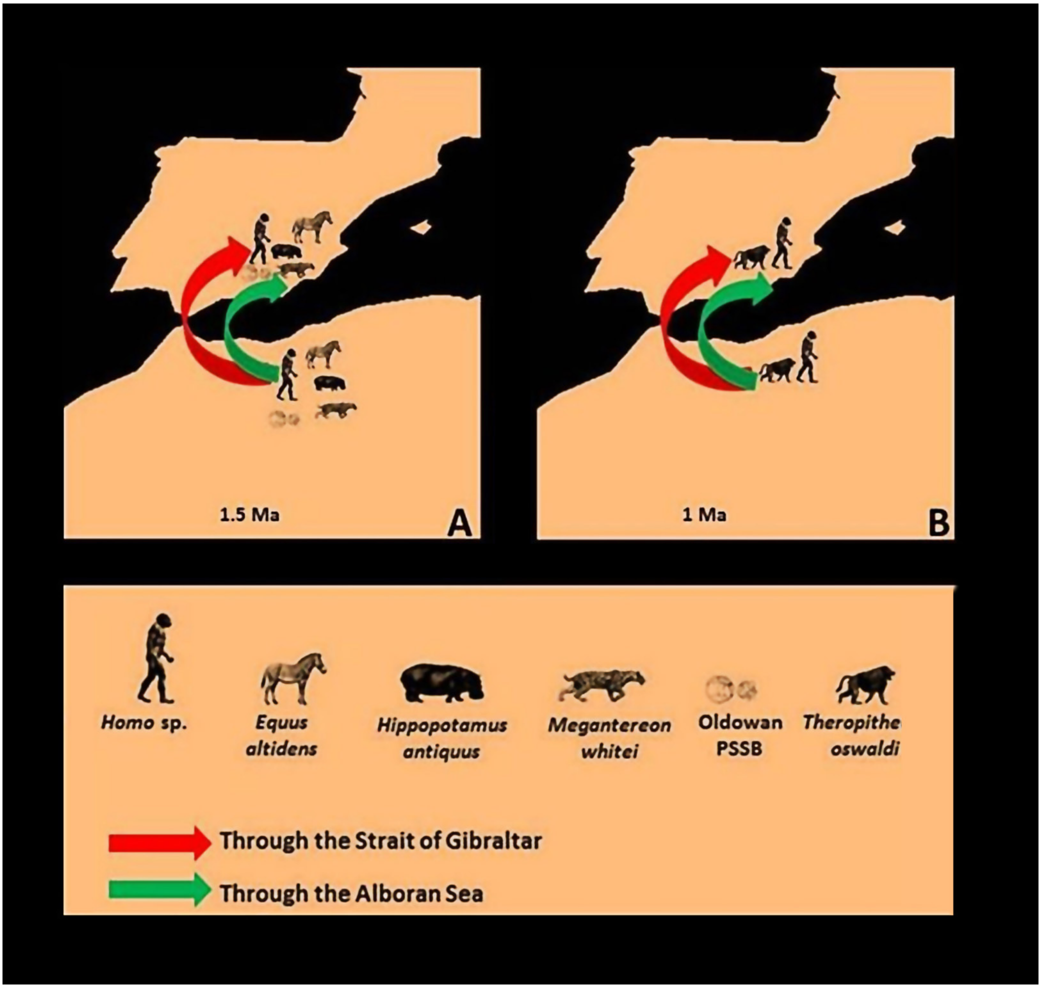

Fig. 4 - Routes of human and fauna dispersal from North Africa. A) First dispersion that reached Europe at 1.5 Ma, specifically the south of the Iberian Peninsula (Orce, Granada). At this migratory moment,* Homo *sp. it carries an archaic industry called Oldowan PSSB (polyhedrons, spheroids, subspheroids and balls), which is located in North Africa and in Barranco León 5 (Orce). Along with some African taxa such as* Hippopotamus antiquus, Equus altidens *and possibly* Megantereon whitei *they were able to reach the European continent by two routes: the Strait of Gibraltar (red arrow) and the Alboran Sea (green arrow). B) Second probable dispersion at 1 Ma. At this time* Homo *sp. and the cercopithecid* Theropithecus oswaldi *would reach Europe again by these two routes. In Cueva Victoria (Cartagena), southeast of the Iberian Peninsula, the only remains on the entire European continent of this African primate have been found, as well as human remains, which reinforces the hypothesis of migratory crossings through these routes maritime. The colour version of this figure is available at the JASs website.

al., 2016a,b; García-Nos, 2019; García-Nos *et al.,* 2019). The cause of this North Africa-Southeast Iberian Peninsula dispersion is unknown. Different hypotheses have been postulated, and the strong aridification discussed above may have played an important role. In addition, in the North Africa site of Tighennif there is a presence of the cercopithecid taxon *Theropithecus oswaldi,* which in Europe is only found in Cueva Victoria (Cartagena, southeastern Spain) at an age between 1 and 0.9 Ma. (Gibert *et al.,* 1995; Ribot *et al.,* 2012-2014; Ferràndez-Cañadell *et al.,* 2014).

Also, the recent discovery of a type of Oldowan industry typical of North Africa, the PSSB (polyhedrons, spheroids, subspheroids and balls), in Barranco León (Orce, Granada) (Titton *et al.,* 2020), with an age between 1,4 and 1,25 Ma (Oms *et al.*,2000; Scott *et al.*, 2007), together with fauna of African origin, such as *Hippopotamus antiquus, Equus altidens,* and possibly *Megantereon whitei,* as well as *Homo* sp., also registered in the Orce deposits from 1.4 Ma (Gibert *et al.,* 2006; Scott *et al.,* 2007), they reinforce the idea of several human and fauna waves from North Africa to the Iberian Peninsula through the Strait of Gibraltar or the Alboran Sea. This supports not only the viability of diversity between one shore and another, but also the idea that hominins used the sea routes to reach the southeast of the Iberian Peninsula from North Africa (Fig. 4) (García-Nos, 2019; García-Nos *et al.,* 2019).

We conclude that the remains of TD6.2, attributed to *H. antecessor,* should be classified as *H. erectus,* because they share an almost identical midfacial morphology. In contrast to what has been reported in a large number of publications, the depression in the zygomatic process of the maxilla of ATD6-69 and ATD6-58 is not a canine fossa. The depression in these fossils is located laterally to the infraorbital foramen, so it is actually the zygomaxillary fossa or Oschinsky‘s fossa. The area below the infraorbital foramen is flat or slightly convex with no trace of cupping, more similar to that of the hominins of the European middle Pleistocene. The origin of European *H. erectus* is an African story and its arrival in Europe from North Africa might been through the Strait of Gibraltar or the Alboran Sea.

Author contributions

All authors have contributed in the same way in the realization of this work.

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