

## A reply to Ribot *et al.*

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Taxonomic issues are always a source of debate in Palaeontology. The taxonomy of hominins, and in particular that of the species of the genus *Homo*, has produced endless discussions. We contend about this matter, because the evidence from the fossil record is limited and because since we are studying ourselves. In these studies, there is an inevitable emotional charge and interest. Some *Homo* species have been named following the rules of the International Code of Zoological Nomenclature: *H. habilis* (Leakey *et al.*, 1964), *H. antecessor* (Bermúdez de Castro *et al.*, 1997), *H. georgicus* (Gabounia *et al.*, 2002), *H. cepranensis* (Mallegni *et al.*, 2003), *H. floresiensis* (Brown *et al.*, 2004), *H. naledi* (Berger *et al.*, 2015), and *H. luzonensis* (Détroit *et al.*, 2019). Other species were named from the finding of one or a few specimens: *H. neanderthalensis* (King, 1864); *H. erectus* (Dubois, 1892, Mayr, 1944); *H. heidelbergensis* (Schoetensack, 1908), *H. rhodesiensis* (Woodward, 1921), or *H. helmei* (Dreyer, 1935). Other *Homo* species have emerged as a result of a review of the fossil record: *H. ergaster* (Groves & Mazák, 1975), *H. rudolfensis* (Alexeev, 1986; Groves, 1989). Some *Homo* species, such as *H. neanderthalensis* and *H. erectus*, receive a wide consensus due to their repeated use for years, even if they were not formally proposed. However, these species are also subject to debate. Thus, some authors consider that *H. erectus* is restricted to the Pleistocene of Asia (Asian *H. erectus* or *H. erectus sensu stricto*, *s.s.*), ranging a temporal age from 1.80-1.66 million years (Ma.) (Swisher *et al.*, 1994; Larick *et al.*, 2001; de Lumley & Lordkipanidze, 2006; Matsu'ura *et al.*, 2020) to 0.117-0.108 Ma.,

which is the last data obtained at the Ngandong site in central Java (Rizal *et al.*, 2020). In contrast, other authors (e.g., Rightmire, 1988; Asfaw *et al.*, 2020) consider that a certain number of Early African *Homo* specimens ought to be included in *H. erectus* as well (African *H. erectus*). Finally, some authors have considered the presence of *H. erectus* in Europe (e.g., Wolpoff, 1971; Vlcek, 1978; de Lumley, 2015), whereas other do not agree with this point of view (e.g., Howells, 1980; Stringer, 1984; Howell, 1986; Manzi, 2011). In formal terms, a wide acceptance of this species in Africa and Eurasia is recognized as *H. erectus sensu lato*, *s.l.* Understood in this way, *H. erectus s.l.* would be a spacious box, a blanket term that would comprise a wide morphological variability, perhaps representing different species (Wood & Collard, 1999; Wood, 2000) or subspecies (e.g., see Howells, 1980).

In their article "Another interpretation of *Homo antecessor*" Ribot *et al.* (2020, this volume) question the validity of *H. antecessor* and its possible origin in Southwest Asia. As an alternative, these authors consider that the fossils recovered from the TD6.2 level of the Gran Dolina cave site should be classified into *H. erectus*. In addition, they consider that the origin of these hominins could be in North Africa, and that they reached the Iberian Peninsula via the Strait of Gibraltar. We really appreciate the comments of these authors, and we are pleased for the interest shown in our work.

Ribot *et al.* (2020) focus their criticisms on the possible presence/absence of a canine fossa in the Gran Dolina-TD6.2 maxillary specimens, with a special mention on the morphology

of ATD6-69. According to these authors, the marked infraorbital depression observed in ATD6-69 is not homologous to the true canine fossa. In contrast, this depression should be considered as what Oschinsky defined as the zigomaxillary fossa (Oschinsky, 1962; Rak, 1983). Oschinsky' fossa is a superolateral extension of the canine fossa, which has been observed in recent Eskimos (Oschinsky, 1962), as well as in other hominin fossils (Rak, 1983; De Ruiter *et al.*, 2018). Ribot *et al.* (2020) support their conclusion in the fact that the bone depression of ATD6-69 is not placed just below the infraorbital foramen. Instead, this depression is located lateral to the infraorbital foramen and only affects the maxillary process of the zygomatic. We agree with Ribot *et al.* (2020) regarding the position of the bone depression of ATD6-69. In fact, Arsuaga *et al.* (1999, p. 442) write "In ATD6-69 the infraorbital depression is placed laterally to the infraorbital foramen". However, in disagreement with Ribot *et al.* (2020) we confirm that the ATD6-69 facial depression affects most of the zygomatic process of the maxilla, and not the maxillary process of the zygomatic (Fig. 1). In addition, Ribot *et al.* (2020) affirm that "In ATD6-69, Oschinsky 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". How can Ribot *et al.* (2020) guess the ontogenetic trajectory of the face of the individual to whom ATD6-69 belonged? Interestingly, in an independent study about the facial ontogeny of ATD6-69, Freidline *et al.* (2013, p. 404) write that "those features that have been suggested to link ATD6-69' morphology to modern humans would not have been significantly altered in the course of subsequent development. In particular, the infraorbital depression on this specimen".

An interesting aspect of ATD6-69 is the distance between the lower orbital margin and the infraorbital foramen (about 12.3 mm). Nanayakkara *et al.* (2016) and Ercikti *et al.* (2017) have obtained significantly shorter distances in modern humans, with ranges below the distance

observed in ATD6-69. Furthermore, the infraorbital foramen of ATD6-69 is placed about 27.0 mm from the anterior nasal spine. Nanayakkara *et al.* (2016) have obtained a distance of  $34.23 \pm 2.56$  mm for this variable in a modern human sample. Thus, the infraorbital foramen in ATD6-69 seems to be placed in a position that it is unusual in recent modern humans. This could be a reason to explain the spatial relationship between the canine fossa and the infraorbital foramen in this specimen and which Ribot *et al.* (2020) try to use as the key argument to question the modern-like morphology of ATD6-69. In other words, assessing the position of the facial depression relative to the infraorbital foramen in *H. antecessor* instead of relative to the zygomatic and maxillary processes may result in an anatomical inaccurate interpretation.

The term canine fossa has been used historically in so many different ways (Maureille, 1994; Maureille & Houët, 1997). Arsuaga *et al.* (1999, p. 442) concluded that ATD6-69 exhibits "an extended infraorbital depression that affects most, if not the entire zygomatic process of the maxilla". Rightmire (1998) observed that specimens attributed to *H. erectus s.l.* (African and Asian *H. erectus*) exhibit a *sulcus maxillaris*, a vertical groove inferior to the infraorbital foramen, first described by Weindenreich (1943) in the Zhoukoudian hominins. This feature, would be plesiomorphic according to Rightmire (1998) and may be confused with the true fossa canine. Due to the lack of consensus about the precise definition of this feature, we could possibly have endless, fruitless and inconclusive debates with Ribot *et al.* (2020) about the presence/absence of a canine fossa in ATD6-69. In this context, it is important to highlight that the modern-like face of *H. antecessor* was defined by several anatomical aspects that can be objectively discussed beyond discussion on the definition of the elusive "canine fossa". In ATD6-69, the modern-like modern face is defined by the fact of having an infraorbital bone plate oriented in the coronal plane and with an anterior surface sloping down and slightly backwards (see Rak, 1983, 1986). This is combined with a sagittal orientation of



**Fig.1 - Specimen ATD6-69, showing what we consider a true canine fossa. Note that this depressed area mainly located at the zygomatic process of the maxilla. The colour version of this figure is available at the JASs website.**

the lateral nasal walls. Furthermore, the inferior margin of the infraorbital plate of ATD6-69 (zygomaticoalveolar crest) is arched, and it shows a zygomaxillary tubercle. This feature is also present in ATD6-19 and ATD6-58. In addition, the comparative study of facial morphogenesis of KNM-WT 15000 (African *H. erectus*) and ATD6-69 has showed that these specimens, which have a similar dental age, differ in the pattern of bone deposition (Lacruz *et al.*, 2013). KNM-WT 15000 shows depositional micro-morphology on the naso-alveolar clivus, right nasal and right maxillary furrow. These features contribute to the anterior growth of the anterior maxilla and so to emphasize the differences in facial prognathism between this specimen and *H. sapiens*. According to Lacruz *et al.* (2013), the pattern of remodeling seen in (African) *H. erectus* resembles the pattern seen in earlier hominins such as *H. habilis* and *Australopithecus* (e.g., Bromage, 1989). In contrast, ATD6-69 exhibits

bone resorption over the naso-alveolar clivus, as is common in *H. sapiens*. In summary, and considering all the features, *H. antecessor* would have earliest occurrence of the modern-like face in the fossil record.

However, we recognize that specimens such as Nanjing 1 and those of Zhoukoudian show a more *H. sapiens*-like mid-facial topography than other coetaneous specimens of the ATD6-69 maxilla (Pope, 1992; Vialet, 2010). These Chinese specimens are more recent than those of the Gran Dolina-TD6.2, so two alternative hypotheses could be proposed: 1) some modern facial features may have developed by convergence in different hominin lineages (Freidline *et al.*, 2013); 2) The Gran Dolina-TD6.2 hominins represent the ancestral facial morphology for the clade containing *H. sapiens* and *H. neanderthalensis* (Bermúdez de Castro *et al.*, 1997; Lacruz *et al.*, 2019; Welker *et al.*, 2020). Additional morphogenetic studies on the origin of the modern

face revealed that the maxillae of Neanderthals and the Sima de los Huesos hominins had a pattern of bone deposition more similar to those of more ancient Pliocene hominins and significantly different to that found in *H. antecessor* and *H. sapiens* (Lacruz *et al.*, 2015, 2019). In this scenario, the most parsimonious interpretation, the one that requires less reversals is that the last common ancestor “may have displayed a morphology of the lower face more like *antecessor* than *heidelbergensis*” (Stringer, 2016, p. 9). This symplesiomorphic morphology was also present in other Middle Pleistocene Asian paleodemes and in the lineage of *H. sapiens* present in Africa from -500 Ky, while it was apparently lost in the *H. heidelbergensis*/*H. rhodesiensis* and *H. neanderthalensis* lineages (Lacruz *et al.*, 2019).

At this point, it is also necessary to consider whether the criticisms of Ribot *et al.* (2020) based on one single feature without clear consensus on its definition is enough to propose that *H. antecessor* should be considered as part of the hypodigm of *H. erectus* s.l. We acknowledge the difficulties to recognize species in the fossil record. Some authors have used the so-called phylogenetic species concept (Kimbel & Rak, 1993), based on the presence of synapomorphies (shared derived characters). This concept is borne from the evolutionary process, a species being the basal group within which there is a parental pattern of ancestry and descent. In this cladistic approach, some have chosen to employ autoapomorphies in species recognition (e.g., Tattersall, 1986) whereas others prefer to use a combination of apomorphies and plesiomorphies. According to Kimbel & Rak (1993) and Harrison (1993), a fossil species could be defined by a unique combination of features, i.e. a distinctive morphotype, regardless of whether it is apomorphies or plesiomorphies. Recognizing the difficulties to assess the cladistics status of certain traits, this is the approach we followed in the naming of *H. antecessor*, a comprehensive approach of the complete anatomical evidence rather than the assessment of an individual feature. After the publication of the *H. antecessor* species in 1997, more than 70 human remains

were recovered from level TD6.2. Various studies were carried out on this material, in which new features were observed. A synthesis of all the dental, cranial and postcranial traits observed in the *H. antecessor* hypodigm have been published by Bermúdez de Castro *et al.*, 2017, and see references therein). Thus, we are in the position to make a more refined diagnosis of *H. antecessor* as follows:

- 1) Primitive (plesiomorphic) features for the *Homo* clade. Among these features, it is interesting to mention the fusion of the styloid process to the basicranium. Asian *H. erectus* exhibits a derived state, since the styloid process is not fused to the basicranium (Martínez & Arsuaga, 1997).
- 2) Derived (apomorphic) features (for the *Homo* clade) shared with Neanderthals and modern humans.
- 3) Derived features shared with modern humans.
- 4) Derived features shared with Neanderthals and the Sima de los Huesos (Sierra de Atapuerca) hominins. Among these features, triangular shovel shape in upper incisors would be a synapomorphy shared with Asian *H. erectus*.
- 5) Derived features shared with Neanderthals.
- 6) Derived features shared with later hominins.

This is a unique species-specific combination of traits, which justifies the inclusion of Gran Dolina-TD6.2 fossils in a different taxon. Importantly, Ribot *et al.* (2020) are overlooking a significant set of potentially autapomorphic dental conformation in classic *H. erectus* that are absent in *H. antecessor* such as the so-called “dendrite-like pattern” of the enamel-dentine junction found in Middle Pleistocene samples like Zhoukoudian, Hexian and Yiyuan (Xing *et al.*, 2018).

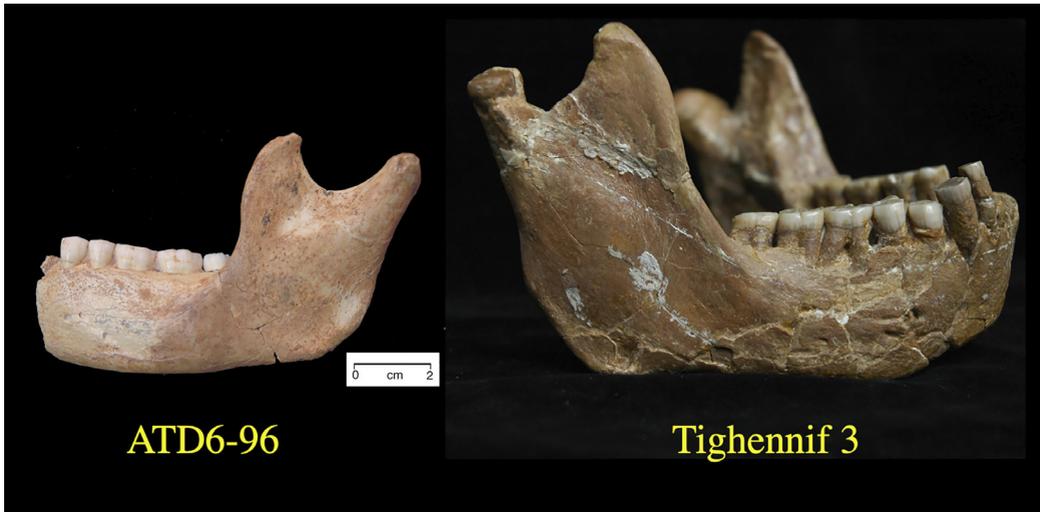
Surprisingly, and although the potential identification of Oschnisky’s fossa in *H. antecessor* is their key argument to assign ATD6-69 to *H. erectus*, Ribot *et al.* (2020) fail to provide a single example of a *H. erectus* specimen where this Oschnisky fossa is found. Instead, they provide

three potential fossil examples (a *H. habilis* and two *Australopithecus*) and numerous examples of modern humans (Fig. 1 and Fig. 2 in Ribot *et al.*, 2020) that would share this feature with ATD6-69. Following their line of reasoning, this seems a contradiction in their own argument as it reinforces the facial similarities between *H. antecessor* and *H. sapiens*.

Particularly important is the dental enamel proteome obtained for *H. antecessor* (Welker *et al.*, 2020). This molecular study places *H. antecessor* as a closely related sister taxon to the clade comprising *H. sapiens*, Neanderthals and Denisovans. Unfortunately, this analysis was unable to obtain conclusive results from a tooth from the Early Pleistocene site of Dmanisi (Republic of Georgia) but opens a promising avenue to explore the phylogenetic relationships among different hominins.

On the other hand, Ribot *et al.* (2020) criticize our hypothesis that Southwest Asia could be a centre for the origin for the ancestors of *H. antecessor* (Bermúdez de Castro *et al.*, 2013; Bermúdez de Castro & Martín-Torres, 2019). To question this possibility, they argue that the most likely route would be the Strait of Gibraltar and/or the Alborán sea area. In order to support this hypothesis, Ribot *et al.* (2020) recall the presence of the extinct cercopithecoid *Theropithecus oswaldi* in the site of Cueva Victoria (South East, Spain), a taxon found in some sites from the South, East and North of Africa (Ferrández-Cañadell *et al.*, 2014; but see Hughes *et al.*, 2008). Furthermore, according to them the continuity of the hominin population in North Africa during the Early Pleistocene could be a better option for the settlement of Europe. Although future discoveries may (or may not) support this migration route, this hypothesis is not mutually exclusive with a hominin colonization through other corridors. Ribot *et al.* (2020) seem focused in only one possibility of colonization of Europe via the Strait of Gibraltar and/or the Alborán sea area. Other possible hypotheses would be irrelevant to them. We advocate for a more scientific approach where all hypotheses should be considered, at least until clear evidence against them is found.

More importantly, in proposing the connection through the Gibraltar strait, Ribot *et al.* (2020), are not considering that the hominin evidence does not support the continuity between the North Africa fossils from Tighennif and *H. antecessor* (Bermúdez de Castro *et al.*, 2007). Both Gran Dolina-TD6.2 and Tighennif sites are approximately contemporary (Sahnouni *et al.*, 2018). The comparison of the two samples (Fig. 2) is highly pertinent in the context of the debate on the origin of *H. antecessor* and its presence in the Iberian Peninsula. The Tighennif mandibles evince a macrodontism and a large size, which may due to regional evolutionary continuity or the adaptation to local conditions (Hublin, 1989). The cladistics analysis of the dental evidence revealed that while Gran Dolina-TD6 hominins were displaying an Eurasian dental pattern, Tighennif and Rabat specimens were showing an African dental pattern clustering with *Homo ergaster* in their primitive dentitions (Martín-Torres *et al.*, 2007). Besides the important differences between the Tighennif mandibles and the *H. antecessor* mandibles (Bermúdez de Castro *et al.*, 2007), the lithic industry of this North African site is Acheulian (Sahnouni *et al.*, 2018), while implements obtained in Gran Dolina-TD6.2 are similar to Mode 1 Technology (Carbonell *et al.*, 1999). Interestingly, the lithic assemblages recovered from the Unit L of Thomas Quarry 1, dated of the Late Early Pleistocene (ca. 1 Ma), consist of Acheulean artifacts made from quartzite and flint (Raynal *et al.*, 2001). In other words, current data does not support a biological and cultural continuity between North African Early Pleistocene populations and the population of *H. antecessor* found in Gran Dolina-TD6.2. In light of the closest similarities between the European populations with the Asian rather than with the African ones (Martín-Torres *et al.*, 2007), as well as taking into account the biogeographic and faunal evidence (e.g. O'Regan *et al.* 2005, 2011), we believe that our proposal of the origin of *H. antecessor* in Southwest Asia should be considered, at least until data against it are found.



**Fig. 2 - Comparison between the mandibles ATD6-96 (*H. antecessor*) and Tighennif 3 (*H. ergaster* or African *H. erectus*). Although differences in tooth size and bone robustness may indicate a marked sexual dimorphism, the shape of the ramus is very different in these two specimens. The colour version of this figure is available at the JASs website.**

Summarizing, Ribot *et al.* (2020) should first explain how they understand the species *H. erectus* (Asian *H. erectus*, [*H. erectus s.s.*] or *H. erectus s.l.*). Any taxonomic proposal (or criticism to it) should be based on the discussion of well-defined features and, ideally, not only one. The only feature they base their criticism on is the alleged absence of a canine fossa in *H. antecessor* in favor of the presence of a “Oschinsky fossa” that surprisingly seems to be present in several modern humans and none *H. erectus* specimens. In any case, one feature is not solid evidence enough to invalidate a species that was defined by an exclusive combination of cranial, dental and postcranial characters. Additionally, beyond criticizing ADT6-69 fossa canina, Ribot *et al.* (2020) do not provide any specific feature that justifies the inclusion of ATD6-69 either in *H. erectus s.l.* or in Asian *H. erectus*.

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### References

- Alexeev V.P. 1986. *The Origin of the Human Race*. Progress Publishers, Moscow.
- Arsuaga J.L., Martínez I., Lorenzo C. *et al.* 1999. The human cranial remains from Gran Dolina Lower Pleistocene site (Sierra de Atapuerca, Spain). *J. Hum. Evol.*, 37: 431-457.
- Asfaw B., Gilbert W.H., Beyene Y. *et al.* 2020. Remain of *Homo erectus* from Bouri, Middle Awash, Ethiopia. *Nature*, 416: 317-320.
- Berger L.R., Hawks J., de Ruiter D.J. *et al.*, 2015. *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. *eLife*, 4: e09560.

- Bermúdez de Castro, J.M. & Martínón-Torres M. 2013. A new model for the evolution of the human Pleistocene populations of Europe. *Quat. Int.*, 295: 102-112.
- Bermúdez de Castro J.M., Martínón-Torres M., Arsuaga J.L. *et al.* 2017. Twentieth anniversary of *Homo antecessor* (1997-2017): a review. *Evol. Anthropol.*, 26: 157-171.
- Bermúdez de Castro J.M. & Martínón-Torres M. 2019. What does *Homo antecessor* tell us about the origin of the “emergent humanity” that gave rise to *Homo sapiens*? *J. Anthropol. Sci.*, 97: 209-213.
- Bermúdez de Castro J.M., Arsuaga J.L., Carbonell E. *et al.* 1997. A hominid from the Lower Pleistocene of Atapuerca, Spain: possible ancestor to Neandertals and modern humans. *Science*, 276: 1392-1395.
- Bermúdez de Castro J.M., Martínón-Torres M., Gómez-Robles A. *et al.* 2007. Comparative analysis of the Gran Dolina-TD6 (Spain) and Tighennif (Algeria) hominin mandibles. *Bull. Mém. Soc. d'Anthrop. Paris*, 19: 149-167.
- Bromage T.G. 1989. Ontogeny of the early hominid face. *J. Hum. Evol.*, 18: 751-773.
- Brown P., Sutinka T., Morwood M.J. *et al.* 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature*, 431: 1055-1061.
- Carbonell E., García-Antón M.D., Mallol C. *et al.* 1999. The TD6 level lithic industry from Gran Dolina, Atapuerca (Burgos, Spain): production and use. *J. Hum. Evol.*, 37: 653-693.
- De Ruiter D.J., Carlson K.B., Brophy J.K. *et al.* 2018. The skull of *Australopithecus sediba*. *PaleoAnthropology*, Especial issue *Australopithecus sediba*, pp. 56-155.
- Détroit F., Mijares A.S., Corny J. *et al.* 2019. A new species of *Homo* from the Late Pleistocene of the Philippines. *Nature*, 568: 181-186.
- Dreyer T.F. 1935. A human skull from Florisbad, Orange Free State, with a note on the endocranial cast by C.U. Ariëns Kappers. *Koninklijke Akademie van Wetenschappen Amsterdam, Proceedings*, 38: 3-12.
- Dubois E. 1892. Paleontogische onderzoekingen op Java. *Verslag van het Mijnwezen. Batavia*, 3: 10-14.
- Ercikti N., Apaydin N. & Kirici Y. 2017. Location of the infraorbital foramen with reference to soft tissue landmarks. *Surg. Radiol. Anat.*, 39: 11-15.
- Ferrández-Cañadell C., Ribot F. & Gibert L. 2014. New fossil teeth of *Theropithecus oswaldi* (Cercopithecoidea) from the Early Pleistocene at Cueva Victoria (SE Spain). *J. Hum. Evol.*, 74: 55-66.
- Freidline S.E., Gunz P., Harvati K. *et al.* 2013. Evaluating developmental shape changes in *Homo antecessor* subadult facial morphology. *J. Hum. Evol.*, 65: 404-423.
- Gabounia L., de Lumley M.A., Vekua A. *et al.* 2002. Découverte d'un nouvel hominidé à Dmanissi (Transcaucasie, Géorgie). *C.R. Paleovol.*, 1: 243-253.
- Groves C.P. 1989. *A Theory of Human and Primate Evolution*. Oxford University Press, Oxford.
- Groves C.P. & Mazák V. 1975. An approach to the taxonomy of the Hominidae: Gracile Villafranchian hominids of Africa. *Caspos Pro Mineralogii A Geologii*, 20: 225-247.
- Harrison T. 1993. Cladistic concepts and the species problem in hominoid evolution. In W.H. Kimbel & L.B. Martin (eds): *Species, Species Concept, and Primate Evolution*, pp. 345-372. Plenum Press, New York.
- Howell F.C. 1986. Variabilité chez *Homo erectus*, et problème de la présence de cette espèce en Europe (1). *L'Anthropologie*, 90: 447-481.
- Howells W.W. 1980. *Homo erectus* - who, when and where: a survey. *Yearb. Phys. Anthropol.*, 23 S1:1-23.
- Hublin J.-J. 1989. Les origines d l'Homme moderne: Europe occidentale et Afrique du Nord. In G. Giacobini (ed): *Proc 2<sup>nd</sup> Int. Congress Hum. Paleont.*, pp. 423-430. Jaca Book, Milan.
- Hughes J.K., Elton S. & O'Regan H.J. 2008. *Theropithecus* and 'Out of Africa' dispersal in the Plio-Pleistocene. *J. Hum. Evol.*, 54: 43-77.
- Kimbel W.H. & Rak Y. 1993. The importance of species taxa in paleoanthropology and argument for the phylogenetic concept of species category. In W.H. Kimbel & L.B. Martin (eds): *Species, Species Concept, and Primate Evolution*, pp. 461-485. Plenum Press, New York.

- King W. 1864. The reputed fossil man of the Neanderthal. *Quat. J. Sci.*, 1: 88-97.
- Lacruz R.S., Bermúdez de Castro J.M., Martín-Torres M. *et al.* 2013. Facial morphogenesis of the Earliest Europeans. *PLoSOne*, 8: e65199.
- Lacruz R.S., Stringer C.B., Kimbel W.H. *et al.* 2019. The evolutionary history of the human face. *Nat. Ecol. & Evol.*, 3: 726-736.
- Lacruz R.S., Bromage T.G., O'Higgins P. *et al.* 2015. Ontogeny of the maxilla in Neanderthals and their ancestors. *Nat. Comm.*, 6: 8996.
- Larick R., Ciochon R.L., Zaim Y. *et al.* 2001. Early Pleistocene 40Ar/39 Ar ages for Bapang Formation hominins, Central Jawa, Indonesia. *Proc. Natl. Acad. Sci. USA*, 98: 4866-4871.
- Leakey L.S.B., Tobias P.V. & Napier J.R. 1964. A new species of the genus *Homo* from Olduvai Gorge. *Nature*, 202: 7-9.
- Lumley M.A. & Lordkipanidze D. 2006. L'Homme de Dmanissi (*H. georgicus*), il y a 1 1810 00 ans. *C.R. Palevol.*, 5: 273-281.
- Lumley M.A. de 2015. L'Homme de Tautavel. Un *Homo erectus* européen évolué. *Homo erectus tautavelensis*. *L'Anthropologie*, 119: 303-348.
- Mallegni F., Carnieri C., Bisconti M. *et al.* 2003. *Homo cepranensis* sp. nov. And the evolution of Africa- European Middle Pleistocene hominids. *C.R. Palevol.*, 2: 153-159.
- Manzi G. 2011. Before the Emergence of *Homo sapiens*: Overview on the Early-to-Middle Pleistocene Fossil Record (with a Proposal about *Homo heidelbergensis* at the subspecific level). *Int. J. Evol. Biol.*, 2011: 582678.
- Martínez I. & Arsuaga J.L. 1997. The temporal bones from Sima de los Huesos Middle Pleistocene site (Sierra de Atapuerca, Spain). A phylogenetic approach. *J. Hum. Evol.*, 33: 283-318.
- Martín-Torres M., Bermúdez de Castro J.M., Gómez-Robles A. *et al.* 2007. Dental evidence on the hominin dispersals during the Pleistocene. *Proc. Natl. Acad. Sci. USA*, 104: 13279-13282.
- Matsu'ura S., Kondo M. & Danhara T. 2020. Age control of the first appearance datum for Javanese *Homo erectus* in the Sangiran area. *Science*, 367: 210-214.
- Maureille G. 1994. *La face chez Homo erectus and Homo sapiens: recherché sur la variabilité morphologique et métrique*. PhD Dissertation, Université de Bordeaux I.
- Maureille B. & Houët F. 1997. Nouvelles données sur caractéristiques dérivées du masif facial supérieur des Néandertaliens. *Anthrop. et Préhistoire*, 108: 89-98.
- Mayr E. 1944. On the concepts and terminology of vertical subspecies and species. *Natl. Res. Council Bull.*, 262: 11-16.
- Nanayakkara D., Peiris R. & Mannapperuma N. 2016. Morphometric analysis of the infraorbital foramen: the clinical relevance. *Anat. Res. Int.*, 2016: 1-8.
- O'Regan H.J., Bishop L.C., Lamb A. *et al.* 2005. Large mammal turnover in Africa and the Levant between 1.0 and 0.5 Ma. *Geol. Soc. London Special Publications*, 247: 231-249.
- O'Regan H.J., Turner A., Bishop L.C. *et al.* 2001. Hominins without fellow travelers? First appearance of Afro-Eurasian large mammals in the Pliocene. *Quat. Sci. Rev.*, 30: 1343-1352.
- Oschinsky L. 1962. Facial flatness and cheekbone morphology in Artic Mongoloids: A case of morphological taxonomy. *Anthropologica*, 4: 349-377.
- Pope G.G. 1992. Craniofacial evidence for the origin of modern humans in China. *Yearb. Phys. Anthropol.*, 35: 243-298.
- Raynal J.-P., Geraads D., Mohi A. *et al.* 2001. The earliest occupation of North-Africa: The Moroccan perspective. *Quat. Int.*, 75: 65-75.
- Rak Y. 1983. *The Australopithecine face*. Academic Press, New York.
- Rak Y. 1986. The Neanderthal: A new look at an old face. *J. Hum. Evol.*, 15: 151-164.
- Ribot Trafi F., García Bartual M., Gracia-Nos E. *et al.* 2020. Another interpretation of "*Homo antecessor*". *J Anthropol Sci.*, 98.
- Rightmire G.P. 1988. *Homo erectus* and later Middle Pleistocene humans. *Ann. Rev. Anthropol.*, 17: 239-259.
- Rightmire G.P. 1998. Evidence from facial morphology for similarity of Asian and African representatives of *Homo erectus*. *Am. J. Phys. Anthropol.*, 106: 61-85.

- Rizal Y., Westaway K., Zaim, Y. *et al.* 2020. Last appearance of *Homo erectus* at Ngandong, Java, 117,000-108,000 years ago. *Nature*, 577: 381-385.
- Sanhouni M., Parés J.M., Duval M. *et al.* 2018. Early *Homo* adaptive and behavioral patterns in North Africa: perspectives from Ain Hanech and Tighennif (formerly Ternifine) sites in Northern Algeria. *15<sup>th</sup> Congress of PanAfrican Archaeological Association for Prehistory and Related Studies (PanAf)*, pp. 5-6.
- Schoetensack O. 1908. *Der Unterkiefer des Homo heidelbergensis aus den Sanden von Mauer bei Heidelberg, Leipzig*, pp. 1-6.
- Stringer C.B. 2016. The origin and evolution of *Homo sapiens*. *Phil. Trans. Roy. Soc. B*, 371: 20150237.
- Stringer C.B. 1984. The definition of *Homo erectus* and the existence of the species in Africa and Europe. *Cour. Forsch. Inst. Senckenberg, Frankfurt am Main*, 69: 131-143.
- Swisher III C.C., Curtis G.H., Jacob T. *et al.* 1994. Age of the earliest known hominids in Java, Indonesia. *Science*, 263: 1118-1121.
- Tattersall I. 1986. Species recognition in human paleontology. *J. Hum. Evol.*, 15: 165-175.
- Vialet A., Guipert G., Jianing H. *et al.* 2010. *Homo erectus* from the Yunxian and Nankin Chinese sites: Anthropological insights using 3D virtual imaging techniques. Étude des *Homo erectus* de Yunxian et de Nankin en Chine. Apport de l'imagerie 3D. *C.R. Palevol.*, 9: 331-339.
- Vlcek E. 1978. A new discovery of *Homo erectus* in central Europe. *J. Hum. Evol.*, 7: 239-251.
- Weidenreich F. 1943. The skull of *Sinanthropus pekinensis*: a comparative study. *Paleontologia Sinica New Series D*, 10: 1-484.
- Welker F., Ramos-Madrigrá J., Gutenbrunner P. *et al.* 2020. The dental proteome of *Homo antecessor*. *Nature*, 580: 235-238.
- Wolpoff M.H. 1971. Is Vértesszöllös II an occipital of European *Homo erectus*? *Nature*, 232: 567-568.
- Wood B.A. 2000. The history of the genus *Homo*. *Hum. Evol.*, 15: 39-49.
- Wood B.A. & Collard M. 1999. The human genus. *Rev. Anthropol.*, 284: 65-71.
- Woodward A.S. 1921. A New Cave Man from Rhodesia, South Africa. *Nature*, 108: 371-372.
- Xing S., Martínón-Torres M. & Bermúdez de Castro J.M. 2018. The fossil teeth of the Peking Man. *Sci. Rep.*, 8: 2066.

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