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The affinities of *Homo antecessor* – a review of craniofacial features and their taxonomic validity

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ABSTRACT: The phylogenetic affinities of *Homo antecessor*, a hominin dating from the early Middle Pleistocene of Europe, are still unclear. In this study we conducted a comprehensive review of the TD6 hypodigm within the context of the historical development of paleoanthropological issues concerning this species. *H. antecessor,* based on all available craniofacial features to date, displays a midfacial morphology very similar to specimens attributed to Classic *Homo erectus*, suggesting that *H. antecessor* is the geographical European variant of Classic *H. erectus*.

KEY WORDS: Atapuerca, Early *Homo*, *Homo erectus*, *Homo antecessor*, midfacial morphology, Middle Pleistocene

Introduction

In 1997, Bermúdez de Castro and colleagues defined a new species, *Homo antecessor* (Bermúdez de Castro et al. 1997), based on craniofacial and dental remains of ATD6-69 specimen, an immature individual found at the TD6 level of Gran Dolina (Atapuerca, Burgos, Spain) and dated between 0.78 Ma (Carbonell et al. 1995) and 0.9 Ma (Parés et al. 2013).The facial morphology features of ATD6-69 were the hallmarks that allowed Bermúdez de Castro and colleagues to define this new species, and also place it as a common ancestor of Neandertals and *H. sapiens* (see "Differential diagnosis of *Homo antecessor*"). However, the phylogenetic status of *H. antecessor* is not widely accepted, as some authors have doubts about its validity as a unique taxon (eg, Delson 1997; Wang 1998; Wang and Tobias 2000a; Rightmire 2001, 2007; Stringer 2002; Etler 2004; Rabadà 2005; Ribot et al. 2006, 2007, 2017, in press 2018; Cartmill and Smith 2009; Ribot and García Bartual 2016).

One of the main problems for the acceptance of this new human species is its diagnosis, which was done on the basis of a subadult individual. Rightmire (1998a) noted that the attribution of a new species, based solely on the facial morphology of an immature specimen is problematic, and also questioned whether the presence of a true canine fossa in a young individual —one of the diagnostic characteristics for this taxon— is an

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appropriate morphological feature for the diagnosis of a new species. In fact, the zygomaxillary fragment from Atapuerca, ATD6-58 (attributed to an adult individual), shows a reduced canine fossa, which differs from to the ATD6-69 fragment attributed to an immature individual (Bermúdez de Castro et al. 1997; Arsuaga et al. 1999) (Fig. 1).

In 2003, a mandible of an adult *H. antecessor* was recovered (ATD6-96) (Carbonell et al. 2005). From the study of this fossil, the authors concluded that: "*[...] none of the mandibular characteristics considered apomorphic in the European Middle Pleistocene and Upper Primitive* Homo *lineage are present in ATD6-96. This evidence reinforces the taxonomic identity of* H. antecessor *and is consistent with the hypothesis of a close relationship between this species and* Homo sapiens" (Carbonell et al. 2005. p. 5674).

While it is not clear if *H. antecessor* represents a new taxon based on diagnostic characteristics, in the study of Carbonell et al. (2005) they compare 14 mandibular characters from the ATD6-96 mandible with those of different *Homo* taxa (Table 4 in Carbonell et al. 2005). The interpretation of the table shows that most of the features present in ATD6-96 are also found in Classic *H. erectus* (see Taxonomic notes). In fact, only one trait can be considered as derived, which is the hollowed posterior subalveolar fossa. This trait is moderately hollowed in ATD6-96 and in some *H. heidelbergensis*, shallow in almost all Classic *H. erectus* individuals, deep in Classic *H. erectus* from Zhoukoudian, and subtle in *H. neanderthalensis* and some *H. heidelbergensis*. However, the distinction drawn by Carbonell et al. (2005) between a shallow and moderately hollowed subalveolar fossa, is very subjective and fossils assigned to either of the two categories are virtually identical. Moreover, in a recent review of *H. antecessor*, Bermúdez de

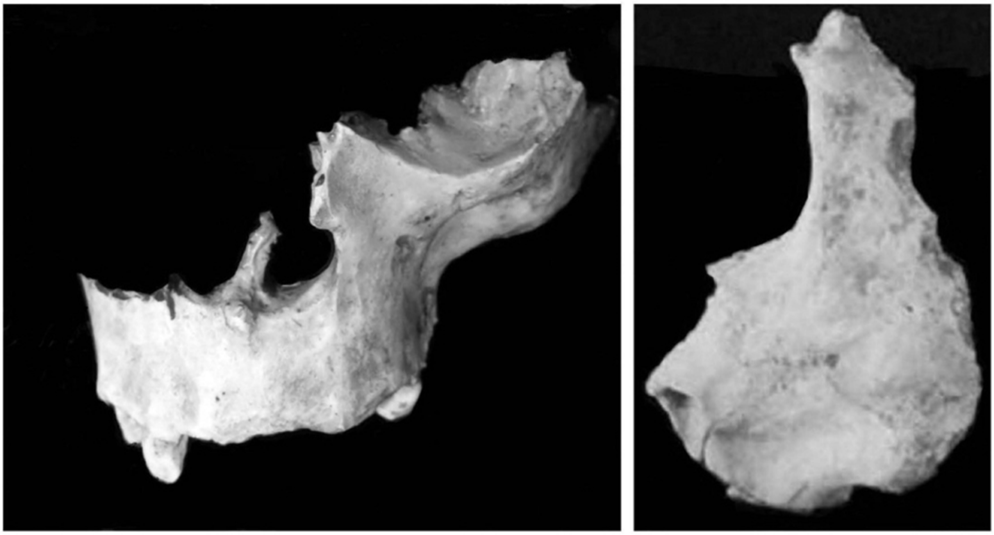

Fig. 1. Comparison between ATD6-69 —juvenile— (right) and ATD6-58 —adult— (left)
Footnote: It can be observed how the canine fossa in ATD6-58 is shallower than that found in ATD6-69. Picture of ATD6-69 courtesy of Roberto Sáez; picture of ARD6-58 taken from Schwartz and Tattersall (2002).

Castro et al. (2017) did not present any derived feature in the *H. antecessor* mandible, with comparison to modern humans (see Table 2 in Bermúdez de Castro et al. 2017).

It has also been argued that the alleged ancestor-descendant relationship between *H. antecessor* and *H. sapiens,* and the recognition of *H. antecessor* as a new taxon, is reinforced by the remodeling pattern of the facial bone of ATD6-69, which shows a strong similarity with that in *H. sapiens* (Lacruz et al. 2013). In both species, there is a retraction at the subnasal region (orthognathic face) associated with the presence of resorptive areas around the nasomaxillary clivus (Lacruz et al. 2013, 2015). This pattern contrasts with that of KNM-WT 15000 —an immature individual of West Turkana Earliest *H. erectus* (or *H. ergaster*) (see Taxonomic notes), dated to approximately 1.7 Ma—, which shows the primitive facial bone remodeling pattern seen in australopiths and early *Homo,* with presence of areas of deposition at the subnasal region (prognathic face) (Bromage 1989; Lacruz et al. 2013, 2015). Thus, Lacruz and colleagues (2013) conclude that the *H. sapiens*-like retraction of the midface in ATD6-69 is a key aspect of *H. antecessor* in its recognition as a new taxon. However, the validity of this characteristic to establish taxonomic relations is problematic considering the findings of previous studies (Kurihara et al. 1980; McCollum 2008).

Regarding the origin of *H. antecessor,* the scientists studying the Atapuerca materials have proposed two different options: the first one states that this taxon had an African origin, in which *H. antecessor* and Classic *H. erectus* share a common ancestor with the Earliest *H. erectus* (or *H. ergaster*) (Bermúdez de Castro et al. 1997, 2017; Arsuaga et al. 1999; Rosas 2000). The second one states that *H. antecessor* has an Asian origin, in which this taxon would be the descendant of *H. erectus* (Carbonell et al. 2005; Martinón-Torres et al. 2007), based on the strong similarities of *H. antecessor* and the Asian Classic *H. erectus* in their mandibles and midfacial morphology, and the shared presence of a zygomaxillary tubercle (Carbonell et al. 2005). Also, these hominins present similarities in some dental features, such as the "morphological robusticity" of the anterior dentition (e.g., triangular shovel shape), and in the posterior dentition, by the simplification of occlusal morphology, high frequencies of non-Y groove patterns, the presence of the mid-trigonid crest, the anterior fovea and the transverse crest in the premolars (Martinón-Torres et al. 2007).

Differential diagnosis for *Homo antecessor*

The erection of the new species, *H. antecessor,* and its relation to *H. sapiens* was based on a series of characters on ATD6-69 (Bermúdez de Castro et al. 1997), which were viewed as derived traits with respect to primitive *Homo* (*H. rudolfensis, H. habilis,* Earliest *H. erectus* [or *H. ergaster*] and Classic *H. erectus*) and to the later appearing European *Homo* (*H. heidelbergensis* and *H. neanderthalensis*). Special emphasis was put on the ATD6-69 midfacial morphology and its related nasomaxillary functional complex (Bermúdez de Castro et al. 1997, 2017; Arsuaga et al. 1999), including: the coronal orientation of the infraorbital surface with inferoposterior slope of its plane; presence of canine fossa; maxillary inflection oriented horizontally and a projection of the nasal bones; arched zygomaticoalveolar crest with a superiorly positioned zygomatic root plus the presence of an *incisura malaris;* spinal and lateral nasal crests nearly fusing to form a lower nasal edge; presence of a zygomaxillary tubercle; modern facial bone remodeling pattern; and convex superior border of the temporal squama. This midfacial and cranial morphological combination found in the ATD6 hominins is considered a modern human synapomorphy that first appeared in the fossil record with the appearance of *H. antecessor* (Table 1, Fig. 2).

Table 1. Craniofacial and mandibular supposedly derived characteristics that are part of the definition of *Homo antecessor** and which are discussed in the present study (see also Fig. 1)

	Diagnostic features of '*H. antecessor*' discussed in this study
1	Coronal orientation of the infraorbital surface with inferoposterior slope of this plane
2	Presence of canine fossa
3	Maxillary inflection horizontally plus projection of the nasal bones
4	Arched zygomaticoalveolar crest with *incisura malaris*
5	Spinal and lateral nasal crests nearly fusing to form a lower nasal edge
6	Presence of zygomaxillary tubercle
7	Modern facial bone remodeling pattern
8	Convex superior border of the temporal squama

*Bermúdez de Castro et al. 1997; Arsuaga et al. 1999; Carbonell et al. 2005; Bermúdez de Castro et al. 2017.

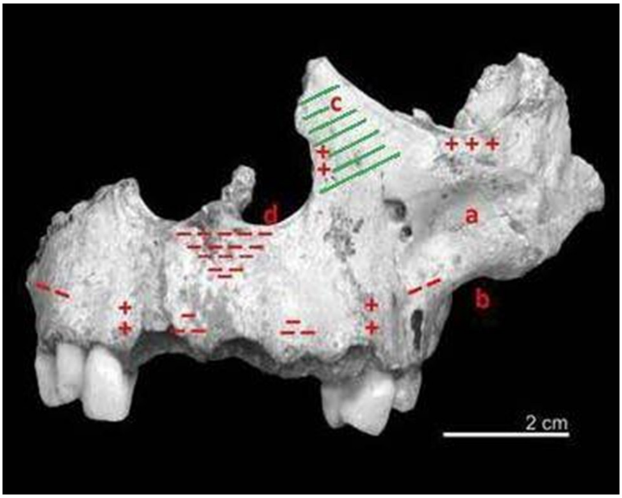

Fig. 2. ATD6-69 facial characteristics considered exclusively derived with respect to *Homo sapiens*, and used to define the species *Homo antecessor* (Bermúdez de Castro et al. 1997, 2017; Arsuaga et al. 1999)
Footnote: *a)* coronal orientation of the infraorbital surface with presence of a true canine fossa; *b)* horizontally arched zygomaticoalveolar crest, with a high zygomatic root and zygomaxillary tubercle; *c)* maxillary inflection determined by the infraorbital plate and the lateral nasal wall (area marked in green lines); *d)* spinal and lateral nasal crests that are very close together and almost fuse forming the lower nasal edge; and modern facial bone remodelling pattern: (+) depository fields; (–) resorptive fields. Modified from Schwartz and Tattersall (2002) and Lacruz et al. (2013).

Material and methods

Material

Materials for this study include casts, images, and description of early *Homo* and penecontemporary Asian Classic *H. erectus* which present midfacial skeleton remains, partially or complete. In particular we studies the following hominin casts: KNM-ER 1470; KNM-ER 1813; OH 24; OH 13; KNM-ER 3883; KNM-ER 3733; KNM-WT 15000; Gongwangling; Sangiran 17; Zhoukoudian (reconstruction of Weidenreich —1937a— and Sawyer and Tattersall —1995 [and Tattersall and Sawyer, 1996]—). Also, a sample of 35 extant human skulls from the Laboratory of Paleopathology and Paleoanthropology of the National Museum of Archeology of Catalonia in Barcelona. Regarding the study of *H. antecessor* remains we used a high-quality replica of ATD6-69 (not the standard cast that is hosted in many laboratories), which was brought by the researchers from the Atapuerca group for a special exhibition at the Miquel Crusafont Institute of Paleontology in Sabadell (Barcelona). One of us (F.R.T.) had access to this replica during several months, and was allowed to study and compare it with the pictures and descriptions of ATD6-69 made by the Atapuerca team. We have also used photos and the original descriptions of the material.

Taxonomic notes

In this study, the midfacial morphology of *H. antecessor* is compared with that of the older *Homo* species (early *Homo* and Earliest *H. erectus* [or *H. ergaster*]), and with the penecontemporary species of Classic *H. erectus*. The taxa used and their representative specimens are as follows.

1. Early *Homo*. We considered as early *Homo* those specimens dated between ~2.4 and 1.4 Ma (Table 2). Although the classification of early *Homo* is controversial, in this work we have opted for a more classic classification and, according to Antón et al. (2014) we distinguish between the 1470 group and the 1813 group (also called *H. rudolfensis* and *H. habilis,* respectively, by several authors —e.g. Wood 1992; Kimbel et al. 1997;

Table 2. Fossil specimens classified here as Early *Homo*

Specimen	Age (Ma)	Author
A.L. 666-1	2.33	Kimbel et al. 1997
1470 group		
KNM-ER 1470	2.03-2.09	Joordens et al. 2013
KNM-ER 62000	1.95-1.98	Joordens et al. 2013
1813 group		
OH 24	1.88	Hay 1976
KNM-ER 1813	~1.86	Feibel et al. 2009
OH 62	1.75-1.85	Johanson et al. 1987
OH 65	~1.78	Blumenschine et al. 2003
OH 13	1.60	Hay 1976
KNM-ER 42703	1.44	Spoor et al. 2007

Strait et al. 1997; Prat 2004; Kimbel 2009; Schrenk et al. 2015; Simpson 2015).

In 1470 group, we include the specimens KNM-ER 1470 and KNM-ER 62000. Leakey et al. (2012) include KNM-ER 1470 and KNM-ER 62000 in the same group because of its morphological similarity.

In 1813 group, we include the specimens OH 24, OH 62, OH 65, KNM-ER 1813 and KNM-ER 42703.

The classification of the OH 65 maxilla is controversial: Blumenschine et al. (2003) and Clarke (2012), they group it with KNM-ER 1470, and Clarke (2012) separates KNM-ER 1470 and OH 65 *(H. habilis)* from KNM-ER 1813 and OH 24 *(Australopithecus* cf. *africanus)*. However, the inclusion of KNM-ER 1470 and OH 65 to the same group has been questioned: Spoor et al. (2007) point out that the morphology of the maxilla KNM-ER 42703 is very close to that of the large specimens of *H. habilis* (OH 65 and KNM-ER 1805) and different from that of KNM-ER 1470. Also, Leakey et al. (2012) and Antón (2012) separates OH 65 from KNM-ER 1470 and KNM-ER 62000, because OH 65 is much more prognathic subnasally and has more posteriorly positioned zygomatic roots, the nasoalveolar clivus is arched at the alveolar margin, and its canine alveoli are not part of the anterior tooth row; the incisors project beyond the bicanine line and the palate is parabolic (like KNM-ER 1813 and different from the 'U-shaped' in KNM-ER 62000). Therefore, we include OH 65 in 1813 group.

Another specimen whose classification is difficult is KNM-ER 1805. Many authors classify it as Early *Homo* (ex, Wood 1991, 1992; Kimbel et al. 1984, 1997, 2004; Wood and Richmond 2000, Williams et al. 2012; Schrenk et al. 2015); however, others include it among the australopiths: Falk (1986) notes that the cortical sulcal pattern of ER 1805 has affinities with *Australopithecus;* Tobias (1980) allocated the specimen to *Paranthropus boisei* on the basis of molar morphology; likewise, Prat (2002, 2004), based on a cladistic analysis with 122 cranial characteristics, concludes that ER 1805 should be included in the genus *Paranthropus*. Finally, Grossman (2009) points out that ER 1805 presents neither the typical morphology of *Homo* nor that of *Paranthropus,* and concludes that the suite of traits presented in KNM-ER 1805 are certainly unique. Due to these different interpretations about this fossil, we prefer to exclude KNM-ER 1805 from this study.

2. Earliest *Homo erectus* (or *Homo ergaster*). We consider as Earliest *H. erectus* (or *H. ergaster*) those hominins that are in a temporal range of approximately 1.8 to 1.3 Ma (Table 3) —classified as Earliest *H. erectus* by Antón 2003. Of the specimens studied by us, Antón includes in the group Earliest *H. erectus* the African specimens KNM-ER 3733 and KNM-WT 15000, the remains of Dmanisi and Sangiran 4 (we added the Asian fossils Gongwangling and Sangiran 17, classified by Antón as Early *H. erectus* for presenting more recent chronologies than the Earliest *H. erectus,* however, the last datings place the remains of Gongwangling at 1.63 Ma —Zhu et al. 2015— and Sangiran 17 between 1.30 and 1.25 Ma —Larick et al. 2001, 2004; Antón et al. 2007). Thus, Antón joins in the same group the specimens from East Africa, those of Dmanisi and Sangiran 4. Likewise, due to the similar morphology, Kaifu et al. (2010) and Lordkipanidze et al. (2013), attributed fossils from East Africa, the Dmanisi and Sangiran sample to the same group.

Table 3. Fossil specimens classified here as Earliest *Homo erectus* (or *Homo ergaster*)

Specimen	Age (Ma)	Author
Africa		
KNM-ER 3733	1.78	Wood 1991
KNM-ER 3883	1.50-1.65	Wood 1991
KNM-WT 15000	1.50	Walker and Leakey 1993
Middle East (Dmanisi)		
D2282	~1.77	Gabunia et al. 2000 Rightmire et al. 2006
D2700	~1.77	Gabunia et al. 2000 Rightmire et al. 2006
D3444	~1.77	Gabunia et al. 2000 Rightmire et al. 2006
D4500	~1.77	Gabunia et al. 2000 Rightmire et al. 2006
Asia		
Gongwangling	1.63	Zhu et al. 2015
Sangiran 4	>1.5	Swisher et al. 1994 Antón 2003 Antón and Swisher 2004 Larick et al. 2001, 2004 Antón et al. 2007
Sangiran 17	1.25-1.30	Larick et al. 2001, 2004 Antón et al. 2007

The difficulty of classifying taxonomically these hominins is clearly observed in the disparity of interpretations between different authors. Thus, Wang and Tobias (2000a) used the term *H. ergaster* for hominins with Facial Pattern I, and Late *H. erectus* (Classic *H. erectus* in this paper) for hominins with Facial Pattern II, making a clear differentiation of the facial models between both groups. On the other hand, Williams et al. (2012) call the remains of East Africa as *H. erectus* (or *H. ergaster*). Recently, Tattersall (2015) demonstrates the need to separate *H. ergaster* from *H. erectus* and points out the great diversity of classifications for Dmanisi remains: *H. erectus* (Gabunia and Vekua 1995; Henke 1995; Bräuer and Schultz 1996; Vekua et al. 2002); *H. ergaster* (Gabunia et al. 2000); *H. georgicus* (Gabunia et al. 2002); *H. erectus georgicus* (Rightmire et al. 2006); and *H. erectus ergaster georgicus* (Lordkipanidze et al. 2013). We have opted for a denomination that combines the one used by Antón (2003) and the one used by Williams et al (2012), and we classify these remains as Earliest *H. erectus* (or *H. ergaster*).

This group presents a facial morphology that distinguishes it from both early *Homo* and the Classic *H. erectus* and *H. sapiens*. Such morphology is characterized by: *a)* absence of canine fossa and presence of *sulcus maxillaris; b)* zygomaticoalveolar crest oblique or straight; *c)* absence of *incisura malaris*; *d)* nasal bones little projected; *e)* weak maxillary inflection; *f)* forward zygomatic root with respect to the lateral nasal margin; *g)* a low origin of the zygomatic; and *h)* rectilinear superior border of the temporal squama.

3. Classic *Homo erectus*. In this study, Classic *H. erectus* included specimens dated between ~1 Ma and ~0.6 Ma (hominins classified as Middle *H. erectus* by Antón, 2003 [Zhoukoudian and Nanjing], we add the Yuxian skulls). In this group, we also included the African specimens KNM-OL 45500, OH 12 and BOU-VP-2/66, although they are not part of this study, since KNM-OL 45500 is a frontal and a temporal fragment, OH 12 is very fragmented and BOU-VP-2/66 is a calvarium (Table 4).

Anatomical features of the midface

The term midfacial is applied to the portion of the anterior skull that is visible in *norma frontalis* and that is vertically delimited by the distance ranging from the alveolar plane of the maxilla to the nasion, and transversally from zygion to zygion (Pope 1991). The topography of this zone is variable in the different hominin groups, but in *H. sapiens* it is highly flexed. The *H. sapiens* flexed face is determined by the orientation of the infraorbital coronal bone plate, with the lower surface that slopes inferiorly and slightly posteriorly (canine fossa), and the more sagittal direction of the lateral nasal wall. Along the joint of these two maxillary surfaces a flexion zone is formed. Likewise, the zygomaticoalveolar crest is generally curved and often presents a malar notch or *incisura malaris* (Rak 1983, 1986; Arsuaga et al. 1999).

For this study, we compare the characteristics described as derived in *H. antecessor*, which are six midfacial features, plus the facial bone remodeling pattern —related to midfacial flexion—, and the form of the superior border of the temporal squama. Moreover, we compare them with those of the most ancestral and penecontemporaneous hominins (early *Homo*, Earliest *H. erectus* [or *H. ergaster*] and Classic *H. erectus*).

Coronal orientation of the infraorbital surface.

Maxillary inflection. This inflection is determined by the eversion of the nasal lateral wall and the slope downwards and

Table 4. Fossil specimens classified here as Classic *Homo erectus*

Specimen	Age (Ma)	Author
Africa		
BOU-VP-2/66	~1	Asfaw et al. 2002
KNM-OL 45500	0.9-0.97	Potts et al. 2004
OH 12	0.78	Tamrat et al. 1995 Antón 2004
Asia		
Yunxian	0.8-~0.94	Yan 1993 Feng 2008 Feng et al. 2011 De Lumley and Li 2008
Zhoukoudian (lower strata of Locality 1)	~0.8	Shen and Jin 1991 Shen 2001 Shen et al. 2009
Tangshan (Nanjing)	~0.62	Zhao et al. 2001

slightly backward of the infraorbital plate (Bermúdez de Castro et al. 1997; Arsuaga et al. 1999). Arsuaga et al. (1999) also add to this morphology the projection of the nasal bones, which advances the upper border of the nasal rim.

Canine fossa. The canine fossa has been defined as an infraorbital depression that encompasses most of the zygomatic process of the maxilla (Mellinger 1940). Some authors add to this definition that this infraorbital depression produces a horizontal incurvation as well as an incurvation of the zygomaticoalveolar crest (Arsuaga et al. 1999; Maddux and Franciscus 2009). This description coincides with what Maureille and Houët (1997) call infraorbital depression. However, Arsuaga et al. (1996, 1999) suggest the inverse by describing the maxillary fragment AT-404 from Sima de los Huesos (Atapuerca) (Figure 4 in Arsuaga et al. 1996, and Figure 7 in Arsuaga et al. 1999), as a possible *Homo heidelbergensis*, which presents a canine fossa and straight-oblique zygomaticoalveolar crest. Likewise, the same morphology of AT-404 is observed in the skull of the probable *H. heidelbergensis* of Steinheim and in some modern specimens (Fig. 3).

Zygomaticoalveolar crest. This crest forms the lower border of the zygomatic process of the maxilla and arises from the lateral wall of the maxilla. The zygomaticoalveolar crest can be best seen in frontal view, and can be determined by the line from alveolar plane to the zygomaxillare (Pope 1991; Koesbardiati 2000). In this study we apply the categories defined by Etler (1994): oblique (straight and diagonally oriented), arched, and horizontal. In frontal view, the zygomaticoalveolar crest is subject to the development of the *incisura malaris* and structures related to the malar tubercle (Rak 1983). The *incisura malaris* may be present or not (Fig. 4).

Lower nasal margin. In the formation of the lower nasal margin three crests are involved: 1) spinal —originates from the anterior nasal spine; a spinal crest can

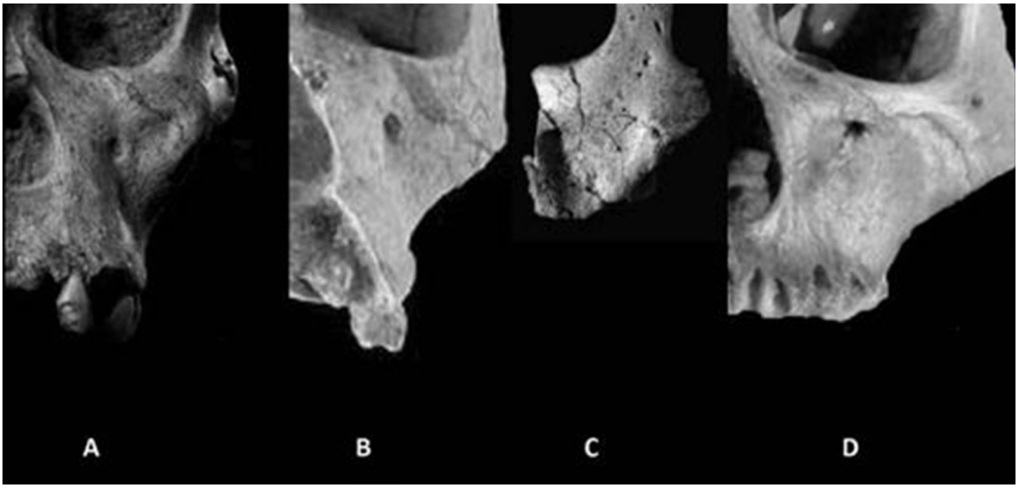

Fig. 3. Examples of canine fossa with straight-oblique zygomatoalveolar crest
Footnote: A) *Australopithecus sediba;* B) Probable *Homo heidelbergensis,* Steinheim (flipped image); C) Probable *H. heidelbergensis,* AT-404, Atapuerca (obtained from Arsuaga et al. 1999); D) Modern human (obtained from Stan et al. 2013).

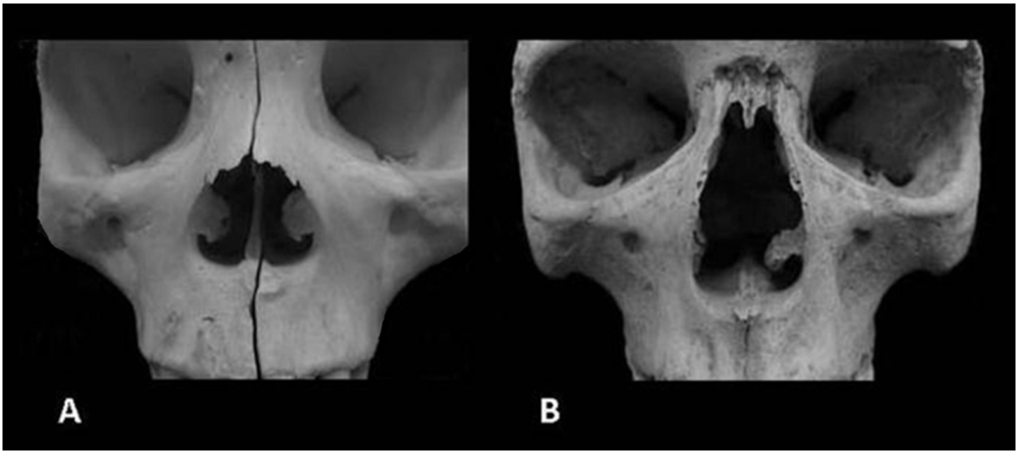

Fig. 4. Modern human faces with curved zygomaticoalveolar crest
Footnote: A) Absence of incisura malaris. B) With incisura malaris. Collection of the Laboratory of Paleopathology and Paleoanthropology, National Museum of Archeology of Catalonia in Barcelona. Photos made by FRT with the authorization of Dr. Domènec Campillo.

be located posteriorly, along the posterior pole of the alveolar process, or anteriorly, along the nasoalveolar clivus; 2) lateral —originates in the lateral margin of the piriform aperture; and 3) turbinal —originates near the anterior end of the inferior turbinate (Gower 1923). This margin can be formed by the presence of a single crest or by the combination of two or three, resulting in up to 6 categories (Gower 1923; Lahr 1994; Franciscus 2003) (absence of lower nasal margin is considered as the seventh category).

The above mentioned anterior nasal spine is the anterior extension of the incisive crest that forms a spinal process that projects anterior to the alveolar process. Hominoids and many fossil hominins do not present this anterior extension, therefore, they do not have a true anterior nasal spine, although they usually present a small protuberance or tuber in the nasoalveolar clivus that indicates the most anterior union of the nasal septum.

Zygomaxillary tubercle. This tubercle occupies the lower part of the anterior face of the zygomatic bone, which marks the anterior origin of the masseter muscle (Rightmire 1998b). It must be distinguished from the malar tuberosity, which is a relatively prominent elevation on the malar surface parallel to the inferior border of the bone, and situated between the orbital and free margins of the malar (Koesbardiati 2000).

Facial bone remodeling pattern. Growth remodeling is an integral component of the craniofacial growth process (McCollum 2008). Growth remodeling refers to various combinations of active bone deposition and resorption on the inner and outer surfaces of a single bony lamina (McCollum 2008). The presence of areas of bone resorption in the maxilla and the nasoalveolar clivus during ontogeny is associated with the orthognathic face, whereas the presence of areas of bone deposition in the maxilla and the nasoalveolar clivus contributes to the formation of the prognathic face (Enlow and Wang 1965; Enlow 1966; Bromage 1989; McCollum 2008).

Superior border of the temporal squama. The superior border of the temporal squama may present two morphologies:

flat or rectilinear, which is associated with a low cranial capacity, and convex or arched, which is associated with increased cranial capacity.

Results

Early *Homo*

In early *Homo* the facial morphology exhibits two possible morphotypes, the one present in 1470 group, and the one present in the 1813 group, on the other hand.

However, prior to these two groups, there is the Hadar maxilla A.L. 666-1, dated ~2.4 Ma and classified as *Homo* aff. *H. habilis* (Kimbel et al. 1997). The configuration of this maxilla could indicate the morphological pattern present in the first *Homo*. Kimbel et al. (1997) describe this fossil as having a nasoalveolar clivus which is not very prognathic; presence of corrugations in the alveoli of the central incisors; slight eversion of the lateral nasal margins; lateral nasal crest that extends and curves medially on the clivus; spinal tubercle (nasal spine not observable in lateral view); spinal crest marking the lower nasal margin; and superficial depression that forms a rudimentary canine fossa in the form of a “tear-drop”.

1470 group

The first morphology, characterized by KNM-ER 1470 and KNM-ER 62000 displays a coronal, flat and anteroinferiorly oriented infraorbital plane, with a small distance between the anterior maxillary surface and the root of the zygomatic process (compressed coronal plane), without canine fossa and with zygomaticoalveolar crest with low and forward origin (on P^3/P^4 in KNM-ER 62000 and on P^4 in KNM-ER 1470 —Leakey et al. 2012), and with straight and diagonally oriented zygomaticoalveolar crest; very little nasal lateral eversion (little sagittal orientation of the lateral nasal wall); orthognathic subnasal plane; infraorbital foramen close to the orbital margin; very broad, flattened nasoalveolar clivus, wich curves backward around the P^3 roots (well defined P^3 jugum), the canine alveoli are fully part of the anterior row; very broad and deep palate; relatively narrow upper face; and forward extension of the maxillary sinus to the coronal plane of the inferior nasal margin. In KNM-ER 1470 the inferior nasal margin is formed by the lateral extension of the spinal crest (nasal margin configuration type 2 —Franciscus 2003). Finally, in KNM-ER 1470, the superior border of the temporal squama is rectilinear.

1813 group

This group includes KNM-ER 1813, KNM-ER 42703, OH 24, OH 65 and OH 62 and presents a different facial model from the previous one: the infraorbital plane is oriented coronally and is posteroinferiorly inclined, and presents a more extensive lateral maxillary surface (not compressed) than in the previous group, giving rise to an extensive and shallow canine fossa (Rak 1983; Kimbel et al. 1997; Schwartz and Tattersall 2003); the zygomatic root is positioned posteriorly to the coronal plane (on P^4/M^1 in all specimens of this group — Leakey et al. 2012), with a higher origin; the zygomaticoalveolar crest is arched (KNM-ER 1813, KNM-ER 42703, OH 24) or straight and diagonally oriented (OH 62, but with a very sallow canine fossa —Schwartz and Tattersall, 2003); also, it does not exhibit an *incisura malaris* nor a zygomaxillary tubercle (Pope

1991); the forward extension of the maxillary sinus to the coronal plane of the inferior nasal margin is not evident in the 1813 group; but there is the presence of maxillary inflection and lateral nasal eversion (marked in KNM-ER 1813 and somewhat weaker in OH 24); the subnasal region is narrow and prognathic; the nasal inferior margin is weakly developed: in KNM-ER 1813 and OH 24 is formed by the lateral expansion of a small blunt spinal crest that does not come together with the lateral crest (category 2 of Franciscus 2003), while the lateral crest descends by the naseoalveolar clivus, whereas in OH 62 the spinal crest extends laterally until it merges with the turbinal crest, both separated from the lateral crest (category 3 of Franciscus 2003).

In most early *Homo,* there is only a small midline tubercle on the inferior nasal margin instead of an anterior nasal spine. The exceptions are OH 24 (Rightmire 1993; Franciscus and Trinkaus 1988; McCollum et al. 1993) and OH 62 (Johanson et al. 1987), both exhibit a well-defined anterior nasal spine. KNM-ER 1813 presents a small elevation on each side of the midline suggesting that *in vivo* there was an anterior nasal spine (Schwartz and Tattersall, 2003). The nasal spine in OH 24 and OH 62 is not observable in lateral aspect.

In OH 13 and SK 27 the facial bone growth remodeling pattern shows strong bone deposition on the anterior face, similar to that found in the australopiths, and possibly related to nasoalveolar prognathism (Bromage 1989).

The morphology of the superior border of the temporal squama is variable: rectilinear in OH 24 or curved (convex) in KNM-ER 1813.

Earliest *Homo erectus* (or *Homo ergaster*)

In the Earliest *H. erectus* (or *H. ergaster*), two midfacial morphologies are found related to life stage (Wang and Tobias 2000a). The morphology found in immature individuals (KNM-WT 15000 and D2700) is characterized by: the orientation of the infraorbital region is positioned in the coronal plane, without being anteroinferiorly or posteroinferiorly inclined (uniplanar); everted nasal bones and sagittal oriented maxillae lateral to the pyriform aperture; and weak maxillary inflection. The zygomatic process of the maxilla is flat, and there is a presence of a *sulcus maxillaris* (partial obliteration of the canine fossa, which becomes a sulcus that descends from the infraorbital foramen). The zygomaticoalveolar crest is arched in D2700 and oblique in KNM-WT 15000, without an *incisura malaris* and with the absence of a maxillary tubercle. The lower nasal margin in KNM-WT 15000 (Rightmire 1998b) is formed by the spinal crest, which is directed laterally towards the lateral crest, but does not merge, since the spinal crest is only a few millimeters posterior to the lateral nasal margin (category 3 of Franciscus 2003), while in D2700 there is no spinal crest. And finally, the presence of nasal spine, although it is not visible in norma lateralis.

The facial morphology found in adult specimens is characterized by marked maxillary flexion (the maxillae lateral to the pyriform aperture face forward), of the following are also present: a *sulcus maxillaris* is evident; the zygomaticoalveolar crest is arched or straight horizontally; nasal bones project anteriorly (nasal prominence); a spinal crest, to a greater or lesser degree of development, form the lower nasal margin (except in Sangiran 17). KNM-ER 3733 and Sangiran 17 exhibit a zygomaxillary tubercle (Pope 1991; Leakey and Walker 1985; Rightmire 1998b; Schwartz and Tattersall 2003). The existence of a prominent nasal spine observable in lateral view is visible in Sangiran 4 (Sawyer and Tattersall 1995; Tattersall and Sawyer 1996; Franciscus and Trinkaus 1988; Rightmire, 1998b; McCollum 2000; Schwartz and Tattersall 2003) and in Gongwangling (Ju-kang 1966; Rightmire 1998b); while the origin of the zygomatic in all Earliest *H. erectus* (or *H. ergaster*) is just lateral to the lateral margin of the nasal aperture. Incisive corrugations are also observed in D2282 (Rightmire et al. 2006), D4500 (Rightmire et al. 2017) and Gongwangling (Rightmire 1998b).

The facial bone growth remodeling pattern has only been studied in the adolescent individual KNM-WT 15000, which shows a primitive pattern, i.e. a flat clivus without corrugations or resorption around the anterior tooth roots (Lacruz et al. 2013, 2015).

In all specimens, the superior border of the temporal squama is rectilinear, except in D3444.

Classic *Homo erectus*

The midfacial morphology in this group, especially in the Chinese Classic *H. erectus* (Yuxian [Li and Etler 1992], Zhoukoudian [Wang and Tobias 2000a; Etler 2004], and Tangshan —Nanjing [Wang and Tobias 2000a,b, 2001; Liu et al. 2005]) is characterized by: infraorbital plate oriented coronally and posteroinferiorly inclined; the *sulcus maxillaris* has become a true canine fossa; the maxillary flexion is fairly pronounced; the zygomaticoalveolar crest is very arched, with a developed *incisura malaris*; there is a significant posterior shift in the origin of the zygomatic relative to the lateral nasal margin; presence of zygomaxillary tubercle; and everted nasal bones (projected nose).

In the skulls of Yuxian the midfacial morphology is described by having a coronally oriented infraorbital plate, a high origin of the zygomatic root, the presence of a canine fossa; and a straight zygomaticoalveolar crest and with a marked *incisura malaris* (Li and Etler 1992). Regarding the midface, in specimens from Zhoukoudian, Wang and Tobias (2000a. p.25) stated: *"Medially, the portion of the maxilla lateral to the pyriform aperture faces laterally, while the infraorbital part faces anteriorly; thus they jointly constitute a concave flexion"*. Effectively, in the new reconstruction of Classic *H. erectus* from Zhoukoudian (Sawyer and Tattersall 1995; Tattersall and Sawyer 1996; Wang 1998), the *incisura malaris* is less restricted that in Weidenreich's (1937a) reconstruction, resulting in a wider zygomaticoalveolar crest. This expansion produces a much more pronounced infraorbital hollow. Unfortunately, it is impossible to ascertain whether this feature is a true canine fossa or a *sulcus maxillaris* (seen in the Weidenreich reconstruction), because the maxilla used in this reconstruction is eroded. Other maxillae from ZKD lower cave are also fragmentary, which makes the actual morphology of the infraorbital region of the maxilla difficult to observe (Tattersall personal communication, 2016). According to Wang (1998) and Wang and Sun (2000), the Weidenreich reconstruction of the female Classic *H. erectus* facial skeleton involves fragments of cranial skeletons from different individuals (both male and female), a female cranial cap (skull XI or LII) and a male maxilla (No V, mentioned as No II); so, the zygomatic bone had to be turned to some degree to make contact with the maxillary and the frontal bones. The zygoma faces laterally to meet the frontal and maxillary bones, leading to lower and larger orbit. Nevertheless, as seen in the reconstructed male skull (Sawyer and Tattersall 1995; Tattersall and Sawyer 1996), the general topography of the midfacial skeleton as reconstructed by Weidenreich (1937a) for the Zhoukoudian population is still useful. In the Tangshan face, the anterior and posterior surfaces of the zygomatic process of the maxilla meet each other in a blunt edge. The edge extends superiorly and laterally, and then turns inferiorly, forming an *incisura malaris* (Liu et al. 2005). Tangshan displays, in the lower area of the zygomatic root, a very well-developed canine fossa associated with a marked midfacial flexion (Wang and Tobias 2000a,b; 2001).

Yunxian 2 and Zhoukoudian Locality 1 Classic *Homo erectus* (crania III, V, XI, and XII) displays a temporal squama with a convex superior border (Rightmire 1998a; Etler 2004; Wu and Poirier 1995). Conversely, the examination of the Tangshan parietal bone shows that the temporal squama is relatively high and curved (convex) (Liu et al. 2005).

Discussion

The knowledge of patterns of facial morphology and topography are important for understanding the variability and evolutionary relationships of early hominins (Tobias 1967, 1991; Rak 1983, 1986; Pope 1991; Rightmire 1998b, 1993; Wang and Tobias 2000a). In the differential diagnosis of *H. antecessor,* some previous scientists have noted that this taxon is derived from the most primitive forms of *Homo* (Early *Homo* —1470 group and 1813 group— Earliest *H. erectus* [or *H. ergaster*] and Classic *H. erectus*), because it presents a flexed midface (i.e., coronal orientation of the infraorbital surface; projecting nose; maxillary inflection — with lateral wall of the nasal opening everted with respect to the adjacent infraorbital surface—; canine fossa; and horizontally arched zygomaticoalveolar crest with high zygomatic root) (Bermúdez de Castro et al. 1997, 2017; Arsuaga et al. 1999; Rosas 2000).

In extant African hominoids (*Gorilla* and *Pan*), East African australopiths, 1813 group and in extant *H. sapiens,* the infraorbital region is oriented coronally and with a posteroinferior slope, which extends towards the zygomaticoalveolar crest; above the infraorbital foramen and immediately below the lower orbital border is the transverse buttress, which forms a ridge that extends medially from the body of the zygomatic bone towards the upper part of the nasal aperture. This transverse buttress is most pronounced in *Gorilla,* and gradually decreases to become rudimentary in *H. sapiens.* Thus, the transverse buttress along with the nasal aperture (more or less pronounced — very elongated in *Gorilla* and modest in *H. sapiens*) and the posteroinferior slope of the infraorbital region form the canine fossa. In the species in which the infraorbital plane slope is anteriorly, the transverse buttress is obliterated (i.e., *A. africanus, Paranthropus,* and 1470 group) and the canine fossa has been modified (maxillary furrow in *A. africanus,* and maxillary fossula in *Paranthropus robustus*) or disappeared (*Paranthropus boisei* and 1470 group). This could be due to the anteroinferior compression of the coronal plane caused by the strong anterior expansion of the maxillary sinus. In this respect, however, Arsuaga et al. (1999)

concluded that the presence of canine fossa and flexed face are derived characters in *H. sapiens* that are produced for the first time in *H. antecessor,* and they argued, citing Kimbel et al. (1997), that in all early *Homo* and Earliest *H. erectus* (or *H. ergaster*) (e.g., KNM-ER 3733 and KNM-WT 15000) a compression of the coronal plane is observed resulting in the typical smooth face in these hominins. But, the real interpretation done by Kimbel et al. (1997) in this respect is different, these authors point out that in 1470 group there is a strong anterior expansion of the maxillary sinus that causes anteroposterior compression of the coronal plane and, therefore, obliteration of the canine fossa, while the anterior surface of the zygomatic process of the maxilla is practically in the same coronal plane as the nasal opening, resulting in the smooth face; while in 1813 group, the maxillary sinus reaches no further anteriorly than the incisive fossa, and in lateral view, the zygomatic process of the maxilla and the nasal opening are separated by a considerable topographical interval, and posteriorly positioned zygomatic process roots, thus forming the canine fossa, and concluding that the latter is the generalized morphology in hominins (in this description KNM-ER 3733 is also included).

On the other hand, the zygomaticoalveolar crest morphology is also complex. Thus, the general curvature of the zygomaticoalveolar crest and the presence or absence of the *incisura malaris* are correlated characteristics, and the expression of these characteristics depend on the height of the masseter origin (Freidline et al. 2013). Species with a low origin of the masseter and a coronal orientation of the infraorbital plane have an arched zygomaticoalveolar crest, and may or may not have an *incisura malaris* (in 1813 group there is no *incisura malaris,* while in Earliest *H. erectus* [or *H. ergaster*] this trait is variable, and in Classic *H. erectus* and *H. sapiens* it is present). On the other hand, species with a high origin of the masseter, and a coronally oriented infraorbital plane, the zygomaticoalveolar crest is straight and obliquely oriented (australopiths and paranthropiths) (Freidline et al. 2013).

The modern human-like facial features of *H. antecessor* are ancestral retentions, relative to later humans, and can be considered to be part of a generalized pattern of facial architecture (Wang and Tobias 2000a; Freidline et al. 2013; Ribot et al. 2017). This conclusion fully coincides with what Rak (1986) calls a generalized face, present in many primates including modern humans and fossil species of the genus *Homo*, which is characterized by: an infraobital surface oriented in the coronal plane and sloping posterorinferiorly, and at the junction with the nasal aperture this inclination forms the canine fossa; the zygomaticoalveolar crest is curved and joins the body of the maxilla at approximately the midpoint of the dental arch or posterior to it; and the nasoalveolar clivus is convex in cross-section.

The face present in *H. sapiens* is in many aspects plesiomorphic (in the most basic sense), and these characteristics are even present very weakly in the East African australopiths and early *Homo*. When each characteristic of the middle facial third is taken independently, or if all of them are taken together, the pattern in *A. afarensis* is a prototypical morphology that could evolve by the relatively simple modifications into the more derived face of *H. sapiens*. The complete transformation of the plesiomorphic face to the current one is a gradual process that culminates with the formation of a more flexed and orthognathic face. Thus, the anterior part of this midfacial region is greatly affected by the bite and occlusion forces of the anterior dentition and premolars, while the zygomatic and the zygomaticoalveolar crest are affected by molar loads (Wang et al. 2010; Rodrigues Freire et al. 2014). The strongest stress of these forces (extensive stress and compressive stress) occurs in the canine fossa and in the frontal process of the maxilla, two of the structures most related to facial flexion. Postnatal ontogeny could be influenced by epigenetic factors, such as biomechanics, which can elucidate functional differences between different facial forms. In this sense, it should be noted that the orthognathic face is better adapted to absorb the masticatory or paramasticatory stress than the prognathic face (Wang et al. 2010).

Compared with East African australopiths, the face of the 1813 group is somehow more flexed, with a more everted wall adjacent to the lateral nasal margin, and to an infraorbital region more sloped posteroinferiorly, which results in a canine fossa less restricted (more expanded) and less deep. This trend of midface flexion increase continues in Earliest *H. erectus* (or *H. ergaster*) (where the canine fossa has been partially obliterated and has become the *sulcus maxillaris*), and culminates in Classic *H. erectus,* where the combination of a greater posteroinferior slope of the infraorbital coronal plane, an arched zygomaticoalveolar crest with *incisura malaris* and a greater eversion of the wall adjacent to the lateral nasal margin are linked to the presence of a "true" canine fossa (Fig. 5).

This midfacial morphology present in Classic *H. erectus* is similar to the one present in *H. sapiens,* and it is identical to that present in *H. antecessor* (Table 5).

In fact, the description of the midfacial morphology of Yunxian Classic *H. erectus* (Li and Etler 1992) is to the same as the description of ATD6-69 (Bermúdez de Castro et al. 1997): *"[…] the face is flattened and orthognathic with moderate alveolar prognathism; the maxilla has a distinct canine fossa; the lateral part of the maxilla is oriented coronally and highly angled to the zygomatic; there is a high origin of the zygomatic root; a horizontal zygomaxillary border and a pronounced malar incisures […]"* (Li and Etler 1992, p. 404). The same morphology is also found in the Tangshan face (Wang and Tobias 2000a,b, 2001; Liu et al. 2005). Also, in table 5 it can be observed that the results for the midfacial morphology in *H. erectus sensu lato* are very variable, but if we divide this group in Earliest *H. erectus* (or *H. ergaster*) and Classic *H. erectus,* it is appreciated that the morphology of the first group is more primitive, while that of the second group is more derived, which justifies the division of *H. erectus sensu lato* in these two groups.

Therefore, the presence of a flexed midface is a plesiomorphic characteristic for all the extant African hominoids (*Gorilla* and *Pan*), the East African australopiths and early *Homo* (except for 1470 group) and in *H. sapiens.* So we agree with Wang and Tobias (2000a) who stated that the flexed face is plesiomorphic and, therefore does not constitute an effective taxonomic basis for the proposed new species, *H. antecessor.*

Regarding the nasal entrance, ATD6-69 presents the category 3 of Gower (Franciscus 2003), the model that occurs primarily in modern humans (the 35.93% in a series of 109 modern skulls [Franciscus 2003]). However, in modern humans all models of combination of crests for forming the lower nasal margin

Table 5. Craniofacial features of examined hominins (see discussion in text) compared with *Homo antecessor*

Craniofacial feature	Examined hominins					
	1470 group	1813 group	*Homo erectus sensu lato*	Earliest *Homo erectus* (or *Homo ergaster*)	Classic *Homo erectus*	*Homo antecessor*
Orientation of the infraorbital surface	Coronal with anteroinferior slope	Coronal with posteroinferior slope	Coronal with posteroinferior slope	Coronal with posteroinferior slope	Coronal with posteroinferior slope	Coronal with posteroinferior slope
Canine fossa	Absent	Present	Variable	*Sulcus maxillaris*	Present	Present
Maxillary inflection	Very weak	Weak	Variable	Weak/variable[a]	Marked	Marked
Zygomaticoalveolar crest	Oblique	Arched/horizontal	Variable	Variable	Arched/horizontal	Arched/horizontal
Incisura malaris	Absent	Absent	Variable	Variable[b]	Present	Present
Lower nasal margin configuration*	2	2 and 3	2 and 3/variable	2 and 3	–	3
Zygomaxillary tubercle	Absent	Absent	Variable	Variable[c]	Present	Present
Superior border of the temporal squama	Rectilinear	Rectilinear	Variable	Rectilinear	Curved	Curved

*The categories of inferior nasal margin used here are those described in Gower (1923) modified by Franciscus (2003).

[a] Marked in Gongwangling and Sangiran 17.

[b] Present in KNM-ER 3733 and Sangiran 17.

[c] Present in KNM-ER 3733 and Sangiran 17.

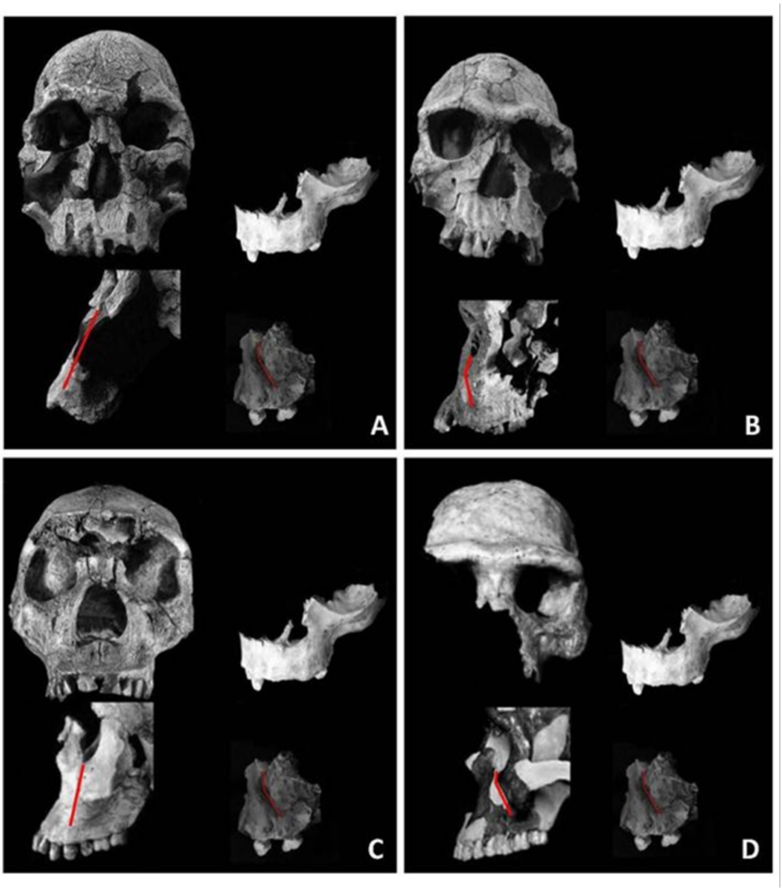

Fig. 5. Morphology of the midface in hominins compared with ATD6-69
Footnote: In all the images, the red line marks the inclination of the infraorbital plane.
A) Early *Homo,* 1470 group. Upper row (front view), left: KNM-ER 1470, right: ATD6-69. Observe in ER 1470 the absence of a canine fossa, the practical absence of maxillary flexion, and a rectilinear/oblique zygomaticoalveolar crest. Bottom row (side view), left: KNM-ER 1470, right: ATD6-69; the infraorbital plane in ER 1470 is oriented anteroinferiorly (uniplanar), which indicates a compressed coronal plane, with low and forward origin of the zygomaticoalveolar crest. B) Early *Homo,* 1813 group. Upper row (front view), left: KNM-ER 1813, right: ATD6-69. Observe in ER 1813 the presence of extended and shallow canine fossa, the low maxillary flexion, and an arched zygomaticoalveolar crest, without *incisura malaris*. Bottom row (side view), left: KNM-ER 1813 (flip image), right: ATD6-69; the infraorbital plane in ER 1813 is oriented posteroinferiorly, with a slightly forward origin of the zygomaticoalveolar crest. C) Earliest *Homo erectus* (or *Homo ergaster*). Top row (front view), left: KNM-WT 15000, right: ATD6-69. Observe in WT 15000 the absence of canine fossa and the presence of sulcus maxillaris, and a rectilinear/oblique zygomaticoalveolar crest. Bottom row (side view), left: KNM-WT 15000, right: ATD6-69; the infraorbital plane in WT 15000 is oriented anteroinferiorly (uniplanar), which indicates a compressed coronal plane, with a slightly backward origin of the zygomaticoalveolar crest. D) Classic *Homo erectus*. Upper row (front view), left: Tangshan skull (Nanjing), right: ATD6-69. Note in Tangshan the presence of a marked canine fossa, the marked maxillary flexion, and an arched zygomaticoalveolar crest with *incisura malaris*. Bottom row (side view), left: reconstruction of the Zhoukoudian skull (Sawyer and Tattersall, 1995; Tattersall and Sawyer, 1996), right: ATD6-69; the infraorbital plane in Zhoukoudian is oriented posteroinferiorly, with a very backward origin of the zigomatic alveolar crest. As can be seen, the morphology of Classic *H. erectus* is identical to that of ATD6-69. Pictures of ATD6-69 courtesy of Roberto Sáez.

are present. Furthermore, category 3 is ancestral for *Homo* as it is present in OH 62, KNM ER 3733 and KNM-WT 15000 (Franciscus 2003).

On the other hand, some researchers have shown that Earliest *H. erectus* (or *H. ergaster*) nasal morphology is practically identical to that of modern humans (Franciscus and Trinkaus 1988), based on the following characters: *a)* presence of anterior nasal spine prominence in some specimens (Sangiran 4 [Franciscus and Trinkaus 1988; Rightmire 1998b; McCollum 2000; Schwartz and Tattersall 2003]; Gongwangling cranium [Woo 1966; Rightmire 1998b]); *b)* smooth nasal cavity entrance with horizontal nasal sill; and *c)* posterior spine. Also in Sangiran 4 (the only specimen in which it can be observed) a vomeral insertion does indeed occur above the nasal sill.

Another important feature of the midfacial morphology of *H. antecessor* is the presence of a zygomaxillary tubercle. Arsuaga et al. (1999), Carbonell et al. (2005) and Bermúdez de Castro et al. (2017) noted that this is a derived feature, and that it is observed for the first time in the remains of Gran Dolina and Zhoukoudian. However, the presence of a zygomaxillary tubercle was noticed for the first time in KNM-ER 3733 —Pope 1991; Leakey and Walker 1985— (dated ~1.8 Ma [Wood, 1991]) and Sangiran 17 —Pope 1991; Rightmire 1998b— (dated 1.25-1.30 Ma [Larick et al. 2001, 2004; Antón et al. 2007]). Thus, the tubercle precedes the appearance of ATD6 and Zhoukoudian hominins. Therefore, the presence of zygomaxillary tubercle in *H. antecessor* is also a plesiomorphic, not a derived trait.

The last feature of the middle facial third described as derived in ATD6-69 is the presence of a bone remodeling pattern of a modern type (Lacruz et al. 2013; Bermúdez de Castro et al. 2017). The midfacial bone remodeling pattern observed in ATD6-69 is present in *H. sapiens*. In both ATD6-69 and *H. sapiens* it is associated with an orthognathic face, a fully flexed maxillary inflection (which anteriorly projects the nasal bones), a coronally oriented infraorbital region and canine fossa, and a curved zygomaticoalveolar crest with an *incisura malaris* (Lacruz et al. 2013).

The orthognathic face is associated with areas of bone resorption during ontogeny (Enlow and Wang 1965; Enlow 1966). In ATD6-69, these resorptive areas are located in the zones of the nasomaxillary clivus, anterolateral maxilla, and in the canine fossa (Fig. 2). Depositional areas in ATD6-69 are close to the canine prominence, in the lateral walls of the nasal aperture and in the anterior part of zygomatic (Lacruz et al. 2013) (Fig. 2). The ATD6-69 and *H. sapiens* facial bone remodeling pattern is very different from that seen in the australopiths (LH 2, LH 21, AL 333-105, Sts 2, Stw 59, Taung, Sts 24, Sts 57, MLD 2 and Sts 52), early *Homo* (OH 13, SK 27) and Earliest *H. erectus* (or *H. ergaster*) (KNM-WT 15000). In all of the latter specimens there is a large deposition area of the maxilla and the nasoalveolar clivus, contributing the development of the prognathic profile (Bromage 1989; Lacruz et al. 2015). However, the facial bone remodeling pattern in *A. sediba* (MH1), which present moderate prognathism, shows that the pattern present in this specimen is identical to that in *H. sapiens,* presenting vertical bands of bone resorption in the lower face (Lacruz et al. 2015). According to the authors, these vertical bands of resorption are reminiscent with the alternating stripes of high and low tension observed in the roots of the anterior teeth during biting, at least as simulated in a human cranial model subjected to finite elements analysis (Wang et al. 2010; Lacruz et al. 2015).

Moreover, variability of this feature should be taken into account. In the study by Kurihara et al. (1980), a sample of 27 modern human skulls aged between 2 and 14 years old was considered, 20 (74%) show a predominantly resorptive anterior lower face; in the remaining 7 specimens (26%), most of the anterior lower face was found to be depository. Also, in a sample of 33 children and subadult chimpanzees, McCollum (2008) found a complete depository pattern in the anterior lower face in only 6 specimens, while in 21 specimens the pattern was partially resorptive and fully resorptive in four. The same author, in a sample of 22 modern human skulls, shows that in 55% *"they were found to display large areas of surface deposition along the nasoalveolar clivus and anterior maxilla"* (McCollum 2008). These studies indicate that there is a close relationship between an orthognathic face and areas of bone resorption during ontogeny, located in the zones of the nasomaxillary clivus, maxillary anterolateral, and in the canine fossa. And, conversely, the bone deposition located in these same facial regions is not always present. Thus, there is variability in the models of resorption and deposition in the nasomaxillary clivus, anterolateral maxilla and canine fossa, which can be present in both orthognathic faces as in prognathic faces.

Although it has not been possible to establish an ontogenetic series for Classic *H. erectus,* based on final midfacial adult form, it is reasonable to argue that their ontogenetic process of the midface must be similar to that found in some modern humans (Wang 1998).

Therefore, the presence of a very similar facial bone remodeling pattern in *Paranthropus, A. sediba,* ATD6-69 and *H. sapiens* could indicate the emergence of this model in different moments in human evolution.

Regarding the morphology of the temporal bone, According to Arsuaga et al. (1999), the ancestral condition would be a low temporal squama with a straight superior border. According to these authors, this morphology is found in *H. habilis,* Earliest *H. erectus* (or *H. ergaster*) and Classic *H. erectus*; while in *H. antecesor,* the presence of a temporal squama with arched superior border represents the derived condition, which is also observed in the hominins of the European and African Middle Pleistocene, in those of the Asian Middle Pleistocene, in Neandertals, and in modern humans. In this regard, Carbonell et al. (2005) add that *H. antecessor* and Classic *H. erectus* must share a hypothetical common ancestor (possibly Earliest *H. erectus* [or *H. ergaster*]) that retained the primitive condition of a low and flat temporal squama, and note that these features are retained in Classic *H. erectus*. However, the skull of Classic *H. erectus* from Bouri (~1 Ma), already presents a high and arched temporal squama (Asfaw et al. 2002, supplementary information). Likewise, many Classic *H. erectus,* as Yunxian 2, Zhoukoudian Locality 1 (crania III, V, XI, and XII), and Tangshan (Wu and Poirier 1995; Rightmire 1998a; Liu et al. 2005; Etler 2004), also present the same morphology. Thus, a temporal squama with a convex superior border is already found in Classic *H. erectus* from Africa and China.

Therefore, regarding the midfacial and cranial morphology, ATD6 hominins and Classic *H. erectus* share the following characters: presence of canine fossa, arched zygomaticoalveolar crest with *incisura malaris* and a high zygomatic root, maxillary inflection, and nasal morphology practically identical to that of modern humans; as well as a convex superior border of the temporal squama. Thus, the facial topography of ATD6-69, considered to be derived (Bermúdez de Castro et al. 1997; 2017; Arsuaga et al. 1999) is actually a plesiomorphic trait, because it is already present in the penecontemporary Classic *H. erectus*. Moreover, in a study by Freidline et al. (2013) on the evaluation of the changes in the shape of the development of facial morphology in *H. antecessor,* these authors conclude that most of the facial characteristics similar to those of current humans, present in ATD6-69, are intercorrelated, and they can be considered ancestral retentions in relation to later humans. They also suggest that these features were present in varying degrees in more plesiomorphic forms, such as Classic *H. erectus* and *H. antecessor,* and have even been retained in recent modern humans.

Conclusions

We conclude that none of the midfacial characters that have been employed to define *H. antecessor* are unique to the Gran Dolina hominins. Any one of them has been found in Classic *H. erectus*. Therefore, it becomes untenable to separate both groups in two different taxa, *H. antecessor* and Classic *H. erectus,* and the Atapuerca hominins of ATD6 should be all classified as Classic *H. erectus* (Wang 1998; Wang and Tobias 2000a; Etler 2004; Rabadà 2005; Ribot et al. 2006, 2007, in press 2018; Ribot and García Bartual 2016).

Therefore, ATD6 hominins would demonstrate the presence of Classic *H. erectus* in the upper lower and middle Pleistocene of Europe (Wang and Tobias 2000a; Rabadà 2005; Ribot and García Bartual 2016; Ribot et al. in press 2018).

Moreover, the low and flexed face with slight to absent prognathism in modern humans could be more readily developed from a low and flexed face such as that seen in Classic *H. erectus*.

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Authors' contributions

FRT was the principal investigator, designed and performed the study, conceived and designed the manuscript; MGB arranged and analyzed the data, wrote part of the manuscript; QW wrote part of the manuscript, and was a proofreader. All authors read and approved the final manuscript.

Conflict of interest

The authors declare that there is no conflict of interest.

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