Human Palaeontology and Prehistory

A "source and sink" model for East Asia? Preliminary approach through the dental evidence

Un modèle de « source et écoulement sans fond » pour l'Est asiatique ? Approche préliminaire à partir des données dentaires

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ARTICLE INFO

ABSTRACT

This study aims to present a preliminary approach to the suitability of the "source and sink" model to explain the human settlement of East Asia. We present a general overview of the hominin dental evidence with a special emphasis in some key localities with human remains that have been recently described. Our analysis suggests that the morpho-dimensional variation of the Pleistocene populations from East Asia cannot be accommodated within one single lineage. This evidence seems supportive of an intense but also more discontinuous pattern of occupation. The severe climatic oscillations, the extent of the desert areas and the possibility of intermittent exchanges between continental and insular East Asia, depending on sea level changes, are key factors to identify possible sink and sources in the region. Future studies should focus in a large-scale characterization of the Asian hominins in order to identify morphologically coherent groups and to understand the evolutionary story behind their spatio-temporal distribution.

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RÉSUMÉ

L'objectif de cette étude préliminaire est de tester la possibilité de proposer le modèle « source et écoulement sans fond » pour expliquer le peuplement humain de l'Asie de l'Est. Nous présentons un panorama général de l'évolution dentaire des homininés et, de façon plus détaillée, quelques localités incontournables ayant livré des restes humains que nous avons décrits récemment. Notre analyse suggère que la variation morphométrique des populations pléistocènes de l'Est asiatique ne peut absolument pas s'inscrire au sein d'une seule lignée. Ce phénomène semble dû à une intensité, mais également à une discontinuité, de peuplement du territoire. Les oscillations climatiques rigoureuses, l'extension des zones

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désertiques et la possibilité d'échanges par intermittence entre l'Est asiatique continental et insulaire en fonction des changements du niveau marin sont des facteurs déterminants pour identifier de possibles sources et écoulements dans cette région. De futures études devront se focaliser sur la caractérisation à grande échelle des homininés asiatiques, dans le but d'identifier des groupes morphologiquement cohérents et de comprendre l'histoire évolutive à travers leur répartition spatio-temporelle.

Recent studies have emphasized the significant morpho-dimensional variation of the Pleistocene populations from East Asia. The detailed analysis of dental samples such as those from Xujiayao, Panxian Dadong, Hexian, Chaoxian, Zhoukoudian or Sangiran (e.g., Bailey and Liu, 2010; Kaifu, 2006; Liu et al., 2013; Xing, 2012; Xing et al., 2015; Zanolli, 2013) reveal that the variability of the East Asian hominin populations is larger than previously thought. Characterising the morphology and spatio-temporal distribution of the Asian hominins would be a critical contribution to the current debate about the pattern of hominin settlement in Asia. Currently, opinions in this topic range from the proposal of a continuous and flourishing occupation (e.g., Ciochon and Bettis, 2009; Keates, 2010; Zhu et al., 2004), based on supposedly benign climatic conditions (Ao et al., 2010; Pei et al., 2009), to the suggestion of a discontinuous and more intermittent settlement of Asia (Dennell, 2009, 2013a, 2013b; Louys and Turner, 2012).

Interestingly, the history of the discussion about the settlement of Asia goes in parallel with the latest research on the Middle Pleistocene of Europe and the origin of *H. neanderthalensis* (e.g., Arsuaga et al., 2014; Dennell et al., 2011; MacDonald et al., 2012; Martinón-Torres et al., 2012). In Europe, the impossibility of satisfactorily fitting the primitive-derived morphological gradients of the human populations along a chronological sequence was the triggering notion for suggesting a discontinuous settlement of the continent, envisaging fragmentation, isolation and recombination of populations, strongly conditioned by biogeographical factors (Dennell et al., 2010, 2011). To the light of this evidence, some of us proposed a population model for Middle Pleistocene Europe that is based on demographic "sources" and "sinks" and where repeated colonization, extinctions and recombination may help explain the morphological variability of the inhabitants of Europe at that time (Bermúdez de Castro and Martinón-Torres, 2013; Dennell et al., 2011; MacDonald et al., 2012).

This paper aims to present a preliminary approach to the suitability of the "source and sink" model to explain the human settlement of the Asian continent. At this stage, we do not intend to perform a thorough analysis of the Asian fossil record and the biogeographical factors that may have shaped the demography of East Asia, but to investigate whether there are reasonable grounds to explore this possibility in future studies. In this context, it would be necessary to:

- characterise the variability of the Asian hominin populations;
- assess whether the primitive-derived gradients can be explained along a chronological scale;
- identify possible sources and sinks in East Asia.

Our objective is to provide a preliminary approach to these three requirements through an overview of the hominin dental evidence from East Asia.

1. "Source and sink" model in Europe

The origin of the Neanderthal lineage has been largely explained by the gradual accumulation of Neanderthal distinctions throughout time, a process that has been coined as *accretion* (Hublin, 1998). Despite their ability to cope with a variety of environments, Neanderthal ancestors would have had problems to survive in extreme glacial conditions. Glacial-interglacial cycles would have led to a pattern of periodical abandonment of northern regions into southern refuges and subsequent recolonisation of higher latitudes when conditions ameliorated (e.g., Bocquet-Appel and Demars, 2000; Turq et al., 1996). This habitat-tracking dispersals, together with an important number of local extinctions (Hublin and Roebroeks, 2009) would have played a major role in shaping these populations, leading to repeated genetic bottlenecks, and subsequent reduction of the variability of the Neanderthal lineage (Hublin, 2009).

However, the recent analysis of the dental and craniofacial evidence from the Middle Pleistocene assemblages of Atapuerca-Sima de los Huesos (Arsuaga et al., 2014; Martinón-Torres et al., 2012) has emphasized the impossibility of aligning in a chronological sequence, the primitive and derived traits of Middle Pleistocene populations. To be specific, our studies revealed that the Atapuerca Sima de los Huesos samples, dated to approximately 420 ka (Arnold et al., 2014), were more Neanderthal not only than other contemporaneous populations like those from Arago and Mauer, but also "more Neanderthal than some Neanderthal themselves" (Gómez-Robles, 2010; Gómez-Robles et al., 2007, 2011; Martinón-Torres et al., 2012; Prado-Simón et al., 2012). Thus, the Atapuerca evidence was not supportive of the statement that earlier specimens would show "incipient" Neanderthal morphology, while the later ones would exhibit full-blown "classic" Neanderthal anatomy (Dean et al., 1998; Harvati et al., 2010; Hublin, 1998).

Based on these findings, we proposed a "source and sink" model, where the variability of the fossil hominin samples in Early and Middle Pleistocene Europe was explained as a result of repeated population dispersals, fragmentation, and re-combination of surviving populations inside Europe (Dennell et al., 2011). The driving force behind this demographic patterning would be the climatic fluctuations, which would also define the windows of opportunity for immigration episodes from Southwest Asia (Bermúdez de Castro and Martinón-Torres, 2013; Martinón-Torres et al., 2011). "Source" populations would have lived in those parts of southern Europe where hominins could have survived glacial periods. "Sink" populations would have been in those areas in higher latitudes that were only suitable for occupation in warm interglacials and often, they would have depended upon "source" populations for recruitment to maintain a stable occupation. When environmental conditions deteriorated, many "sink" populations would have become extinct and/or retreated to the southern refugia where they would have mixed with the resident groups. This recombination would explain the high morphological variability maintained by European populations throughout the Middle Pleistocene despite the demographic decline.

While the European fossil record is relatively well-characterized, only recently new specialized studies on old and new dental findings have started to contribute to a more precise picture of human evolution in Asia (e.g., Bae et al., 2014; Bailey and Liu, 2010; Kaifu et al., 2005a, 2005b; Liu et al., 2001, 2013; Xiao et al., 2014; Xing et al., 2009, 2014, 2015; Zanolli, 2013; Zanolli et al., 2012). As we will outline in this paper, these studies expand the morphological variability known for the Pleistocene human populations of East Asia and outline complex evolutionary scenarios, with persistence and survival of primitive lineages.

The challenge to properly investigate the applicability of the "source and sink" model in Asia requires the identification of morphologically coherent groups where fossil samples/specimens could be interpreted as "representative of prehistoric populations or lineages acting as portions of dynamic evolutionary units" (Trinkaus, 1990). These units would approach the "paleodemes" concept of Howell (Howell, 1999) and would constitute the basis for the assessment of phylogenetic affinities, for recognition of evolutionary trends and for deciphering the evolutionary story (dispersals, isolation, extinctions and interbreeding) behind their spatio-temporal distribution.

Here, we present a general overview of the hominin dental evidence from several Pleistocene localities of Asia. We will focus in the primitive versus derived status of three original fossil samples that have been recently published: Hexian, in the Anhui Province (Eastern China), Panxian Dadong, in the Guizhou Province (Southern China), and Xujiayao (Northern China) (Fig. 1). The morphological variability of these fossil teeth will be discussed in the context of the variability described for some classic *H. erectus* samples such as those recovered from Zhoukoudian and Java (Table 1).

Table 1
List and chronology of the main sites discussed in the text.
Tableau 1
Liste et chronologie des principaux sites évoqués dans le texte.

Site	Chronology	
Hexian	412 ± 25 ka (Huang et al., 1981; Grün et al., 1998)	
Panxian Dadong	190-300 ka (Zhang et al., 2015)	
Xujiayao	160-220 ka (Tu et al., 2015)	
Chaoxian	> 310 ka (Shen et al., 1994)	
Zhoukoudian	770-800 ka (Shen et al., 2009)	
Sangiran	Grenzbank/Sangiran (Pucangan) Formation	1.5 M.a. (Larick et al., 2001) - 900 ka. (Hyodo et al., 1993)
	Kabuh Formation	800 ka. - 500 ka. (Sémah, 2001)

2. Hexian

Hexian site is located in the Anhui Province (31°45′N, 118°20′E) and the surveys and excavations performed during the 1970s and 1980s have provided several human remains including a nearly complete skullcap, a left partial mandible with two teeth in situ, and ten isolated teeth. The latest chronological assessment, based on the combined ESR/U-series techniques, has provided an estimation of around 412 ± 25 ka which is also consistent with the faunal composition (Grün et al., 1998; Huang et al., 1981).

Recently, the Hexian teeth were compared in detail to a wide sample of *Australopithecus* and *Homo* fossils (Xing et al., 2014). Summarizing, we can highlight the expression of several *mass-additive* traits (term by Irish, 1998) that provide to these teeth with a primitive and robust morphology (Fig. 2). Namely, the upper central incisor presents several finger-like projections on its lingual aspect and, notably, pronounced vertical grooves in its labial surface, similar to the ones expressed at the buccal aspect of the upper third premolar. These features, together with conspicuous protostylids on lower molars, could have acted as a cingulum-like or buttresing system evincing its primitive status.

In the same line, Hexian molars and premolars are characterized by complex occlusal morphologies with wrinkled enamel and dentine surfaces and the expression of several accessory grooves and ridges. The presence of bifurcated essential crests, the elevated frequencies of deflecting wrinkle, C6 and C7 in lower molars and the highly crenulated occlusal surfaces, contribute to the primitive aspect of this sample. The crown outline of the upper premolar and upper and lower molars is also primitive, similar to early *Homo* specimens but with a characteristic Asian pattern in the bucco-lingual projection of the mesial cusps with regard to the distal ones.

The root number and shape are particularly informative. The three independent roots of the upper third premolar can be only found in East Asia in one specimen from the Early Pleistocene of Sangiran (Pucangan). The bifurcaton of the roots in upper and lower molars is high and strongly divergent, more primitive than in other roughly contemporaneous populations like those from Zhoukoudian
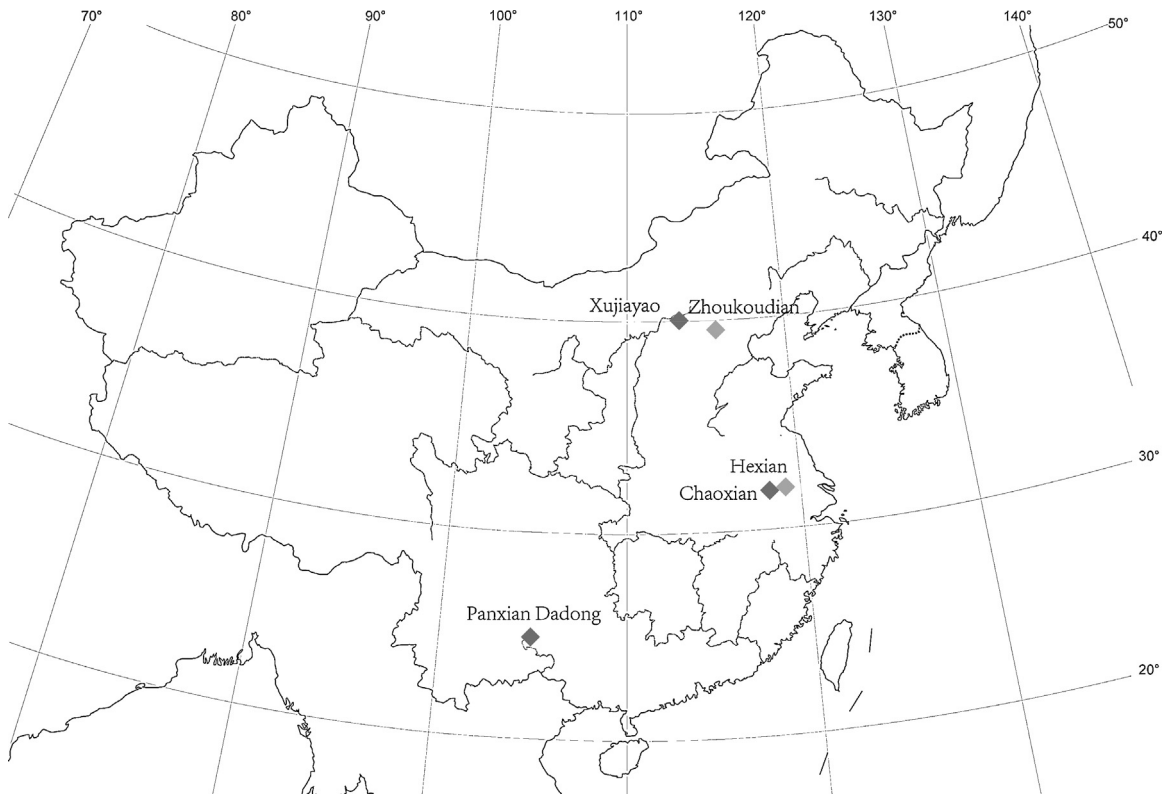
Fig. 1. Map showing the location of some of the key fossil localities discussed in the text.
Fig. 1. Carte présentant la situation de quelques-unes des localités fossiles clés, discutées dans le texte.

Fig. 2. Hexian teeth. Top (from left to right): occlusal and buccal view of PA832 (right P^3), occlusal view of HXUP3 (left P^4), occlusal view of PA836 (left M^1), occlusal view of PA833 (left M^2) and occlusal view of PA837 (right M^2). Bottom (from left to right): occlusal view of PA835 (right I^1), occusal view of PA839 (left M_2), buccal view of PA838 (left M_2) and lingual view of PA834-1 and PA834-2 (left M_2 and M_3).
Fig. 2. Dents d'Hexian. En haut (de gauche à droite) : vues occlusale et buccale de PA832 (P3 droite), vue occlusale de HXUP3 (P4 gauche), vue occlusale de PA836 (M1 gauche), vue occlusale de PA833 (M2 gauche) et vue occlusale de PA837 (M2 droite). En bas (de gauche à droite) : vue occlusale de PA835 (I1 droite), vue occlusale de PA839 (M2 gauche), vue buccale de PA838 (M2 gauche) et vue linguale de PA834-1 et de PA834-2 (M2 et M3 gauches).

where the roots are less divergent and even coalescing in some specimens. The section of the root is rounded and they barely narrow towards the root tip, a feature that seems to be characteristic of Early Pleistocene samples from both continental Asia and Sangiran (Kaifu et al., 2005a, 2005b). We do not find taurodontism, a feature that has been cited as typical of the Neanderthal lineage but can be found in variables percentages in other samples like Zhoukoudian, according to Weidenreich estimations (Weidenreich, 1937).

All these features reveal that Hexian is close in some aspects to *H. ergaster* and to East Asian Early and mid-Middle Pleistocene fossils. However, compared to Zhoukoudian, Hexian hominins have larger teeth. Indeed, the metric analysis reveals that all Hexian teeth are remarkably large, falling always in the lower limit of *Australopithecus* and African early *Homo* variation despite the younger age of the site. Hexian teeth are even larger than the earliest specimens from Sangiran, particularly the upper central incisor and the upper third premolar (Xing et al., 2014).

Overall, Hexian teeth show a primitive conformation for the genus *Homo* and expand the variation known for the East Asian hominins before the mid-Middle Pleistocene. Both metric and morphological aspects are more typical of Early Pleistocene specimens from Africa and Asia. In particular, despite Hexian is ca. 300 ka younger than Zhoukoudian (see Shen et al., 2009), the general crown dimensions and the number and shape of Hexian roots are more primitive (Xing et al., 2014).

3. Panxian Dadong

Panxian Dadong is a site located at the western part of the Guizhou Plateau, in South China (25°37′38″N, 104°8′44″E) and, to date, it has provided four isolated teeth dated to an interval ranging from 300 to 190 ka (Zhang et al., 2015): an upper central incisor, an upper first premolar, a lower first premolar and a lower canine (Fig. 3).

With the exception of a more primitive upper central incisor (see below), the rest of the dental sample expresses derived features that make Panxian Dadong different from early *Homo* and *H. erectus sensu lato* specimens, and closer to later member of the genus *Homo*, including recent humans (Liu et al., 2013).

The lingual features of the upper central incisor are archaic. The strong basal eminence and the well-developed finger-like projections make this tooth similar to early *Homo* specimens such as KNM-WT 15000, and some Early and Middle Pleistocene hominins from Asia (Martinón-Torres et al., 2008; Weidenreich, 1937; Xing, 2012; Xing et al., 2014). Unfortunately, the labial surface is broken preventing an assessment of its convexity. If the straight incisal edge of Panxian Dadong upper central incisor can be used as a proxy of a flat labial surface (see Crummett, 1995), this would be one of the few features that can be considered typical and even exclusive of *H. sapiens*. However, due to the labial fracture, this assessment has to be made with caution.

The Panxian Dadong canine is derived for the genus *Homo*, with a symmetrical incisor-like crown and faintly elevated lingual central ridge. This pattern is more derived than in *H. ergaster* and some *H. erectus* specimens from Zhoukoudian and the Pucangan and Kabuh Formations from Sangiran (Brown and Walker, 1993; Grine and Franzen, 1994; Weidenreich, 1937) where the crown is more asymmetrical, a cingulum is present in some cases and the central ridge is relatively swollen. However, typical *H. sapiens* canines are more slender and show smoother labial and lingual surfaces than Panxian Dadong specimen. The upper third premolar has a relatively symmetrical crown outline and light basal swelling that contrasts with the marked cingulum expressed in other Middle Pleistocene specimens like some Zhoukoudian or Hexian specimens. In particular, the geometric morphometric analysis of the upper third premolar shape reveals that Panxian Dadong specimen clusters with Late Pleistocene specimens and modern humans (Liu et al., 2013). The lower third premolar shows a relatively symmetrical crown outline, relatively small lingual cusp and smooth buccal surface. This pattern is more derived than that of the Early and Middle Pleistocene *Homo* specimens from Africa and Asia (Tobias, 1991; Wood and Uytterschaut, 1987; Xing, 2012) and it is also different from the typical Neanderthal conformation, characterized by a bulbous metaconid and a small occlusal polygon that is lingually displaced (Gómez-Robles et al., 2008; Martinón-Torres et al., 2007).

Our study shows that the Panxian Dadong teeth combine archaic and derived features that align them with Middle and Late Pleistocene fossils from East and West Asia and Europe. However, the derived traits are not diagnostic enough to specifically link the Panxian Dadong teeth to *H. sapiens*. Indeed, the dental distinctiveness of *H. sapiens* is still an open research topic (Bailey and Hublin, 2013). Although there are some traits that in their pattern of expression can be considered as typical of *H. sapiens*, those features can be variably present in other "*non-sapiens*" hominins. In other words, with the possible exception of a flat labial surface in upper incisors (grade 0 of ASUDAS) (Martinón-Torres et al., 2007), we have not identified so far any dental autapomorphy for modern humans. However, the derived status of Panxian Dadong points to a larger morphological variability during the Middle Pleistocene in China, and poses the possibility of different evolutionary trends at the same time in the continent.

4. Xujiayao

The Xujiayao site, located in northern China (40_06′02″N, 113_58′39″E) has provided several hominin remains that include a partial maxilla with six teeth in situ (upper central incisor, upper canine, upper third and fourth premolars, and upper first and second molar), and four isolated teeth (upper first and third molars and lower third molar) (Xing et al., 2015) among other skeletal parts (Wu and Trinkaus, 2014; Wu et al., 2014). The latest chronometric study of this collection provides an age older than 140 ka and likely between 160-220 ka (Tu et al., 2015).

The Xujiayao teeth show consistently large dimensions and morphological features that are more typically found in the Early and Middle Pleistocene populations from Asia

Fig. 3. Panxian Dadong teeth. Top (from left to right): occlusal, buccal and mesial view of right lower C, occlusal buccal and mesial view of left P₃. Bottom: occlusal, buccal and mesial view of right P³, lingual and occlusal view of right I¹.

Fig. 3. Dents de Panxian Dadong. En haut (de gauche à droite) : vues occlusale, buccale et mésiale d'une canine inférieure droite, vues occlusale, buccale et mésiale d'une P₃ gauche. En haut (de gauche à droite) : vues occlusale, buccale et mésiale d'une P3 droite, vues linguale et occlusale d'une I¹ droite.

(Fig. 4). The mesiodistal and bucco-lingual diameters fall generally outside the range of variation of other Late Pleistocene samples except for the Denisova specimen (Reich et al., 2010) which is also remarkably large in comparison with other contemporaneous specimens.

Both the upper central incisor and canine display a constellation of mass-additive features such as pronounced shovel shape, strong tuberculum dentale, labial convexity and mesial canine ridge that have been described as typical of the Neanderthal lineage, although not exclusive to this group (Bailey and Hublin, 2006; Bailey et al.,

2008; Martinón-Torres et al., 2007). Interestingly, these features would match the morphological assessment of other skeletal parts recovered from the Xujiayao locality. The analysis of a temporal bone and a mandibular fragment revealed features that were classically considered as distinctive of Neanderthals, although they were interpreted as the result of regional variation and without taxonomic resolution (Wu and Trinkaus, 2014; Wu et al., 2014). The Xujiayao upper third premolars shows a symmetrical contour and relatively simplified occlusal and buccal surfaces as it is commonly found in *H. sapiens*,
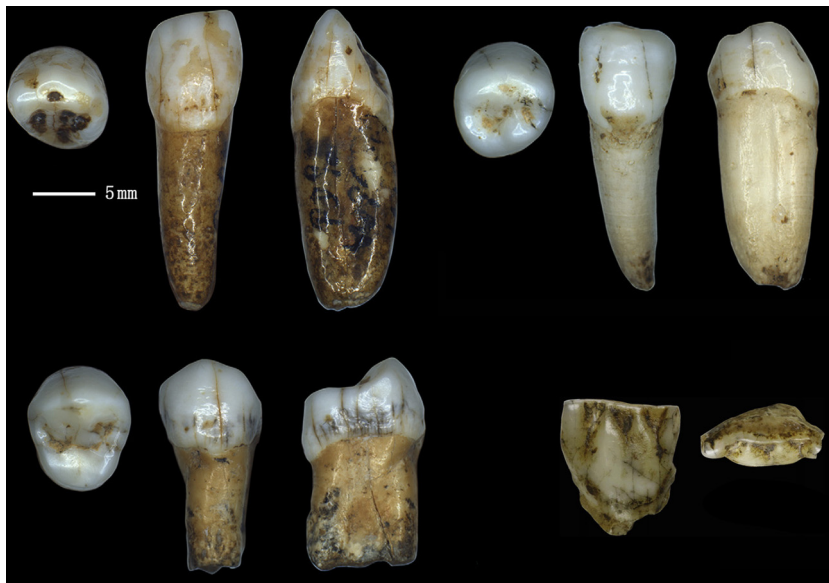

Fig. 4. Xujiayao teeth. Top (from left to right): occlusal view of left partial maxilla (PA1480) with M¹ in situ and associated left I¹, C, P³, P⁴ and M². The P³, P⁴ and M² images are obtained from micro-CT reconstruction. Bottom (from left to right): occlusal and mesial view of PA1481 (right M³), occlusal and mesial view of PA1496 (left M₃) and occlusal and buccal view of PA1500 (right M₃).

Fig. 4. Dents de Xujiayao. En haut (de gauche à droite) : vue occlusale d'un fragment de maxillaire gauche (PA1480) avec M¹ in situ et I¹, C, P³, P⁴ et M² gauches associées. Les images des P³, P⁴ et M² ont été obtenues par reconstruction à partir des données acquises par micro-tomographie. En haut (de gauche à droite) : vues occlusale et mésiale de PA1481 (M³ droite), vues occlusale et mésiale de PA1496 (M³ gauche) et vues occlusale et buccale de PA1500 (M₃ droite).

H. neanderthalensis and can be also identified in the Panxian Dadong specimen (Liu et al., 2013). While this dental class, in particular, is more derived than the Early and Middle Pleistocene specimens found at Sangiran, Zhoukoudian, Hexian or Chaoxian (Bailey and Liu, 2010; Gómez-Robles et al., 2011), the upper fourth premolar presents a more primitive and asymmetrical shape. The Xujiayao upper molars display the characteristic trapezoidal crown outlines of the East Asian Early and Middle Pleistocene hominins, with a relative expansion of the bucco-lingual dimension at the mesial aspect, and a tapering distobuccal corner due to a proportionally lower reduction of the hypocone with regard to the metacone. The occlusal surface of upper and lower molars is complicated by several accessory ridges, crests and cusps, that are also expressed at the enamel-dentine junction (Xing et al., 2015). The molar root system is remarkably large and robust, with long and divergent radicals that remain relatively wide throughout the whole length. This pattern seems to be typical of East Asian Early and mid-Middle Pleistocene hominins (Grine and Franzen, 1994; Kaifu, 2006; Kaifu et al., 2005a, 2005b; Weidenreich, 1937) and different from that found in other Asian Late Pleistocene localities such as Tubo, Huanglong, Maba, Luna or Zhiren (Bae et al., 2014; Liu et al., 2010a,b; Xiao et al., 2014). Indeed, despite the tendency towards crown reduction ascertained in the Eurasian Early and Middle Pleistocene populations (Kaifu, 2006; Martinón-Torres et al., 2008), the root system remains proportionally more robust in the Asian than in the European and African hominins. This pattern could be evincing different ontogenetic mechanisms behind the dental size reduction in the Asian groups with regard to the European populations (Bermúdez de Castro and Nicolás, 1995; Gómez-Robles et al., 2012; Martinón-Torres et al., 2012).

The mosaic of primitive and derived dental features for the Xujiayao hominins reveals the existence in Asia of a population of unclear taxonomic status with regard to other Late Pleistocene groups such as *H. sapiens* and *H. neanderthalensis*. The scarcity of fossil information available from the also Late Pleistocene sample from Denisova prevents a sound comparison with the Xujiayao hypodigm. However, there is an intriguing parallelism between the morphological and genetic mosaic of the Xujiayao and the Denisova samples, respectively, which point in both cases to a hominin lineage that:

- is different from *H. sapiens*;
- shares features with *H. neanderthalensis*;
- preserves the heritage of a "mysterious" and primitive hominin, which in the Xujiayao fossils could be reflected in the preservation of some typical Asian Early and Middle Pleistocene features.

This is obviously a speculative statement that could only be tested either by extracting and analysing Xujiayao DNA (if preserved), or by increasing the Denisova fossil sample that could be directly compared. Still, it is worthy to highlight the primitive status of the M^3 from Denisova (Reich et al., 2010), with a large and morphologically complex crown and a stout and divergent root

system with radicals that do not narrow towards the tip.

5. The morphological variability of the Asian dental record

Summarizing, we believe that a preliminary approach to the Pleistocene human dental evidence in Asia reveals high levels of morphological variability. The combination of dental features in these hominins cannot be organized along a chronological sequence, since later forms are not always more derived than earlier ones. In our opinion, this pattern would be more supportive of an intermittent and/or discontinuous settlement of the continent. Fragmentation and isolation would have favored the retention of primitive features in certain groups and the development of new and/or more derived features in others.

From our analysis, it is clear that Xujiayao is morphologically more primitive than other Late Pleistocene samples from Asia, with the possible exception of Denisova (Reich et al., 2010) and Penghu, from Taiwan (Chang et al., 2015). This could be evincing the persistence in Asia of a primitive lineage that coexisted in time with *H. sapiens* and contributes to the ongoing debate about the presence of primitive and/or local groups in Asia before the appearance of *H. sapiens* (Chang et al., 2015; Curnoe et al., 2012). This also keeps open the question about the type of interaction that may have existed between these lineages, since the preservation of archaic features in some Late Pleistocene fossils from Asia has been interpreted for long time in the context of possible assimilation, admixture and gene flow between demes (e.g., Etler, 2004; Wolpoff et al., 2001; Wu, 2004; Wu and Trinkaus, 2014; Wu et al., 2014). These studies are also in line with the latest molecular studies on ancient DNA that support scenarios with persistence of primitive lineages and introgression (e.g., Green et al., 2006, 2008; Kim et al., 2015; Krause et al., 2010; Meyer et al., 2013; Reich et al., 2010) and are far from picturing a linear scenario for the genus *Homo* evolution, particularly in Asia.

Furthermore, Xujiayao is morphologically more primitive than the Middle Pleistocene population from Panxian Dadong which, in turn, is more derived than other roughly contemporaneous samples that have been classically considered as typical of the Asian *H. erectus* taxon. These samples would include fossils from Hexian, Chaoxian, Zhoukoudian and most of the Sangiran specimens discussed by Grine and Franzen (1994) and Kaifu and his collaborators (Kaifu, 2006; Kaifu et al., 2005a, 2005b), but not those analysed by Zanolli (2013), that are characterized by more derived conformations. We tentatively suggest that Panxian Dadong could represent a deme that is different from those usually classified as classic *H. erectus*, although its origin and fate still need further research. To support this statement, we face the difficult but exciting challenge of defining the features that can dentally characterize *Homo erectus sensu strictu (s.s)*. There is a need for more detailed and specific analyses of the large Asian dental samples in the search of a common *bauplan* that despite the variability, could be employed to identify *H. erectus s.s*. Indeed, despite the variability observed between the

Java and the Chinese material (e.g., Aguirre and de Lumley, 1977; Antón, 2002, 2003; Kidder and Durband, 2004), several authors have pointed to a common cranial *bauplan* that unifies the *H. erectus* taxon (Antón, 2002). We tentatively suggest that part of the dental *bauplan* of the Asian *H. erectus* taxon could comprise features in upper and lower molars such as the relative bucco-lingual expansion of the lateral walls of the mesial cusps with regard to the distal ones; a profuse and particular "dendrite-like" crenulation of the enamel-dentine junction; and the stout, round in section and divergent roots that are thick throughout their entire length without narrowing towards the tip in upper and lower molars (Kaifu et al., 2005a; Xing et al., 2014, 2015).

Even within the samples that we could tentatively considered as typical of *H. erectus s.s.* (but see Chang et al., 2015 for Hexian assessment), Zhoukoudian is morphologically more derived than Hexian despite being roughly contemporaneous or likely older than Hexian (Shen et al., 2009). Hexian would be also more primitive than the Chaoxian fossils, particularly in their large crown sizes (Bailey and Liu, 2010; Xing et al., 2014). Hexian could represent the persistence in time of a *H. erectus* group that would have retained primitive features that were lost in other contemporaneous populations from Asia. In this line, several studies have already pointed to biogeographical isolation as one of the mechanisms that would explain the discontinuity, regional evolution and morphological divergence of the populations within China and between continental Asia and Java (Kaifu, 2006; Zanolli, 2013).

6. Where are the sinks and sources in East Asia?

In Europe, sources were mostly referring to southern latitudes or coastal areas in which populations could find refuge during glacial periods as climatic conditions remained relatively mild and tolerable for survival (Bermúdez de Castro et al., 2013; Dennell et al., 2010, 2011; MacDonald et al., 2012). Thus, glacial-interglacial cycles would be the main forces constraining the expansion and settlement of hominins in Europe, particularly during the Middle Pleistocene. In Asia, there is evidence that occupation may have been also limited to the moist and warmer interglacial and inter-stadial periods (e.g., Dennell, 2009, 2013a; Ranov, 1995; Ranov et al., 1995). To this, we can add the difficulty (or impossibility) of permanently occupying the vast desert areas that dominate the Asian landscape. Indeed, recent studies point to deserts as a key elements preventing also the settlement and free dispersal of hominins across the Asian territory (Dennell, 2013a, 2013b). It is logical to assume that the repeated expansion and contraction of deserts throughout the Pleistocene (Liu et al., 1999) had a major impact in the settlement of Asia in certain periods and regions. In addition, hominins were particularly sensitive to rainfall variation (Dennell, 2009), so weather systems like the monsoon, that are predominant in a large area of continental Asia, probably played a major role in the demographic shaping of the Asian human groups.

The recent analysis of the pattern of hominin settlement of the Nihewan Basin and adjacent Loess Plateau

suggests that hominins occupation was likely intermittent and linked to favourable warm periods (Dennell, 2013b). During cold periods of the Middle and Late Pleistocene, much of the central and western Asia areas were hostile for hominin settlement, and the steppe-like conditions of China north of the barrier conformed by the Qingling Mountains would have been equally inhospitable (see Dennell, 2009; Ferguson, 1993; Louys and Turner, 2012). All these regions could have potentially worked as "sinks", being depopulated during the dry and cold periods (Ao et al., 2010; Pei et al., 2009). Northern China may have acted as a population "sink" and the repeated incursions and excursions into and out of this region of warm-adapted mammals could be likely consequence of climatic changes (Dennell, 2013b; Louys and Turner, 2012; Tong, 2006, 2007).

In investigating the applicability of the "source and sink" model to Asia, it is important to bear in mind that semi-arid regions, bordering the deserts, are the regions that potentially contained the source populations (Dennell, 2009, 2013a, 2013b). Since the limits of deserts are not immutable, when demographic levels allowed expansion or climatic conditions were more benign, hominins could expand to adjoining areas that were previously hostile for hominin settlement. The climatic instability and environmental changes in Asia might have favoured a pattern of fragmentation and isolation leading to the high morphological variability of the Asian hominin record and the possibility of persistence of primitive hominin lineages throughout time (Dennell, 2013a, 2013b).

Another important issue to understand the dynamics of the human settlement of Asia is the potential of islands to act as sources or sinks depending on how the sea level changes may have created or blocked land bridges with continental Asia (Dennell et al., 2014; Louys and Turner, 2012). Recently, Louys and Turner (2012) draw very enlightening parallels with the population "source and sink" model proposed for northern Europe (Dennell et al., 2011; MacDonald et al., 2012). Louys and Turner (2012) defended the potential of Southeast Asia and in particular, the increased land area represented by Sundaland, to act as "a refugium for savannah-adapted species, and particularly hominin during the period of lowered sea level and environmental changes that characterised so much of the Pleistocene" (Louys and Turner, 2012).

Another interesting example about islands potentially acting as refugia comes from the recent publication of the first hominin from Taiwan (Chang et al., 2015). Chang et al. (2015) highlight the unexpected late survival of primitive dentognathic features in Penghu 1, a fragmentary mandible with molars and premolars in place, that was dredged by a fishing net 25 km off the western shore of Taiwan together with a fossil faunal assemblage typical of Middle/Late Pleistocene. Based on similar contents of fluorine and sodium, authors conclude that the human and the faunal assemblages share similar depositional histories and thus, Penghu 1 is dated as younger than 450 ka and likely 190-10 ka based on the faunal morphology. The study of Penghu 1 specimen reveals differences with classic *H. erectus* materials from Java or northern China, and suggest affinities with the Hexian assemblage (Chang et al.,

2015; Durband et al., 2005; Xing et al., 2014). In this context, Hexian and Penghu could be potentially considered as a morphologically coherent group or paleodeme *sensu* Howell (1999) despite the chronological distance.

The varying degrees of sea level and land connections between islands would undoubtedly influence the degree of isolation and interaction of hominins from continental Asia and Java. Indeed, despite the morphological differences found between the chronologically younger and older specimens from the Sangiran series, several authors point to certain degree of morphological stasis in this region (Kaifu, 2006; Kaifu et al., 2005a, 2005b) and thus, certain degree of isolation from continental Asia. However, recent additional evidence from the Sangiran Dome highlights the expression of derived features that are unusual for the Early and early Middle Pleistocene populations such as the strong dental reduction, with reduction and/or loss of hypoconulid or the high frequencies of non-Y groove patterns (Zanolli, 2013). According to this author, these teeth would support intermittent exchanges between continental and insular Southeast Asia through the Pleistocene or, in other words, it would suggest that the pattern of isolation was far from being continuous. Although Zanolli (2013) allocates this new Java material to *H. erectus s.s.*, he also acknowledges that the remarkable differences between this sample and the rest of the specimens recovered from the Kabuh Formation could be suggestive of a different species/demes. In our opinion, this material does not fit within the variability usually observed in Early and Middle Pleistocene populations from Asia and cannot be comfortably accommodated with *H. erectus s.s.* Such a degree of dental reduction, from both a morphological (i.e., molar inter-ratio, loss of main cusps) and a metric perspective has been only identified in the Middle Pleistocene sample from Sima de los Huesos, in Atapuerca (Bermúdez de Castro and Nicolás, 1995; Martinón-Torres et al., 2012, 2013a, 2013b). In addition, the study of the inner structure confirms that the combination of non metric features are unusual for this period and more frequently found in recent humans (Zanolli, 2015). From our perspective, this large morpho-dimensional variability in the Sangiran material is beyond the degree of time-related structural reduction occurred in Javanese *H. erectus* and would suggest more complex scenarios envisaging frequent population interchanges (possibly from sources to sinks) and/or regional variation by isolation. Future studies should aim to a detailed but also macro-scale study of the dental evidence. This would assist in understanding the longitudinal (Dennell, 2009, 2013a, 2013b; Zanolli, 2013, 2015) but also the transversal evolutionary dynamics across Asia, particularly the nature and intensity of possible connections between Asia and Europe (Bermúdez de Castro and Martinón-Torres, 2013; Martinón-Torres et al., 2007, 2011).

Acknowledgments

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