Two new Mio-Pliocene Chadian hominids enlighten Charles Darwin's 1871 prediction

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The idea of an evolutionary sequence for humans is quite recent. Over the last 150 years, we have discovered unexpected ancestors, numerous close relatives and our deep evolutionary roots in Africa. In the last decade, three Late Miocene hominids have been described, two about 6 Ma (*Ardipithecus* and *Orrorin*) in East Africa and the third dated to about 7 Ma (*Sahelanthropus*) in Central Africa. The specimens are too few to propose definite relationship to other species, but clearly these belong to a new evolutive grade distinct from *Australopithecus* and *Homo*. Moreover, all of them were probably habitual bipeds and lived in woodlands, thus falsifying the savannah hypothesis of human origins. In light of all this recent knowledge, Charles Darwin predicted correctly in 1871 that Africa is the birthplace of humans, chimpanzees and our close relatives.

Keywords: earliest hominids; central Africa; evolutionary grade; woodland origin

1. INTRODUCTION

Who our ancestors were, and when and how they arose, are questions that are always topical.

The notion of fossil humans is quite recent: the first Neanderthal specimen from the Neander Valley of Germany was first described only in 1856 (Fuhlrott 1859, 1865) and Darwin's masterpiece 'On the Origin of Species' only published in the middle of the nineteenth century (Darwin 1859).

By the 1980s early hominids were known just from south and east Africa (figure 1).

But from 1994 in the Djurab desert of Northern Chad the M.P.F.T.¹ unearthed successively a new australopithecine dated to 3.5 Ma (Brunet *et al.* 1995; Lebatard *et al.* 2008), *Australopithecus bahrelghazali* (Brunet *et al.* 1996; figure 2), the first ever found west of the Rift Valley; and a new hominid, *Sahelanthropus tchadensis* (Brunet *et al.* 2002a,b), from the Late Miocene (figures 3–6), dated to 7 Ma (Vignaud *et al.* 2002; Lebatard *et al.* 2008). This earliest known hominid is a new milestone suggesting that an exclusively southern or eastern African distribution of the early hominids is unlikely to be correct.

And so in the last 15 years our roots have been shown to be deeper, from the Lower Pliocene (4.4 Ma) to the Late Miocene (7 Ma), with three new species: *Ardipithecus kadabba* (Haile-Selassie 2001; Haile-Selassie & Woldegabriel 2009; 5.2–5.8 Ma, Middle Awash, Ethiopia), *Orrorin tugenensis* (Senut *et al.* 2001; ca 6 Ma, Lukeino, Kenya) and, the earliest one, *S. tchadensis* (Brunet *et al.* 2002a,b; 7 Ma, Chad).

Sahelanthropus tchadensis (figures 3–6) displays a unique combination of plesiomorphic and apomorphic characters that clearly illustrate its hominid affinities

temporally close to the last common ancestor of chimpanzees and humans, and also that it cannot be related to chimpanzees or gorillas (Brunet *et al.* 2002a,b, 2004, 2005; Vignaud *et al.* 2002; Guy *et al.* 2005; Zollikofer *et al.* 2005; Brunet 2006, 2009a,b; Lebatard *et al.* 2008). In Chad, the Late Miocene sedimentological and palaeobiological data are consistent with mosaic landscapes probably very similar to the present Okavango Delta (Central Kalahari, Botswana; Brunet *et al.* 2005). As with the other Late Miocene hominids, *S. tchadensis* represents a new evolutionary grade (Brunet 2009b), surely a habitual biped with its usual habitat probably a wooded one.

So, now, it is completely clear that the earliest hominids are not dependent on savannah and were not living just in south and east Africa.

Accordingly, this early hominid history enlightens the Charles Darwin prediction of 1871 (Darwin 1871) and must be reconsidered from a completely new viewpoint.

2. A NEW STORY ... WEST OF THE RIFT VALLEY

In the 1980s, the distribution of hominid remains in Africa, with the earliest being in east Africa (Ethiopia and Tanzania) (figure 1), led Coppens (1983) to propose an 'East Side Story' scenario in which early hominids appeared and evolved in the Pliocene primary savannah east of the Rift Valley, while the tropical forest, west of the Rift Valley, was thought to represent the early African ape habitat.

In 1994, I received a research permit from the Chadian authorities to conduct geological and palaeontological survey in the Djurab desert of northern Chad. With the M.P.F.T., one year later (January 1995), at a site east of Koro-Toro, we found a Lower Pliocene vertebrate fauna with a partial lower jaw belonging to a new australopithecine that we nicknamed 'Abel', the first ever found west of the

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Figure 1. Map of Africa showing the main Mio-Pliocene hominid localities. 1, Taung; 2, Drimolen; 3, Sterkfontein; 4, Swartkrans; 5, Kromdraai; 6, Makapansgat; 7, Malema; 8, Laetoli; 9, Olduvai; 10, Peninj; 11, Lukeino; 12, Chesowanja; 13, Lothagam; 14, Kanapoi; 15, Chemeron; 16, W. Turkana; 17, Koobi Fora; 18, Allia Bay; 19, Omo; 20, Konso; 21, Maka; 22, Aramis; 23, Hadar; 24, Koro-Toro; 25, Toros-Menalla.

Rift Valley (Brunet *et al.* 1995). We named it *A. bahrelghazali* (Brunet *et al.* 1996; figure 2).

Other australopithecine sites have been discovered in the Koro-Toro area since 1995 (Brunet *et al.* 1997), all having the same fauna with mammals (proboscidiens, suids, rhinocerotids and equids) indicating a biochronological age of 3.5 Ma, congruent with more recent ^{10}Be dating (Lebatard *et al.* 2008).

Geological and palaeontological survey in the Djurab desert from 1994 to 1997 yielded three new fossiliferous areas, biochronologically dated to: (i) the Early Pliocene (4–4.5 Ma), at Kollé (Brunet *et al.* 1998); (ii) the Mio-Pliocene boundary (5–5.5 Ma), at Kossoum Bougoudi (Brunet *et al.* 2000); and (iii) the Late Miocene (*ca* 7 Ma), at Toros-Menalla (TM) (Brunet *et al.* 2002a,b). To date, more than 500 fossiliferous localities have been discovered in the Djurab desert, representing up to now around 20 000 vertebrate (mammals, reptiles, birds and fish) specimens.

Figure 2. Mandible holotype specimen (KT12-95-H1) of *A. bahrelghazali* (Brunet *et al.* 1996).

In 2001, the M.P.F.T. unearthed a new hominid, *S. tchadensis* (Brunet *et al.* 2002a,b), from the locality TM 266. The holotype cranium (figure 3), nicknamed

Figure 3. Cranium holotype specimen (TM 266-01-060-1) of *S. tchadensis* (Brunet *et al.* 2002a,b). Scale bar, 1 cm.

Figure 4. Right lower jaw paratype specimen (TM 266-02-154-1) of *S. tchadensis*. Scale bar, 1 cm.

‘Toumai’, is associated with a fauna (more than 70 species) of which the mammalian component indicates a biochronological age estimate congruent with the ^{10}Be dating, close to 7 Ma (Vignaud *et al.* 2002; Lebatard *et al.* 2008). This earliest known hominid, *S. tchadensis*, unearthed at least 2600 km west of the Rift valley, is a new milestone suggesting that an exclusively eastern or southern African origin of the hominid clade is unlikely to be correct.

The discovery of *S. tchadensis* occurred in a particular scientific context. With three new Late Miocene species, *Ar. kadabba* (5.2–5.8 Ma, Ethiopia), *Or. tugenensis* (ca 6 Ma, Kenya) and *S. tchadensis* (ca 7 Ma, Chad), our roots went deeper, from 3.6 Ma in the 1970s to about 7 Ma today.

Since 1994, all these discoveries have had a scientific impact equivalent to that of Dart's naming of *Australopithecus africanus* (Dart 1925). During the last 10 years the framework of the hominid evolutionary story has changed markedly. Now, we have a new understanding of the environments inhabited by early hominids, and the models established in the 1980s must be reconsidered. Potential representatives of the earliest members of the human clade are now twice as old and are shown to be spread much wider over the African continent. Moreover, the hominids described during the last 15 years, while extending the geographical and temporal limits of our family,

Figure 5. Stereolithocast of the *S. tchadensis* cranium, three-dimensional reconstruction. Scale bar, 1 cm.

Figure 6. Illustration of the Toumai head.

show original associations of characters and morphotypes that lead us to revise our definitions of the Hominidae *per se*. In fact, we have to study our evolutionary history within completely new paradigms.

But, as palaeontologists and palaeoanthropologists, we have always to remember that our interpretations have, at most, a life expectancy that usually does not go beyond the next new major fossil discovery.

3. THE CHADIAN EARLY HOMINIDS

The material referred to as the Chadian australopithecine ‘Abel’ is an anterior lower jaw (figure 2), with the body missing beyond the P₄ level, and to a right P³. This pre-human has a new mosaic of derived and primitive anatomical characters such as: a flat mental

surface of the lower jaw; a subvertical symphysis, bulbous in its outline with a shallow genioglossal fossa; and an incisiform and very asymmetric canine with a strong bifid lingual crest. Each premolar exhibits a three pulp canal rooting pattern and the P_4 s are submolariform with a large talonid. This original combination of anatomical features has been interpreted as being sufficiently distinct to name a new species: *Australopithecus barhelghazali* (Brunet *et al.* 1996).

To date, only three Late Miocene species may claim the 'enviable status' of being among the earliest hominids. Two of them are from eastern Africa: *Ar. kadabba* (5.8–5.2 Ma, Ethiopia; Haile-Selassie 2001; Haile-Selassie *et al.* 2004; Haile-Selassie & Woldegabriel 2009) and *Or. tugenensis* (ca 6 Ma, Kenya; Senut *et al.* 2001; Galik *et al.* 2004; Ohman *et al.* 2005; White 2006); the third one, the oldest known hominid, is from central Africa: *S. tchadensis* (7 Ma, Chad; Brunet *et al.* 2002a,b, 2005). The geographical location of *S. tchadensis*, 2600 km west of the Rift Valley, along with its great antiquity, suggests an early (at least by 6 Ma) widespread hominid distribution (Sahel and eastern Africa). The material referred to as the Chadian hominid 'Toumai' consists of a distorted but nearly complete cranium (figure 3), as reconstructed in three-dimensions (figures 5 and 6), associated with several mandibular specimens (figure 4) and isolated teeth. *Sahelanthropus tchadensis* displays a unique combination of primitive and derived characters. Identifiable derived features of *S. tchadensis* are: an anteriorly-positioned foramen magnum linked to a rather short basioccipital and a sub-horizontal nuchal plane; a downward lipping of the nuchal crest; lower jaw with a vertical symphysis with weak transverse tori; and for the dentition, the anatomical characters are: a non-honing C/P3 complex; no diastema between C and P^3 ; small-crowned canines with a long root, the upper one without any honing distal crest and the lower one with a large distal tubercle, both shoulders being very low; a P^3 with a strongly sloping buccal surface; postcanine teeth with maximum radial enamel thickness intermediate between chimpanzees and australopithecines; and bulbous, slightly crenulated postcanine occlusal morphology. It is interesting to note that all the hominid mandibular specimens from TM have the same root pattern in the postcanine teeth, with two roots and three separate pulp canals for each premolar (Brunet *et al.* 2002a,b, 2004, 2005; Vignaud *et al.* 2002; Guy *et al.* 2005; Zollikofer *et al.* 2005; Brunet 2006, 2009a,b).

As known since Darwin, all these derived characters show that *S. tchadensis* cannot be related to an ape (chimpanzees or gorillas) but clearly suggest that it must be related to later bipedal hominids, and may be temporally close to the common ancestor of chimpanzees and humans (Brunet *et al.* 2002a,b, 2005; Guy *et al.* 2005; Zollikofer *et al.* 2005).

Scientifically it is impossible to understand why some authors ignore these derived characters and concentrate on primitive ones to reach the conclusion that *S. tchadensis* is related to modern apes and even more precisely to a palaeogorilla (Wolpoff *et al.* 2002, 2006; Pickford 2005). This attempt to undermine the clear affinity of the Chadian hominid is curious mainly

when it is coming from, among others, two who have not yet had the opportunity to check Toumai casts in their laboratory. Is it what they believe, or is it only because they want to keep *Orrorin* as the earliest hominid?

The East Side scenario of Coppens (1983) emphasized the major role of savannah in early hominid evolution. Are the earliest known hominid environments in agreement with such a model?

4. THE LATE MIOCENE HOMINID ENVIRONMENTS AS WE KNOW THEM

In Chad, the sedimentological evidence from the Late Miocene TM fossiliferous area demonstrates that, at least since 7 Ma, successive wet (mega-lake Chad events) and arid periods (desertic events) occurred. These successive events are identified by a sedimentological series comprising aeolian sandstones (desertic episode); perilacustrine sandstones (lacustrine transgression); and green pelite and diatomite (true lacustrine environment; Vignaud *et al.* 2002; Schuster *et al.* 2006). *Sahelanthropus tchadensis* and its associated vertebrate remains have been uncovered from the perilacustrine sandstones (Anthracotheriid Unit). Sedimentological data are in agreement with this mosaic of environments, indicating a vegetated perilacustrine belt between lake and desert (Vignaud *et al.* 2002). The Okavango Delta in central Kalahari (Botswana) appears to be a good modern analogue in presenting similar habitat diversity (mosaic of lacustrine and riparian waters, swamps, patches of forest, wooded savannah, grassland and desertic areas). Although the precise habitat of the TM 266 hominid among this mosaic of landscapes available is still uncertain, it was probably a wooded one (Brunet *et al.* 2005). Other significant hominid discoveries associated with wooded environments in Middle Awash, Ethiopia (*Ardipithecus ramidus* and *Ar. kadabba*) and Lukeino, Kenya (*Or. tugenensis*) also rule out the role played by an open environment or savannah in favouring the acquisition of bipedal posture in the course of hominid evolution. Thus, sedimentological and faunal data rather suggest wooded environments for *Ar. ramidus* (White *et al.* 1994; Woldegabriel *et al.* 1994) and *Ar. kadabba* (Woldegabriel *et al.* 2001; Haile-Selassie & Woldegabriel 2009). In 2001 those authors noted: 'It therefore seems increasingly likely that early hominids did not frequent open habitats until after 4.4 Myr. Before that, they may have been confined to woodland and forest habitats' (p. 177). Moreover, according to the recent description of a partial skeleton of *Ar. ramidus* (White *et al.* 1994, 2009a,b) from Aramis, Ethiopia at 4.4 Ma, it appears that this hominid may be the same new evolutionary grade as are the three late Miocene taxa. It was a climbing biped, both terrestrial and arboreal, with an opposable grasping big toe (without arched feet and walking flat-footed), living in a woodland landscape (Lovejoy 2009; Lovejoy *et al.* 2009a,b,c,d; Suwa *et al.* 2009a,b; White *et al.* 2009a,b).

A wooded habitat (open woodland with denser stands of trees in the vicinity) has been also suggested for the Kenyan *Or. tugenensis* (Pickford *et al.* 2002).

This is of fundamental importance since the three late Miocene taxa, *Ar. kadabba*, *Or. tugenensis* and *S. tchadensis*, were all probably habitual bipeds. All these Late Miocene hominids demonstrate that the savannah hypothesis is now falsified.

5. NEW PARADIGMS ... FOR A NEW EARLY HOMINID STORY

During the last 150 years, most of the models for hominid evolution have been overturned by successive discoveries. This fact obviously highlights the importance of fieldwork, as our understanding of our evolutionary story has, at most, a life expectancy that usually does not go beyond new findings.

Twenty years ago, available fossil hominid remains led us to consider eastern African savannah as the cradle of mankind. Now, it appears that the earliest members of our family have favoured wooded environments, and were not restricted to eastern or southern Africa but were rather living in a wider geographical region, including at least central and eastern Africa.

In the last decade, the number of recognized hominid taxa and the length of our geological roots, from 3.6 Ma in the 1970s to 7 Ma today, have doubled. These new hominids, while extending the geographical and temporal limits of our family, are Late Miocene ones with new associations of anatomical characters representing a new evolutionary grade.

In Chad, the radiometrical dating of *S. tchadensis* indicates that the divergence between chimpanzee and human lineages occurred before 7 Ma, which is earlier than generally (Kumar & Hedges 1998; Pilbeam 2002) or more recently thought by the molecular phylogenists (Patterson *et al.* 2006).

Besides, from a palaeobiogeographical point of view, published results derived from fieldwork show that central Africa was, at least between 3 and 7 Ma, a crossroad region marked by sporadic faunal exchanges with northern and eastern Africa (Brunet *et al.* 1995, 1996, 1997, 1998, 2000, 2002a,b, 2004; Brunet & White 2001; Geraads *et al.* 2001; Vignaud *et al.* 2002; Boissérie *et al.* 2003, 2005; Likius *et al.* 2003; Mackaye *et al.* 2005; Peigné *et al.* 2005; Lihoreau *et al.* 2006).

Better identification of the migratory patterns and the faunal exchanges between northern, central, eastern and southern Africa during the Mio-Pliocene is a key element that is indispensable for a new understanding of the origin and dispersal of the first members of the human clade and therefore its evolutionary history. We need more data from these geographical areas and notably from north-eastern Africa (e.g. Libya, Egypt and Sudan).

Finally, for a better understanding of the early human story palaeontologists and palaeoanthropologists need more data, and thus will have to conduct more and more geological and palaeontological field surveys.

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ENDNOTE

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