The International Union of Anthropological and Ethnological Sciences
The 16th World Congress IUAES
July 13 to July 23 2008, postpoined to July 27 to July 31, 2009 in Kunming, Yunnan Province of China

Embryogenic cranial evidences in fossil hominids, taxonomical and phylogenetical implications in human palaeontology

Anne DAMBRICOURT MALASSÉ

Department of Prehistory, National Museum of Natural History, UMR 5198 CNRS,
Institut de Paléontologie Humaine, 1, rue René Panhard, 75 013 Paris France
e-mail : iphadm@mnhn.fr

After a long period focused on East Africa, the debate on the origins of Anatomically Modern Human, *Homo sapiens* sensu stricto, as well as that of the oldest species of the genus Homo, is again topical. This focus is due for the most part to the outstanding conditions for fossilisation and excavations of plio-pleistocene fossils and, on the other hand, to the increasing research programmes in those areas of the Old World. North Africa (Ain El Hanech, Algeria) and South East Asia (*Homo erectus* child from Modjokerto) raised also the question of the great age of Homo genus (1,8 Myr), but this is during the last decades that the geographic areas expanded from the Arabic peninsula to Southern Europe, India and China (Majuangou, 1.66 Myr (Zhu *et al*. 2004, Huang and Zhang 2007).

The four remarkably preserved skulls from Dmanissi in Georgia, dated around 1.8 Myrs belong to the same morphological pattern than their African contemporaries *Homo habilis* and *Homo erectus* (Lordkipanidze *et al.* 2006), but they show sufficient exocranial diversity to distinguish them as *Homo georgicus* (Lumley M.A. *et al.* 2004, Spoor *et al.* 2007). This variability, well dispersed in geographic space, is a small sample of what really was the anatomical diversity of the oldest known human species. This species lived in East and South Africa, but quite certainly too in West Africa (Tchad, Niger, Mali, Mauritania (de Lumley *et al*. 2006)), as well as on the Indian peninsula where the human presence is confirmed in the Potwar plateau by artefacts dated 1.8 myr in Riwat (Rendell *et al* 1989, Allchin 1995) and in Central India at Isampur (Blackwell *et al.* 2001). The Indus basin is one of the oldest migration paths between East Africa and Eurasia (Central Asia, Iran, western China), a geographical situation which can explain the sustainability of the Indian Soanian industries (mode 1) during the Pleistocene (Gaillard *et al*. 2002, Dambricourt Malassé 2008, Gaillard and Dambricourt Malassé 2008).

The oldest artefacts were recorded in East Africa at Kada Gona and Ounda Gona (2,6 – 2,5 Myrs), Omo (2,5 Myrs), but also in the North of the Yiron Rift (Israël, 2,4 Myrs) and in France (Saint Elbe, 2,4-2,2 Myrs). Such a geographical dispersal implies the great ancienity of the genus Homo around 3 Myrs ago (Boeda 2005). The convergences of these discoveries call into question the African origins of Homo genus.

In the same time, better knowledge developed to understand what means an erected posture from the axial skeleton to the endocranial part of the clivus that can explain why Eurasian or Asian origins are possible without an Australopithecine ascendance (Deloison 2004). These new data have implications for the geographical and phylogenetical understanding of *Homo sapiens* emergence.
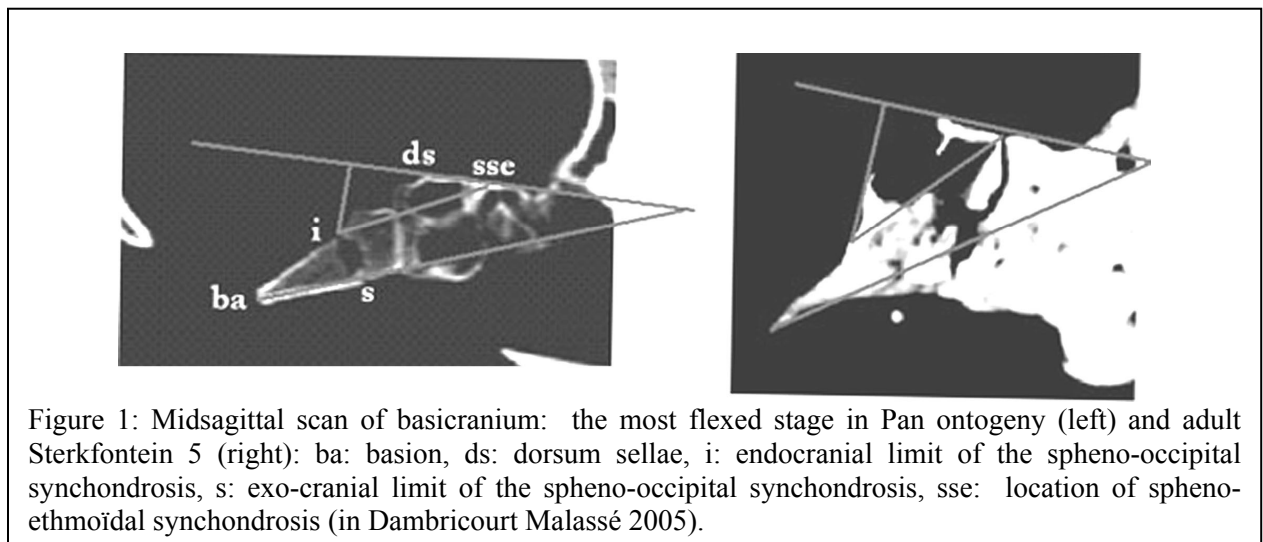
Embryogeny and convergences in hominids lineages

The oldest fossil showing the emergence of an upright position, well asserted up to the endocranium (i.e. the spheno-occipital flexure), is an isolated part of a cranial base (petrous, basi-occipital and mastoid process) discovered in Ethiopia and attributed to *Ardipithecus ramidus,* with an age of 4.4 Myrs (White et

al. 1995). This fossil has been associated with like-pongid teeth belonging to an oldest geological layer far from 1 km, nevertheless such an association is not in accordance with the occluso-postural equilibrium well known in posturology (Bonnier 1997) nor with the embryogenesis of the cephalic tissue. Teeth and brain share the same neuroblastic steam cells. The Australopithecine as well as the Homo genus developed an embryonic differentiation completely changed when compared with Paninae and Ponginae, not only for the brain, the teeth and the occlusion, but also for the all cephalo-caudal axis (Dambricourt Malassé 1987, 1988, 1993, 2004, 2006, Caro 2004).

The great anatomical craniofacial resemblance between two south African fossils SK847 (Swartkrans) and STW53 (Sterkfontein) is such that to establish a taxonomic diagnosis, it becomes necessary to take into account the features acquired during embryonic development, such as the spatial organisation of the semi-circular canals (Spoor *et al* 1994). Each one of the canals occupies one of the three Euclidian planes; an angle separates the lateral (or horizontal) canal from the posterior that differs between Paninae and modern humans. This angle is closed in Paninae, whereas it is more open in modern humans as well as in *Homo habilis* (Spoor *et al. ib*). A Gorilla foetus or a new born Chimpanzee both have a 10° angle that does not change until the adult stage, whereas in modern humans, it measures 20° (Dambricourt Malassé *et al.* 2000). The CT scan study of a 5 months human fetus devoided of flexion, shows that the angle is acquired without kinetic influence of the embryonic sphenoidal rotation. This means that such a morphogenetic change is closely related to Hox genes (Dambricourt Malassé and Lallouet 2008).

Compared to Paninae and Ponginae, and whatever the post-natal development stage, the australopithecine skull, on one hand, and that of human on the other, are modified in the three spatial plans towards a straightening of the whole face with a less projecting profile. In the vertical plan one can clearly observe 1) the straightening of the anterior pillars of the middle face closer of the anterior cranial fossa (McCollum 2008), 2) the same changes for the mandible with the straightening of the symphysis. The combination causes a withdrawal of the dental row towards the pharyngeal sphere. In the transversal plane, a rotational motion re-organized the two deciduous dental arches towards the frontal plane. These re-adjustments are in accordance with those of the cranial base observed in the sagittal and transversal planes (Dambricourt Malassé 1987); the sphenoid shows an endocranial surface clearly vertically oriented compared with Paninae and Ponginae (fig.1).

Figure 1: Midsagittal scan of basicranium: the most flexed stage in Pan ontogeny (left) and adult Sterkfontein 5 (right): ba: basion, ds: dorsum sellae, i: endocranial limit of the spheno-occipital synchondrosis, s: exo-cranial limit of the spheno-occipital synchondrosis, sse: location of spheno-ethmoïdal synchondrosis (in Dambricourt Malassé 2005).

Correlation are observed between this endocranial verticality and 1) a forward motion of the petrous pyramids in the transversal plane (Dean 1986, Dean and Wood 1981), 2) a more curved temporo-mandibular joint and 3) a posterior cranial fossa in a lower position. Those reorganizations associated between the base and the faces are finding in orthopaedics, and considered as dynamics that underlies the cranio-facial growth (Björk and Skeller, 1984, Deshayes 1991, 2006a, b, Deshayes *et al.* 2002). The applied analyses to great anthropoids find the same principles (Deshayes and Dambricourt Malassé 1990).

The restructuration concerns not only the skull, but also all the cranio-sacral and endocranial architectonics. Nevertheless, unlike Homo, in Australopithecine there is no generalization of the verticality to the exocranial side of the clivus (fig.2), while the semicircular canals remain unchanged. In this respect, one of the two South African fossils, SK847, shows an open angle, it is therefore a *Homo habilis*, whereas the Sterkfontein fossil STW53 is like a Paninae, so this is an Australopithecus. The anatomical convergences of the two new organisms characterized by permanent bipedalism, come from an evolutionary process acting on the embryonic pattern shared by the Ponginae, Paninae and their common ancestors. This embryonic and dynamic pattern common to numerous fossil and living species, has been define as "fundamental ontogeny". (Dambricourt Malassé 1987, 1988, 1993, Dambricourt *et al.* 1998, Chaline 1999).
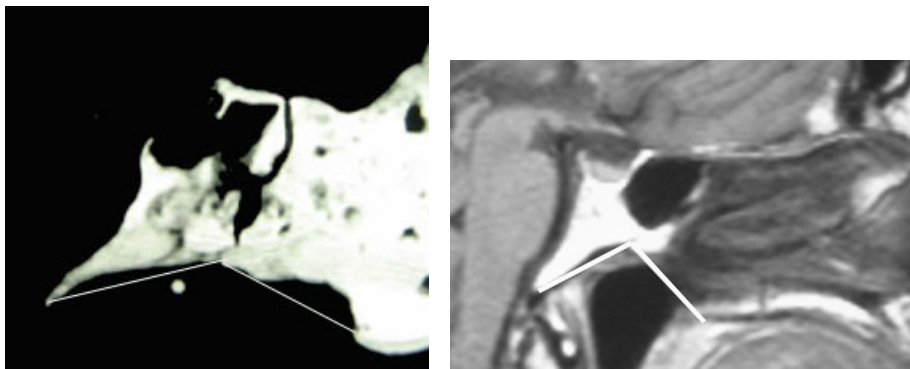

Figure 2: Midsagittal scan and IRM of the basi-spheno-ethmoïdal complex : Sterkfontein 5 (left) and *Homo sapiens* (right) The lines and the angle visualize the exocranial straightening of the clivus and the repositioning of the palate below the anterior cranial fossa.

Embryonic origin of the posterior cranial fossa position and facial straightening

Many scholars have searched for the origins of the straightened clivus that characterizes the hominid lineage (i.e. the spheno-occipital flexure), making reference to the winding of the telencephalon and the cerebellum, more important than in any other primates. Thanks to the new medical imaging techniques and 3D reconstructions, Jeffery (2002), Jeffery and Spoor (2002, 2004) could study a series of human foetuses from the end of the embryonic stage until birth. The encephalon winding (cerebral hemispheres and cerebellum) follows an irregular pace, while the sphenoidal angle fluctuates without correlation. Authors conclude to the lack of physiological links between the flexion and the rolling up of the brain, putting in mind that the flexion marks the end of the embryonic period.

Orthodontists dealt with this issue in order to better correct the children malpositions of the two dental arches and the deficiencies in transversal growth. This medical field focuses on the flexion mechanisms located at the spheno-occipital synchondrosis, and bases the treatments on the morphogenic principles seen above. The success of extraoral forces reveal that during the growth, the midfacial morphogenesis is under the influence of the three dimensional dynamics of the spheno-occipital flexion and of the frontalization of the two petrous pyramids (fig.3). Correlations exist between the posterior cranial fossa and some angles of maxillae and mandible (like the symphyseal angle).

Our research works show that these relationships start very early in embryogenesis, between the 7th and 8th week (Dambricourt Malassé 1987, 1988, 1993, 2005, 2006a). On the 6th week the cartilaginous base of the skull, that is to say the chondrocranium or *planum basale*, is flat, formed with the basi-occipital, the postsphenoïd and the presphenoïd aligned but separated by the spheno-occipital and the interspheноïdal synchondrosis (fig.4,5). This organization is the ancestral mammal condition, that of all fossil species, Australopithecine, Homo or any Dryopithecine.

Right from the beginning of the 20th century, anatomists like Levi (1900) very accurately described the development stages of the human basi-cranium, while other naturalists compared primates such as Cercopithecus, Tarsier or other mammals. The most detailed description is Levi's, illustrated with high-quality drawings which had no equivalent until the recent perfecting of Magnetic Resonance Microscopy (MRM, fig. 4). From the 7th week, the sphenoid body rotates on its axis, followed shortly by a basi-occipital straightening. This dynamics causes the vertical dimension of the skull and the vertical orientation of the facial growth vectors (fig.5).
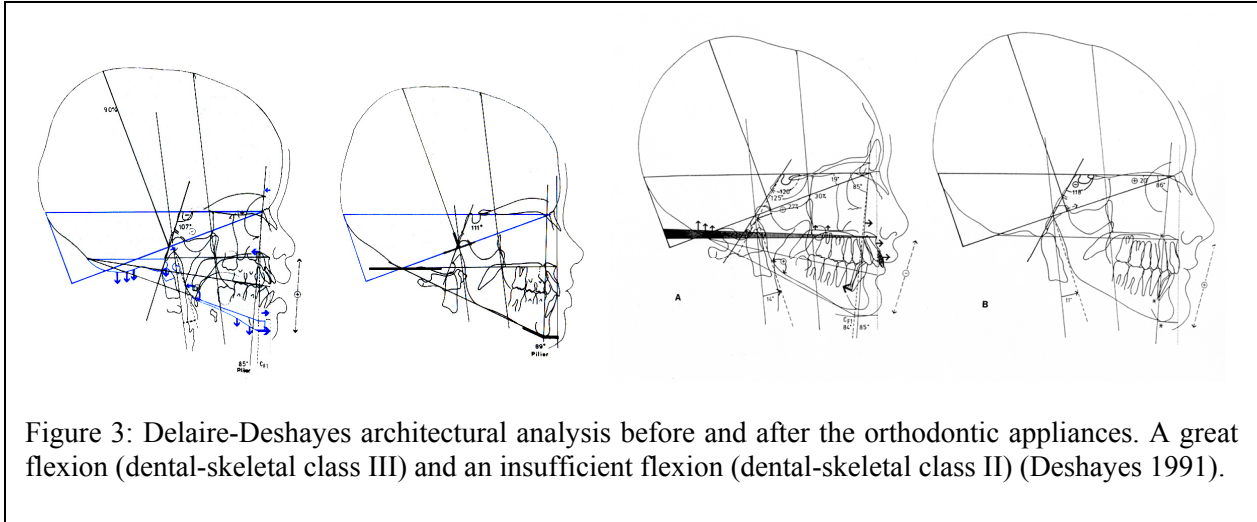
Figure 3: Delaire-Deshayes architectural analysis before and after the orthodontic appliances. A great flexion (dental-skeletal class III) and an insufficient flexion (dental-skeletal class II) (Deshayes 1991).
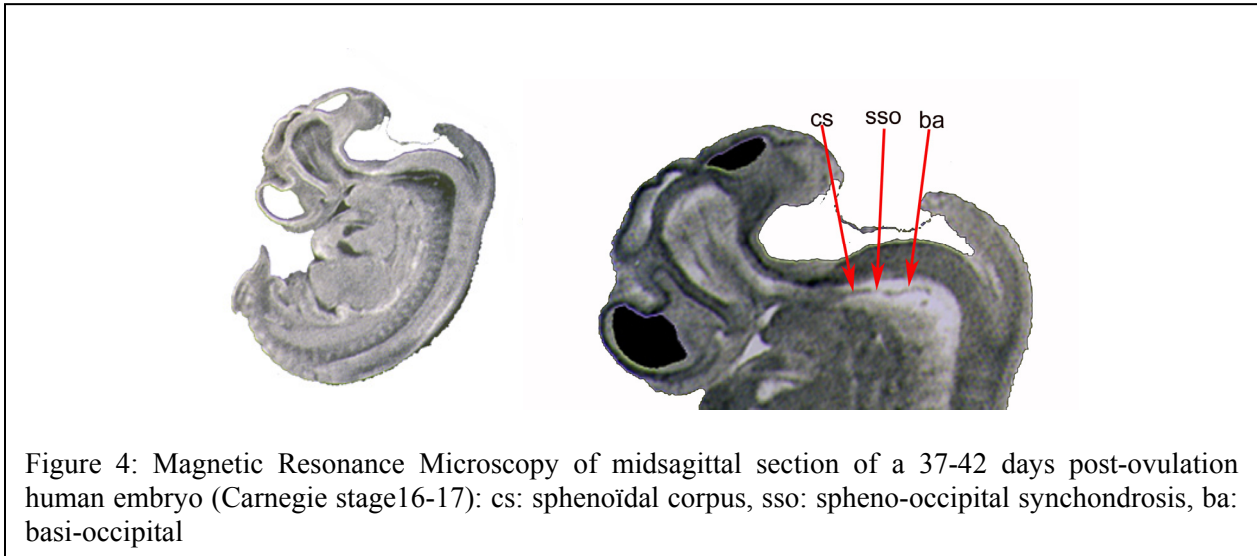

Figure 4: Magnetic Resonance Microscopy of midsagittal section of a 37-42 days post-ovulation human embryo (Carnegie stage16-17): cs: sphenoïdal corpus, sso: spheno-occipital synchondrosis, ba: basi-occipital
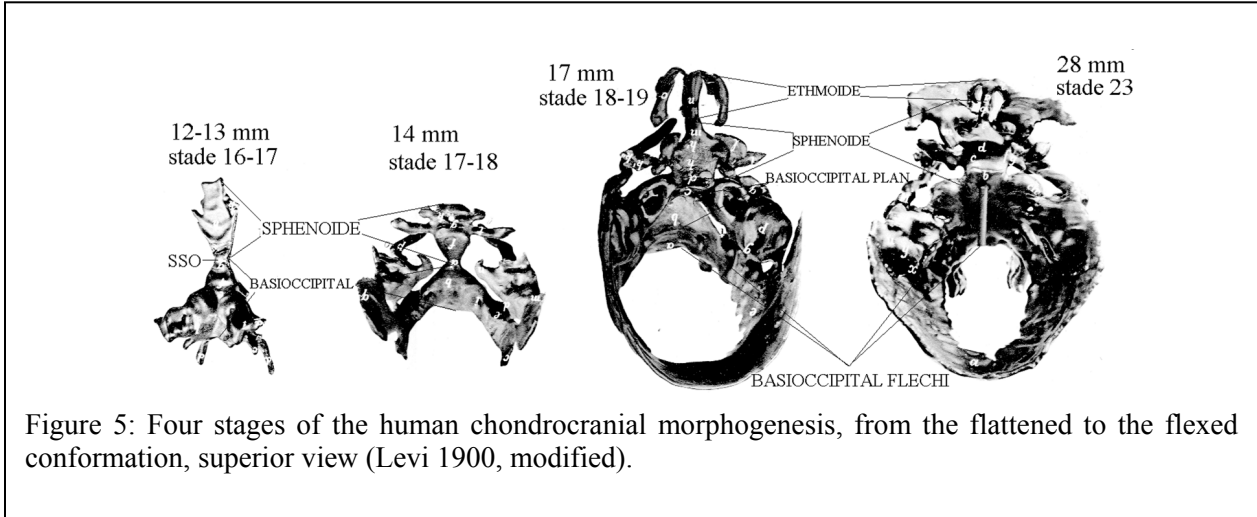

Figure 5: Four stages of the human chondrocranial morphogenesis, from the flattened to the flexed conformation, superior view (Levi 1900, modified).

However, any cephalic details illustrate the morphological stages. In order to understand the cause of the spheno-occipital rotation, one must compare the whole of cephalic tissues without isolating them from the cephalo-caudal unit. Figure 6 synthesizes the result. Whatever the primate species, the future central nervous system, or neural plate, grows along the underlaying dorsal chord. By doing so, the plate invaginates to form the neural groove and progressively closes to give rise to the neural tube. Its cephalic end, formed by three vesicles (proselencephalon, mesencephalon, rhombencephalon), stretches in the anterior part of the chord, but instead of following a longitudinal direction, it begins to rotate antero-posteriorly centred on the end of the chord.
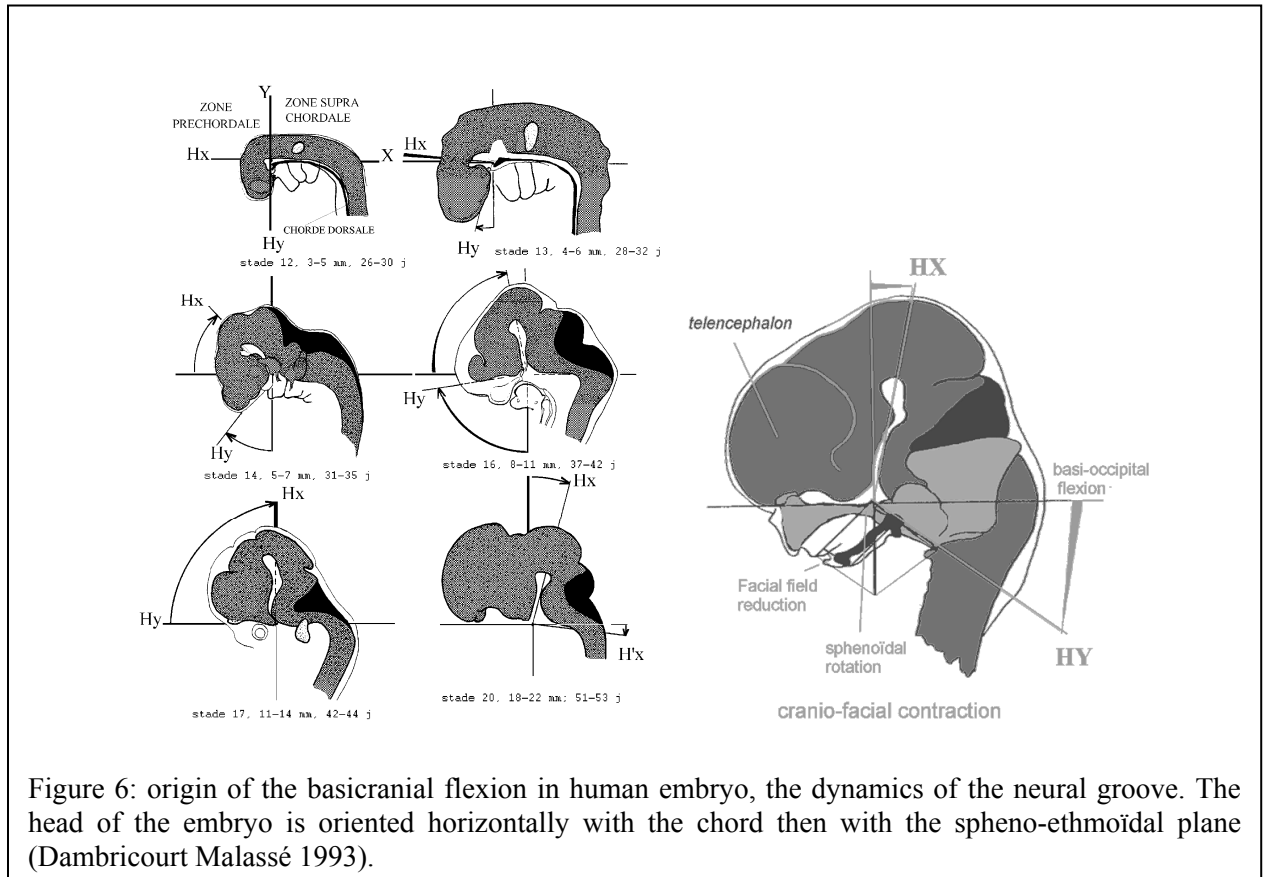
Figure 6: origin of the basicranial flexion in human embryo, the dynamics of the neural groove. The head of the embryo is oriented horizontally with the chord then with the spheno-ethmoïdal plane (Dambricourt Malassé 1993).

The neural vesicles follow a front to back motion, in relation with the kinetics of some neuroblastic cytoskeletal fibers. The differences between the species appear as soon as the rotation goes beyond the vertical line, going through this chordal apex. For instance, there are no possible confusions between Homo genus, Macaca and Pan. In fact, the divergences are those of the consensual Linnaean classification and phylogenetic distribution of extinct and living primates: Prosimian, monkeys, great apes, homininae and Homo (Martin and Pilbeam, The Cambridge Encyclopedia of Human Evolution, 1994).

The trajectories of Macaca and Homo for instance, are similar but the human rotation increases with simultaneous changes that occur in the underlaying sphenoidal synchondrosis, close to the apex of the chord. The basi-occipital, postshenoïd and presphenoïd are repositioned with a gain of verticality and a reduction of the antero-posterior length more important in Homo than in Macaca, where the three cranial fossae are less storied vertically, the mandibular cartilage longest and the *septum nasi* prognatic (fig. 7).
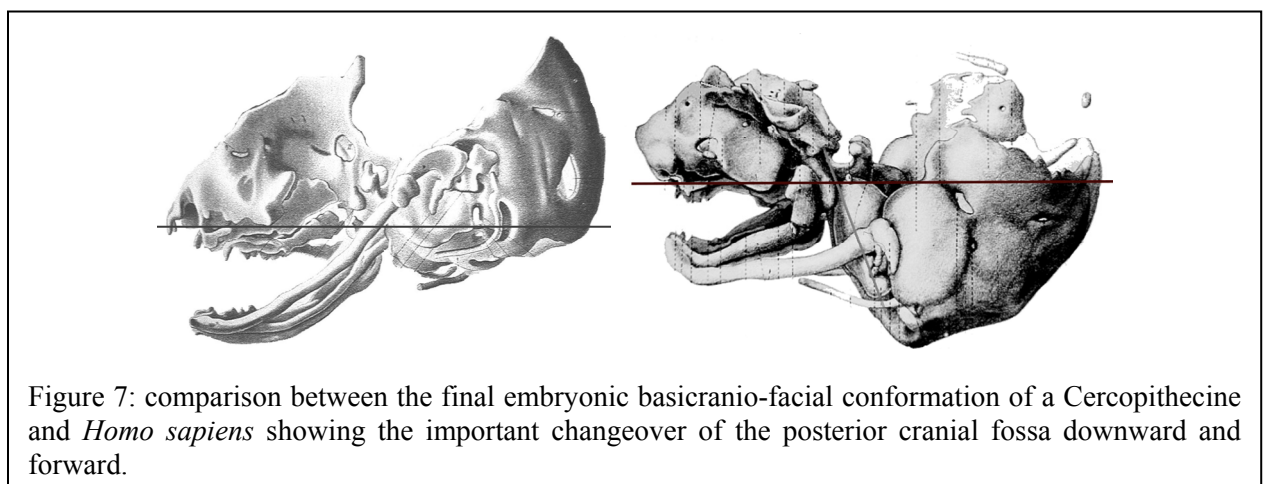

Figure 7: comparison between the final embryonic basicranio-facial conformation of a Cercopithecine and *Homo sapiens* showing the important changeover of the posterior cranial fossa downward and forward.

The differences in range mean that, right from the emergence of the neural plate, the neuroblastic tensional dynamics are different. Yet the straightening of the clival plane, the more downward and lowered position of the posterior cranial fossa, are dependant on this rotation, and not on the development of the most anterior vesicle, the telencephalon (future cerebral hemispheres).

The petrous pyramid do not exist at that stage, their counterparts are the two otic capsules located on each side of the basi-occipital. Their endocranial face connects them to it, while the exocranial is in connexion with to the cartilage of the first branchial arch; the Meckel's cartilaginous of the future mandible (figure 7). They therefore move downward and forward, inducing the repositioning of the mandibular cartilage, the temporo-mandibular joint (TMJ) and the straightening of the anterior part in the junction of the two right and left cartilaginous sticks. It straightens slightly in Macaca and very strongly in Homo, leaving a triangular space, the future ossified trigonum mentale that does not exist in any monkey nor great ape; only Australopithecines and Homo have it, in correlation with the low position of both basioccipital and TMJ. The facial tissues re-organize themselves according to the repositioning of the basal cartilaginous tissues, which confirms the clinical observations in infantile dento-maxillo-facial orthopaedics.

Phylogenetic origins of the posterior cranial fossa lower position and facial straightening in Australopithecines and Homo.

All the extant primate species shared this dynamics, but the cranial bases differ in the range of their sphenoidal rotation. Non-primate mammals like Chiropters (bats) for example, have barely flexed cartilaginous base, the rotation of the three vesicles does not go further than the vertical line passing through the end of the chord. Later, during the fetal period, the cerebellum, pons and medulla (rhombencephalon), the tectum and tegmentum (mesencephalon), the cerebral hemispheres and the cerebellum (telencephalon), are lying on a flat base; the foramen magnum is not visible in inferior vie,. It cannot be seen either in fossil species like Plesiadapiforms.

When the medial sagittal section of the skull shows a long base and face, as in the oldest or extant prosimians (Adapiform, Lemuriform, Lorisiform), the mandibular body is low and the dental arches narrow. With fossil monkeys such as the Aegyptopithecus, the winding neural tube exceeded that of any prosimian species, fixing that of the oldest simiiforms: none of the Platyrrhine, Cercopithecidae or Hylobatidae has gone beyond the limit. It is no longer the case in extant Ponginae and Paninae, their sphenoidal flexion is clearly greater than that of a monkey; their mandibles, which illustrate this flexion, have the same conformation, whatever the ontogenetic stage (Dambricourt Malassé 1987).

Unfortunately there is no complete base of Proconsulidae, Dryopithecinae, neither Ramapithecinae nor Sivapithecinae, while the endocranial profile of *Sahelanthropus tchadensis* is still published. Nevertheless by comparing the numerous mandibles of fossil species (Dryopithecinae, Ramapithecinae, Proconsulidae), with the corresponding values from Ponginae and Paninae, it is possible to conclude that their posterior cranial fossae had the same growth vectors, a greater lowering than that of any monkey's fossil. The emergence of this embryonic flexion, yet observed within the living great apes, could therefore be dated around 20 millions years ago (*Proconsul africanus*) (fig. 8). However, by comparing external reconstructed profile of *Sahelanthropus tchadensis* (fig.9), the growth pathway of the occipital (membranous squama, cartilaginous basi-occipital) did not differ from that of Ponginae-Paninae pattern, the profile is that of their juvenile stages (Dambricourt Malassé 2004a, 2006a). Even the occlusion with the canine lock (the crown longest than premolar's), is in conformity with this juvenile conformation of the base. As known in occluso-posturology, this is not the size that is significant, but the type of occlusion. In the opposite, on Australopithecine and Homo, the inion is below the Frankfurt plane. The embryonic development of this fossil never exceeded the limits already common to Ponginae-Paninae pattern. The shape of the isolated mandibles can confirm this. Our occluso-postural and organogenetic analysis reaches to the same conclusion than Wolpoff, Pickford, Senut and Hawks (2002), adding an ontogenetic interpretation in the sense of heterochronies (Dambricourt Malassé 2006b).
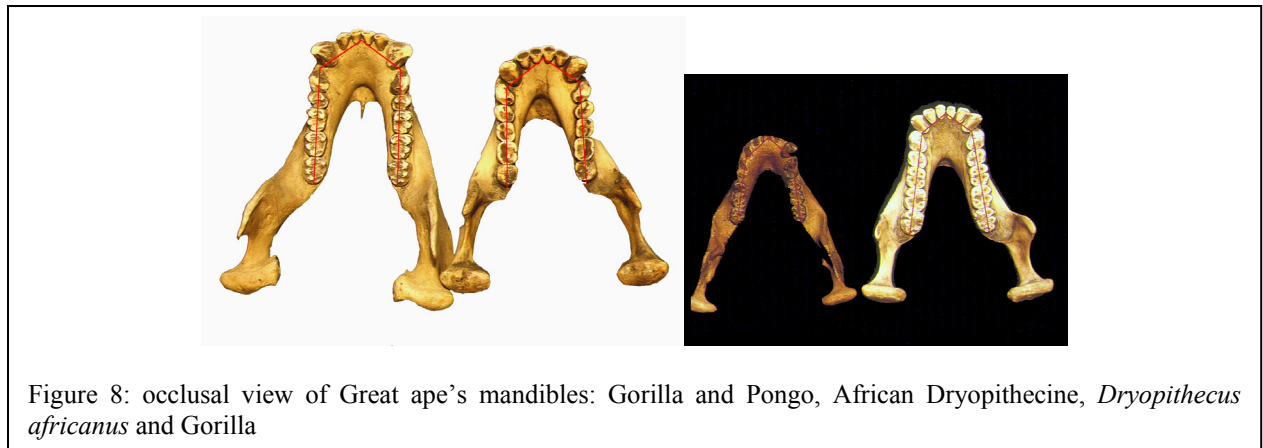
Figure 8: occlusal view of Great ape's mandibles: Gorilla and Pongo, African Dryopithecine, *Dryopithecus africanus* and Gorilla
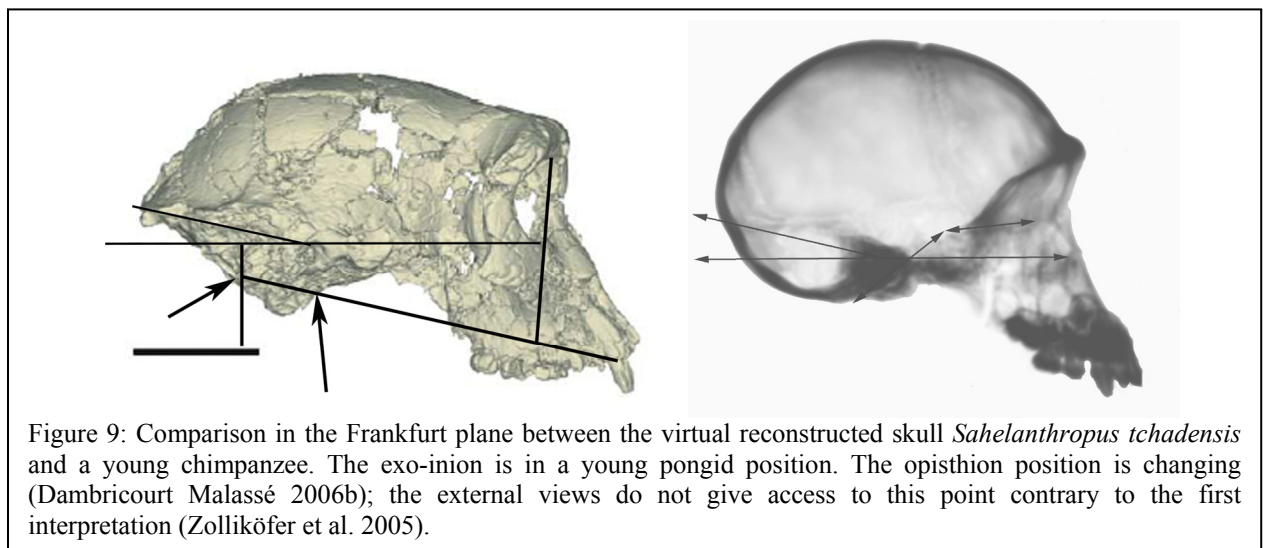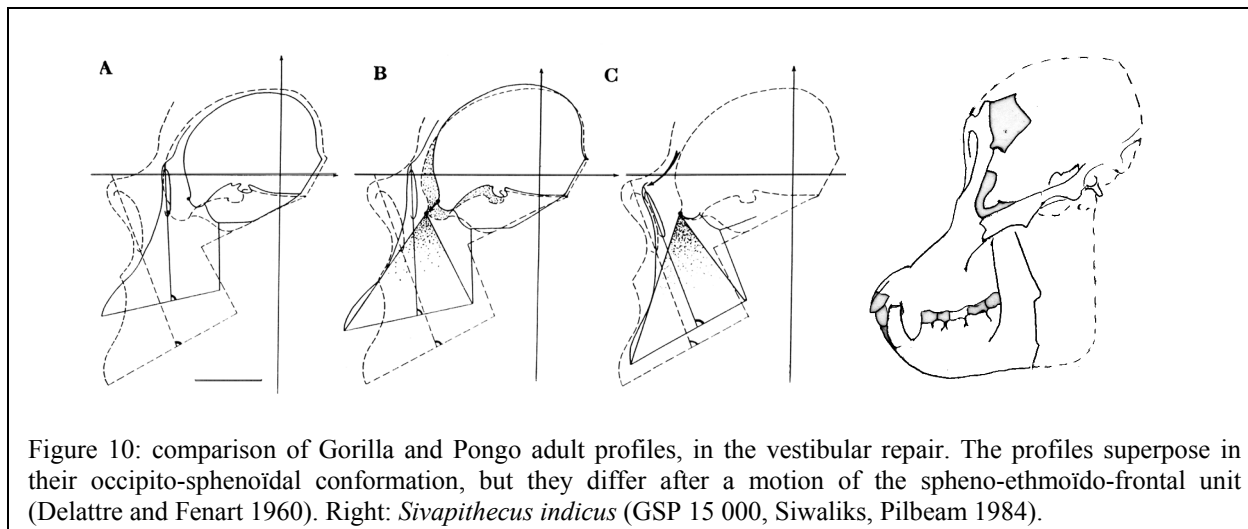

Figure 9: Comparison in the Frankfurt plane between the virtual reconstructed skull *Sahelanthropus tchadensis* and a young chimpanzee. The exo-inion is in a young pongid position. The opisthion position is changing (Dambricourt Malassé 2006b); the external views do not give access to this point contrary to the first interpretation (Zolliköfer et al. 2005).

The lower and upper faces are known with European, African, and Asian species (*Ouranopithecus macedoniensis* and *Greacopithecus freybergi* (Greece), *Proconsul africanus* (Kenya), *Sivapithecus indicus* (India), *Rudapithecus hungaricus* (*Dryopithecus brancoi*, Hongrie) *Pierolapithecus catalaunicus, Dryopithecus laietanus* and *Dryopithecus major* (Spain). They show no contradiction with the morphogenetic data from the three living great apes. On the contrary, there are homologies in the variability of the intersphenoidal synchondrosis activity. In *Pongo pygmeus* the intersphenoidal synchondrosis fuses at birth while it remains active in Paninae. This stabilisation causes a change in the growth trajectories of the spheno-ethmoido-frontal complex that topples upward and backward (Deshayes 1991). Those differences cannot be seen with mandibles (fig. 8), but they can be observed on the upper face with the absence of frontal sinus and a pteriac suture that comes in contact with the sphenoid greater wing and the parietal bone, whereas that of the Paninae comes in contact with the frontal and temporal bones. Miocene Asian species, *Sivapithecus indicus* already established those circumnatal differences (fig. 10).

The human pteriac sutures are the same than in Pongo. Yet, in the oldest human species the lack of newborn does not enable to know the ontogenetic modalities of this synchondrosis, but the angular opening between the lateral and posterior semi-circular canals indicates a complete change in the neural tube dynamics, corroborated by the downward and forward expansion of the posterior cranial fossa. In other hand, in modern *Homo sapiens,* the intersphenoidal synchondrosis undergoes complete closure by 3 months of age. This was very probable acquired with the first human species. Now a question is to know if such ontogenetic changes are only convergences between Asian fossils and Homo, or a genetic inheritance.

Figure 10: comparison of Gorilla and Pongo adult profiles, in the vestibular repair. The profiles superpose in their occipito-sphenoïdal conformation, but they differ after a motion of the spheno-ethmoïdo-frontal unit (Delattre and Fenart 1960). Right: *Sivapithecus indicus* (GSP 15 000, Siwaliks, Pilbeam 1984).

In first conclusion, an increase of the "rolling-up" kinetics in the range above the dorsal chord can explained why adult primate shows a flexed base in association with a facial shortening and a transversal enlargement compared to other species. The prolonged winding dynamics of the neural tissue goes with a fetal and post-natal encephalization such as the myelinization, particularly prolonged in *Homo sapiens* corresponding to the most recent evolutionary stasis.

The upright position of the Australopithecine and Homo species result of new tensional dynamics specific of the neural tube with their consequences on the sphenoidal rotation. Thus, unlike the common idea, ontogenetic encephalization was neither the prime mover of hominization nor the physical cause of the posterior cranial fossa repositioning. All the cranio-sacral organogenesis evolved and at the stage of hominids, the amplification of the three vesicles dynamics was sufficient to generate a vertical positioning of the basicranium. This is concomitant with axial skeleton remodelling.

This distinction between organogenesis and fetal growth enables to understand why Jeffery *et al.* did not find correlations between fetal telencephalization and the basal angle and then why there are difficulties to distinguish between an evolved *Homo erectus* and an early *Homo sapiens*. This is a matter of chronological distinctions, not from a gradual phylogenetic point of view, but from an understanding of the mode and tempo of ontogenetic evolutionary process.

The endocranial and facial closeness between species of Australopithecines and the oldest human species, reflects that of the mutations affecting the embryogenesis common to Ponginae, Paninae and to their ancestors. This is a first rate observation, for it means that the type of mutations may have occurred in African Dryopithecines as in Asian Ramapithecines

The second observation is the consensual phylogenesis showing an increasing contraction of the chondrocranium since 55 million years, occurring with long stasis punctuated by new embryonic patterns, moving the three cranial fossae upward with a shortening of the basi-cranio-facial complex. This evolution follows the punctuated equilibrium theory as defined by Gould and Eldredge: very long periods of stasis followed by anatomical discontinuities. Macro-evolutionary process and anatomical discontinuity are not in contradiction; 1) discontinuity is a natural process well observed in development genetics (Montandon *et al.* 2008) and 2) the transmission of a type of mutations with constant effects can explain the evolutionary continuity with integration of previous mutations. The emergence of a more complex central nervous system is necessary for the posture control (Dambricourt Malassé 1993, 2004, 2006a, Dambricourt Malassé *et al.* 1998, Chaline 1999, Chaline *et al.* 1996, 1999, 2000). The high degree of integration between the social tissues and the environment characterizes the Primates; ecological crises offer greater chances for these new organisms to survive, because of the reflexive abilities, which increase. Those parameters including palaeo-embryogenetic data enable to reconsider the relationships between Australopithecines and Homo.

Ecological conditions of phylogenetic convergences

Many palaeontologists, among whom P.V. Tobias (1999) gave up the savannah paradigm which prevailed to the emergence of Australopithecines. The reason is the discovery in South Africa, of the Australopithecine Stw573 skeleton dated of 3.3 millions years. The animal died in a wooded environment and its anatomy was adapted to arboricolism (Clarke, 1999). It is therefore no longer surprising, as soon as one understands the embryonic origin of the erected postures. The two Australopithecine and Human embryogeneses might have therefore emerged separately in the same ecological conditions, the tropical habitats of the Afro-Eurasia supercontinent, recorded in deposits that extended now from Spain to Southeast Asia.

A global warming took place from 5 Myrs ago with the drying up of the Mediterranean sea, the European great anthropoids became extinct (Spain, France, Greece, Hungary), in Africa *Ardipithecus kadabba* (5,5 Myrs) survived in wooded conditions (teeth of *Ardipithecus ramidus,* Aramis 4,4 Myrs) whereas some populations engendered the first Australopithecines (isolated fragmented base, Aramis 4,4 Myrs). They may have formed a monophyletic group with the extinct Paranthropus. In Asia, *Sivapithecus indicus, Sivapithecus sivalensis, Sivapithecus parvada, Ramapithecus punjabicus, Indopithecus (Gigantopithecus bilaspurensis)* which lived in sub-Himalayas disappeared during the late Miocene (Patnaik *et al.* 2005, Pillans *et al.* 2005)*,* as the Chinese *Lufengpithecus lufengensis* and Ramapithecines *(*Rukang and Oxnard 1983, Gaur 1987, Zhao and Zhang 2008), whereas *Gigantopithecus blacki* survived until the Pleistocene. Other species in Thaïland engendered Pongo (Chaimanee, Y. *et al.* 2003). However, where the oldest Homo species emerged 3 millions years ago? On the geological scale, the both erected postures nearly occurred at the same time. The main question remains to know why these convergent genetic mutations – dependant on the same past mutations – occurred 15 millions years after the great ape pattern (Chaline *et al.* 1999). Palaeontology cannot solve this evolutionary process, but it is possible to take into account the palaeo-environnemental circumstances favourable for parturition and longer learning phases. There is no reason for them to be different from the ones of the great anthropoids. This can be a clue to look for the oldest human species within the Pliocene layers, known for holding a wide variety of great anthropoid species. Reconsidering the ancient human ascendance rooted in pliocene Asian habitats, seems as interesting as prospecting in the East-African deposits.

Distinction between a *Homo erectus* sensu largo and a *Homo sapiens*: the posterior cranial fossa conformation before the dermal bones of the vault

It is therefore necessary to make the difference, on an adult skull, between the basicraniofacial conformation, established during embryogenesis, and the neurocranium, differentiated with the cerebral hemispheres whatever their shape, volume and dimensions. The boundary between the territories formed in accordance with the embryonic "rolling-up" and those induced by fetal brain development, is complex to delimitate in external view, probably the pteriac and asteriac sutures mark those limits. However, more details are necessary on the endocranial side of the bones in the clivo-petrous limits and temporo-exo-occipital sutures. Such investigation needs well preserved skulls and CT scan explorations.

One of the best cases that give strong support for this deduction is the fossilized skull of *Homo floresiensis* in Southeast Asia. The sagittal section is sufficient to deduce that this skeleton belongs to a late subspecies of *Homo erectus*: no chin, high position of the posterior cranial fossa, lesser rolling up of the cerebellum and of the occipital lobe. The bones of the wrist confirmed those embryonic and fetal conformations as the comparison of the scapular girdle (Broom *et al.* 2006, Tocheri *et al.* 2007, Larson *et al.* 2007).

In the middle Pleistocene, any human fossil shows a development of the neocortex, visible with greater high of the temporal and parietal squama. However, this encephalization occurred without the downward and forward remodelling of the posterior cerebral fossa, in a highest position than in *Homo sapiens* (fig. 11). The neuroblastic tensions of the neural plate did not evolved, the embryonic pattern is the one shared by the oldest species and remained unchanged.
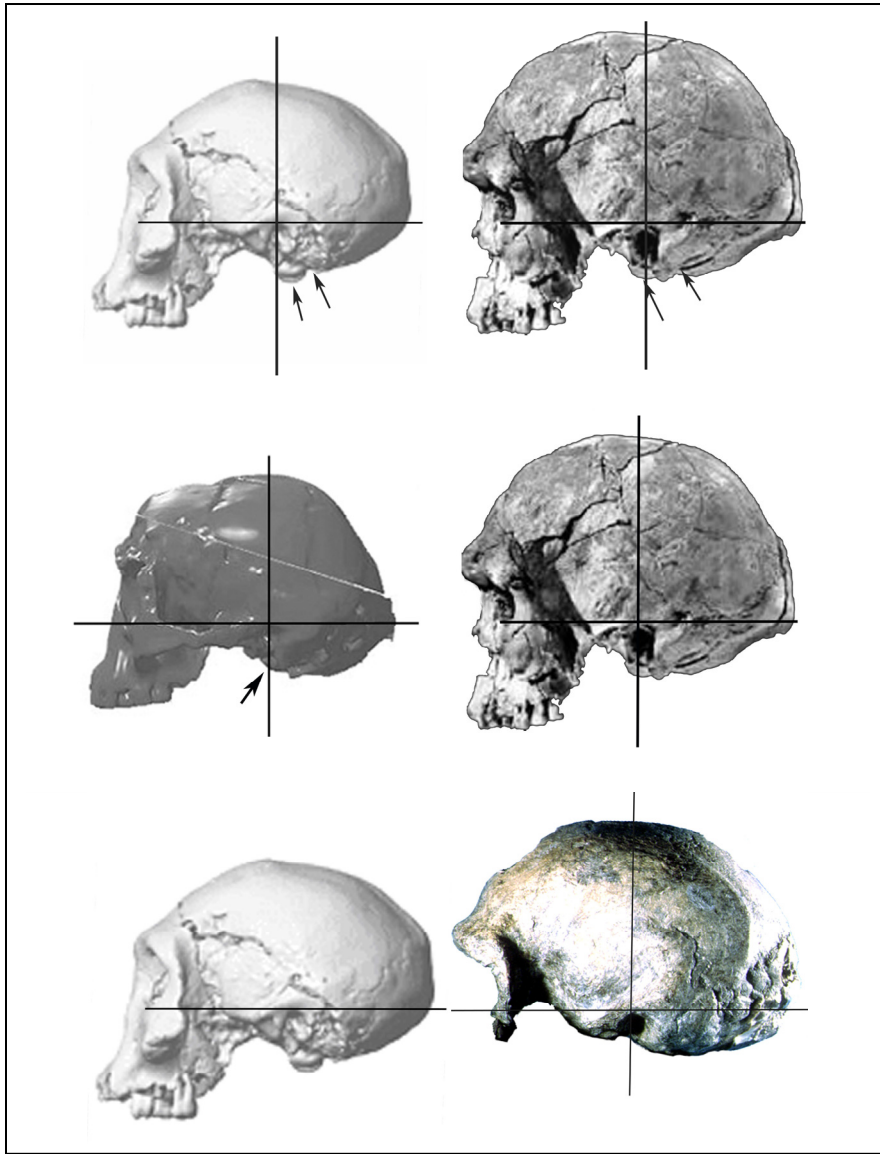
Figure 11: *Homo georgicus* D 2700 and Herto-*Homo sapiens* with the forward position of the occipital condyle, the lowering of the posterior cranial fossa relatiouely to the condyle, the closure of the external flexion and the motion of the alveolo-dental arch. Middle: *Homo floresiensis* and Herto-Homo sapiens. Low: *Homo georgicus and* Hathnora (Dmanissi: in Mafart B. 2004, Flores: in Falk et al. 2005, Herto: in White et al. 2003, Hathnora: Institut de Paléontologie Humaine)

In Europe, the encephalization increased during upper Pleistocene with the Neanderthal lineage, but the posterior cranial fossa stayed as high as in *Homo ergaster* with a specific evolutionary trend. The occipito-spheno-ethmoidal complex was expanding, like shown by 1) the formation of a third malar sinus (Heim 1989), 2) the overall pneumatization of the frontal sinuses with continuous supra-orbital ridge between the two arcades, 3) the retro-molar space between the anterior border of the mandibular ascending ramus and the last dental alveole, since youngest ontogenetic stage, 4) a lateral semicircular canal less lowered than in the oldest species (Hublin *et al*. 1996). In Asia, the lower Pleistocene fossils like Sangiran 17 (*Homo erectus*) also fluctuate toward extension (Dambricourt Malassé 2002) although they were less cephalized than the late Neanderthals. The neocorticalisation is a polycentric and gradual evolutionary trend, independent of the basicranial dynamics that lead its own evolutionary parameters, without never gone beyond the limit of the oldest species.

There are no *Homo sapiens* before 160 kyr, the oldest skulls come from Africa with Herto and in Near East with Kafzeh (95 kyr), the posterior cranial fossa is clearly in a more forward and downward position and the frontal cephalic curvature is more expressed, but it follows, chronologically, the new sphenoidal rotation. The tensional dynamics of the neural plate must have evolved under the influences of the previous genetic mutations effects of which amplifie the increasing complexity of neocorticalisation and vascularization. Therefore, the basicraniofacial complex evolved with a decreasing longitudinal growth of

the face, the two dental arches still in « end to end» occlusion and the exocranial features still robust, but the chin is clearly saillant. With Neolithic skulls, the occlusion changes again, with an alveolo-dental mandibular retrognathie and a general gracilization of the exocranial table.

The encephalization was gradual but this trend did not lead gradually to *Homo sapiens*, this neo-corticalisation should not to be confused with the transition to *Homo sapiens*, which is a punctuated equilibrium. In this respect, the Narmada skull alternately interpreted as a *Homo erectus* or *Homo sapiens* (Lumley and Soniakia 1985, Kennedy et al. 1991, Sonakia and Biswas, 1998), is not sapiens (fig. 11). Since all the populations evolved with the neocorticalisation, how to distinguish, among non-sapiens populations, those that were the ancestors of the oldest *Homo sapiens*? Did the late forms of Asian *Homo erectus* contribute to the emergence of *Homo sapiens*? Discrete traits enable to observe phyletic continuity. Among the significant exocranial features for a plausible lineage between *Homo sapiens* and Asian *Homo erectus* (Pope 1992), one can mention the shovel-shaped incisors, the presence of three roots on the first inferior molar, and the bony exocranial superstructures such as the supramastoïd crest and the torus angularis. This eminence is a thickening of the cortical bone next to the asteriac suture.

The frequency and geographical dispersion of the torus angularis is an interesting data as shown by the comparison of 50 well-preserved skulls or *os parietalis* from lower Pleistocene until the first "modern" *Homo sapiens* (Herto, Kafzeh, Omo Kibish 1). In Europe and Near East (n=21), the torus angularis is already present in Dmanissi on one skull, then on 4 late lower Pleistocene skulls (Ceprano, Tautavel, Castel di Guido, Reilingen), but it is never visible on middle Pleistocene and Neanderthals skulls including the Near Eastern fossils (n= 17). On African skulls (11 adults, 1 sub-adult) it is never visible (OH 9 has a pseudo-torus), one exception is the late middle Pleistocene skull of Kabwe (ca 200 ky). On the opposite on Asian *Homo erectus* (13 skulls), there is a highest frequency (n=9): in India with Hathnora, in China with Dali, Sinanthropus III and X, in Indonesia with Ngawi and Sangiran 17, then Ngandong 1, 5 and 6 (upper Pleistocene). The Kabwe skull shows a significant encephalisation, but it keeps the *Homo erectus* basicranial pattern, this is also the only known African fossil with a torus angularis that may attest to genetic flows, or migrations, from India. The torus angularis lack on the oldest African *Homo sapiens* (Herto, Omo Kisbish 1) and the Near-East Kafzeh. However, we could observe a well-developed torus angularis on an Indian Neolithic skull from Tekka Lakota (Karnataka).

Its presence on *Homo sapiens* skull is therefore independent from the lowering of the posterior cranial fossa. Taking into account its phylogenetic frequency, only the more recent Asian *Homo erectus* could transmit this discrete character. If *Homo sapiens* emerged only in Africa, the hypothesis of interbreeding between Asian *Homo erectus* and African *Homo sapiens* is very unlikely for two reasons; the first comes from the punctuated mutations we observe now, with the type of genes coding for cephalocaudal embryogenesis. This is not any more the same genetic program. The second because Asian *Homo erectus* have derived from the oldest human species at least since 2 millions years without embryonic change; the genetic barrier with extreme East populations should be established long time ago. It is therefore undeniable that Neolithic Indians from Tekka Lakota were remote descendants of Indian *Homo erectus* such as Hathnora. The embryonic approach of human origins gives strong support to this hypothesis (Sankhyan and Rao, 2007).

If, in the coming years, discoveries will confirm the Asian ape roots of the human lineage, it will be necessary to solve the origins of the oldest *Homo sapiens* of East Africa and the Near East. One hypothesis is that genetic flows occurred in the Middle Pleistocene, within *Homo erectus* populations living between the Indus delta and the shores East Africa; Kabwe supports this model. In fine, the origin of *Homo sapiens* could have been more like a kind of « fertile crescent » spreading through the eastern shores of the Arabian Peninsula**,** as well as through the great migration paths that are the major river valleys like the Indus and its tributaries, the Tiber, the Euphrate and the Nile.

References

ALLCHIN B. 1995. Early Human occupation in the Northern Punjab, Pakistan: an overview of the Potwar Project of the British Archaeological Mission to Pakistan (1981 - 1991). In Wadia, S., Korisettar R. and Kale V. S. (Eds.) Quaternary Environments and Geoarchaeology of India. Bangalore: Geological Society of India, 150-167.

BJORK, A. SKEILLER V. 1984 La croissance du maxillaire dans les trois dimensions, comme le révèle radiographiquement la méthode des implants, *Revue d'Ortho.Dento-Maxillo-Faciale*. 18, 11 : 281-298.

BLACKWELL B.A.B, FEVRIER S., BLICKSTEIN J.I.B, PADDAYYA K., PETRAGLIA M, JHALDIYAL R., SKINNER A.R..2001 ESR dating of an Acheulean quarry site at Isampur, India, Indian *Journal of Human Evolution*, 40: A3.

BOËDA E. 2005 Paléotechnologie ou anthropologie des techniques ? Arob@se, Ed. Université de Rouen, vol.1, pp : 46-64.

BONNIER L. 1997 La modification de l´occlusion a-t-elle une répercussion immédiate sur le système postural fin? In Lacour M., Gagey P.M., Weber B. (Eds) *Posture et Environnement*. Sauramps: 77-86.

CARO P. 2004 Développement embryonnaire et évolution. Entretien avec Anne Dambricourt Malassé. *La Lettre de l'Académie des Sciences*, Paléontologie, 13 : 14-15.

CHAIMANEE Y, JOLLY D, BENAMMI M, TAFFOREAU P, DUZER D, MOUSSA I, JAEGER JJ 2003 A Middle Miocene hominoid from Thailand and orang-utan origins. *Nature* 422:61–65.

CHALINE J. 1999 Origines de l'homme *Encyclopaedia Universalis*, Ed. Albin Michel.

CHALINE J., DURAND A., MARCHAND D., DAMBRICOURT MALASSÉ A., DESHAYES M.J. 1996 Chromosomes and the Origins of Apes and Australopithecines, *Human Evolution*, 11, 43-60.

CHALINE J., DAMBRICOURT MALASSÉ A., DID, B., MAGNIEZ-JANNIN, F., MARCHAND D., COURANT F. MILLET J.J. 1999. Quantification de l'évolution morphologique du crâne des hominidés et hétérochronies. *Comptes Rendus de l'Académie des Sciences de la Terre et des Planètes*, 326 : 291-298.

CHALINE J., DURAND A., DAMBRICOURT MALASSÉ A. DAVID B., MAGNEZ-JANNIN F., MARCHAND D. 2000.Were climatic changes a driving force in hominid evolution? In: Climates: Past and Present. M.B. Hart (Ed.). *Geological Society*, London, Special Publication, 181: 185-198.

CLARKE, R.J. 1999 Discovery of complete arm and hand of the 3.3 million-years old Australopithecus skeleton from Sterkfontein. *South African Journal of Science*, 95, 477-480.

DAMBRICOURT MALASSÉ A 1987 Ontogenèses, Paléontologenèses et Phylogenèse du corps mandibulaire catarhinien. Ph. D. National Museum of Natural History, Paris.

DAMBRICOURT MALASSÉ A 1988 Hominisation et Foetalisation, *Comptes Rendus de l'Académie des Sciences*, 307, II : 199-204.

DAMBRICOURT MALASSÉ A. 1993 Continuity and discontinuity during modalities of hominization. In: "Modes and Tempos in Evolution in the Quaternary" *Quaternary International*, 19: 85-100.

DAMBRICOURT MALASSÉ A**.** 2002. Nouvelles approches de l'évolution crânienne des Homo erectus de Java. In : " *Origin of settlements and chronology of Palaeolithic cultures in Southeast Asia"* (in French). Eds F. Sémah, C. Falguères, D. Grimaud Hervé, A.M. Sémah, Artcom, Paris.: 377-396**.**

DAMBRICOURT MALASSÉ A. 2005 Un nouvel angle de la base pour une meilleure compréhension de la morphogenèse basi-crânienne des hominidés et des modalités évolutives. *Biométrie Humaine et Anthropologie*, 23 : 1-2.

DAMBRICOURT MALASSÉ A. 2006a. Evolution du chondrocrâne et de la face des grands anthropoïdes miocènes jusqu'à Homo sapiens, continuités et discontinuités**.** *Paléovol* Proceedings of the French Academy of Sciences. Tome 5 : 109-117.

DAMBRICOURT MALASSÉ A. 2006b La question des origines de la lignée humaine : les modèles évolutionnistes confrontés aux fossiles, implications en orthopédie et posturologie. Centre d'Etude d'Ostéopathie, de Posturologie et Sciences Annexes (Eds). Actes du 4ème Symposium, Toulouse.

DAMBRICOURT MALASSÉ A. 2008. Le peuplement humain en Eurasie : la Haute Asie et les piémonts sous-himalayens du Plio-Pléistocène à l'Holocène, origines, évolution humaine et migrations. *L'Anthropologie,* Asie, vol. 111, n°3:

DAMBRICOURT MALASSÉ A, F. LALLOUET 2008 Etude au scanner des canaux semi-circulaires d'un crâne sec d'anencéphale dépourvu de flexion sphéno-occipitale ; implications pour l'interprétation

paléo-embryologique des hominidés fossiles. Abstract. XVè Colloque de la Société de Biométrie Humaine – novembre 2008, Muséum national d'Histoire naturelle, Paris.

DAMBRICOURT MALASSÉ, A. DESHAYES M.J. 1992 Modeling of the craniofacial architecture during ontogenesis and phylogenesis. A. Berthoz, P. P.Vidal, W. Graf (Eds), The Head-Neck Sensori-Motor System. New York-Oxford, Oxford University Pres: 37-46.

DAMBRICOURT MALASSÉ A., DESHAYES M.J., MAGNIES-JANNIN F. CHALINE, J., MARCHAND D. 1998. A solution to human paradox: fundamental ontogenies and heterochronies. *Human Evolution*, 14-4: 277-300.

DAMBRICOURT MALASSÉ A., MARTIN J.P., DE KERVILER E. 2000 Neural tube, spheno-occipital flexion and semi-circular canals in fossil and modern hominids. *Acta Anthropologica Sinica*, suppl. to Vol. 19: 82-89.

DEAN M.C., 1986 Homo and Paranthropus similarities in the cranial base and developing dentition, in : B. Wood, L. Martin, P. Andrews (Ed) Major topics in primate and human evolution. Camb.. Univ. Press () 249-265.

DEAN M.C., WOOD B.A. 1981 Metrical analysis of the basicranium of extant hominoïds and Australopithecus, *Am. J. Phys. Anthropol.* 59, 53-71.

DELATTRE A., FENART R. 1960 L'hominisation du crâne étudiée par la méthode vestibulaire, Ed. CNRS, Paris.

DELOISON Y. 2004 La Préhistoire du piéton, Plon.

DESHAYES M.J. 1991 Reconsideration of craniofacial growth during development and evolution. Orthodontic consequences *Rev Orthop Dento Faciale.* 25(3):353-65.

DESHAYES M.J. 2006a Cranial asymmetries and their dento-facial and occlusal effects, *Orthod Fr.* 77(1):87-99.

DESHAYES M.J. 2006b Growth of the skull and bony kinetics interfering with facial morphogenesis. Conceptual bases of success in orthopaedic treatments before the age of 6 *Orthod Fr.* 77(1):63-78.

DESHAYES M.J., DAMBRICOURT MALASSÉ A. 1990, Analysis of various craniofacial architectural types using the ontogenic approach of humanization. *Rev Stomatol Chir Maxillofac.* 91(4):249-258.

DESHAYES MJ, M. DESVIGNES, B. ROMANIUK, J. ROBIALLE, M. REVENU, DESHAYES B. 2002 Cranial analysis for early treatment and the biodynamic concept of cranio-facial morphogenesis. *Orthod Fr.* 73(4):395-406.

FALK, D.; HILDEBOLT, C.; SMITH, K.; MORWOOD, M.J.; SUTIKNA, T.; BROWN, P.; JATMIKO, SAPTOMO W.E.; BRUNSDEN, B., F. PRIOR. 2005 The brain of LB1, *Homo floresiensis*. *Science* 308:242-245.

GAILLARD CL, DAMBRICOURT MALASSÉ A, MAGRANER, J. MAITREROBERT A., VOISIN J.L. NASIR A. 2002. Discovery of recent lithic industries with archaïc features in the Hindu Kush range (Chitral district, North Pakistan). *Bulletin of the Indo-Pacific Prehistory Association*, vol. 6: 25-33.

GAILLARD CL, DAMBRICOURT MALASSÉ A. 2002 Early human occupations in the western Himalaya and border regions. Extended Abstract of the International Conference on Quaternary Climate, Tectonics and Environment of the Himalaya, Kuman University, Nainital, India: 78.

GAILLARD CL. DAMBRICOURT MALASSÉ A. 2008 Les principales étapes de l'occupation humaine en bordure de l'Himalaya occidentale, *L'Anthropologie*, Asie, vol. 111, n°3.

GAUR R. 1987 Environment and Ecology of Early Man in Northwest India, B.R. Publishing Corporation, New Delhi.

HEIM J.-L 1989 Une nouvelle reconstitution du crâne néandertalien de la Chapelle aux Saints. *Comptes Rendus de l'Académie des Sciences*, Paris, t. 308, série II n°6, 1187-1192.

HUANG W., ZHANG P. 2007 Les plus anciennes occupations humaines en Chine, *L'Anthropologie*, 111, 2: 166-181.

HUBLIN J.J. SPOOR F, BRAUN M, ZONNEVELD F, CONDEMI S. 1996 A late Neanderthal from Arcy-sur-Cure associated with Upper Palaeolithic artefacts. *Nature,* 381:224–226.

JEFFERY N. 2002 Differential regional brain growth and rotation of the prenatal human tentorium cerebelli, *J Anat.* 200, 135-44.

JEFFERY N., SPOOR F. 2002 Brain size and the human cranial base: a prenatal perspective, *Am J Phys Anthropol*, 118, 324-340.

JEFFERY N., SPOOR F. 2004 Prenatal growth and development of the modern human labyrinth, *J Phys Anthropol.* 123, 78-90.

KENNEDY, K. A. R., SONAKIA A., CHIMENT J., VERMA K. K. 1991 Is the Narmada hominid an Indian Homo erectus? *American Journal of Physical Anthropology*, 86:475-496.

LARSON, S G, W.L. JUNGERS, M.J. MORWOOD, T. SUTIKNA, E. SAPTOMO, E. R DUE, DJUBIANTONO, T. 2007 Homo floresiensis and the evolution of the Hominin shoulder. *J.H.E, 53,* 6:718-731.

LEVI G., 1900 Beitrag zum studium der Entwicke ung des knorpelingen primordial craniums des Menschens, *Arch. Mikros. Anat. Entwick.* 55, 341-414.

LORDKIPANIDZE D., VEKUA A., FERRING R., RIGHTMIRE G.P., ZOLLIKOFER C., PONCE DE LEON M., AGUSTI J., KILADZE G. MOUSKHELISHVILI A., NIORADZE M., TAPPEN M. 2006 A fourth hominin skull from Dmanisi, Georgia. The Anatomical Record Volume 288A, 11 : 1146 – 1157.

LUMLEY DE M.A, SONAKIA A. 1985 Premières découvertes d'un Homo erectus sur le continent indien à Hathnora, dans la moyenne vallée de la Narmada. *L'Anthropologie* (Paris), 89, 1 : 13-61.

LUMLEY DE M.A., GABOUNIA L., VEKUA A., LORDKIPANIDZE D. 2004 Les restes humains du Pliocène final et du début du Pléistocène inférieur de Dmanissi, Géorgie (1991-2000) I- Les crânes 2280, D 2282, D 2700, *L'Anthropologie*, 110 : 1-110.

B. MAFART, G. GUIPERT, M.-A. de LUMLEY, G. SUBSOL 2004 Three-dimensional computer imaging of hominid fossils: a new step in human evolution studies. *Canadian Association of Radiologist Journal* JACR 55(4): 264-270.

MARTIN R. D., D.R. PILBEAM 1994 The Cambridge Encyclopedia of Human Evolution. Ed S. Jones.

McCOLLUM M.A. Nasomaxillary remodeling and facial form in robust Australopithecus: a reassessment. Journal of Human Evolution, vol. 54, 1: 2-14.

MONTAVON T., LE GARREC J.F., KERSZBERG M. D.DUBOULE 2008 Modeling *Hox* gene regulation in digits: reverse collinearity and the molecular origin of thumbness, *Genes Dev.* 2008 February 1; 22(3): 346–359.

PATNAIK R., D. CAMERON, J.C. SHARMA, HOGARTH J. 2005 Extinction of Siwalik fossil apes: a review based on a new fossil tooth and on palaeoecological and palaeoclimatological evidence. *Anthropological Science,* Vol. 113, 1, pp. 65-72.

PILBEAM D. 1984 The descent of hominoids and hominids. *Scientific American*, 250, 3: 84-96.

PILLANS B., M. WILIAMS, D. CAMERON, R. PATNAIK, J. HOGARTH, A. SAHNI, J. C. SHARMA, F. WILLIAMS, BERNOR R.L 2005 Revised correlation of the Haritalyangar magnetostratigraphy, Indian Siwaliks : implications for the age of the Miocene hominids Indopithecus and Sivapithecus, with a note on a new hominid tooth. Journal of Human Evolution, vol. 48, n°5, pp. 507-515

POPE G.P. 1992 Craniofacial evidence for the origin of modern humans in China. Yearbook of Physical Anthropology. 35: 243-298.

RENDELL H.M. R.W. DENNEL, HALIM M.A. 1989 Pleistocene and Palaeolithic Investigations in the Soan Valley, Northern Pakistan. *British Archaeological Report*, International Series 544, 364p.

RUKANG W., C.E. OXNARD 1983 Ramapithecines from China: evidence from tooth dimensions. *Nature*, 306, 258 -260.

SANKHYAN A. R, RAO V.R 2007 Genome and Peolple of India: Genomic, Palaeontological and Archaeological Perspectives. New Delhi.(India): Allied Publishers

SONAKIA A., BISWAS S. 1998 Antiquity of the Narmada Homo erectus, the early man of India. *Current Science*, 75, 24: 391-393.

SPOOR F., M. G. LEAKEY, P. N. GATHOGO, F. H. BROWN, S. C. ANTÓN, I. MCDOUGALL, C. KIARIE, F. K. MANTHI, LEAKEY L. N. 2007 Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya, *Nature* 448, 688-691.

TOBIAS P.V. 1995 *Lecture.* University College London, November 14.

Tocheri M.W., C.M. Orr, S.G. LARSON, T.h. SUTIKNA Jatmiko, Saptomo E., R. A. Due, T. Djubiantono, M.J. Morwood, W.L. Jungers 2007 The Primitive Wrist of *Homo floresiensis* and Its Implications for Hominin Evolution. *Sciences*, 317, 5845: 1743 – 1745.

WHITE T.D., ASFAW B., DEGUSTA D., GILBERT.H. , G. D. RICHARDS., SUWA GEN, CLARK HOWELL F. 2003 Pléistocène *Homo sapiens* from Middle Awash, Ethiopia, *Nature* 423: 742-747.

WANPO H., R. CIOCHON, G. YUMIN, R. LARICK, F. QIREN, H. SCHWARCZ, C. YONGE, J. DE VOS, RINK W. 1995. Early Homo and associated artefacts from China. *Nature* 378: 275-278.

WOLPOFF, M. H., B. SENUT, M. PICKFORD, HAWKS J. 2002. Palaeoanthropology – *Sahelanthropus* or *'Sahelpithecus'*? *Nature* 419, 581-582

ZOLLIKOFER C. P. E., M. S. PONCE DE LEÓN, D.E. LIEBERMAN, F. GUY, D. PILBEAM, A. LIKIUS, H. T. MACKAYE, P. VIGNAUD, BRUNET M. 2005 Virtual cranial reconstruction of *Sahelanthropus tchadensis*, *Nature* 434, 755-759.

ZHAO L, Q.L.W. ZHANG 2008 Age at first molar emergence in Lufengpithecus lufengensis and its implications for life-history evoltuion. *Journal of Human Evolution,* vol. 54, 2: 251-257.

ZHU R.X., POTTS R., XIE F, HOFFMAN K.A, DENG C.L., C.D. SHI 2004 New evidence on the earliest human presence at high northern latitudes in northeast Asia, *Nature* 431, pp. 559–562.