

Original Synthetic Article

The relationships between occlusion and posture in the hominid lineage, implications for the transition between mesolithic and neolithic populations

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Abstract – Background and Aim: Connecting the occlusion to the posture during growth consists in studying the correlations between the contact of both dental arches and the constraints acting within the skull base, at the level of the sphenoidal synchondroses. They articulate the ethmoid, sphenoid and basi-occipital anlagen which are in the same alignment during the first weeks of the embryonic period. The basi-occipital belongs to the metameresed axial skeleton (petrous bones, exo-occipital, vertebral column and sacrum), the sphenoid and ethmoid belong to the prechordal territories. The simiiforms are the only mammals where embryonic kinetics breaks the alignment by a flexure sitting at the chordal-prechordal limit because of increasing tensions acting during neurulation. The degree of verticality of both facial and axial skeletons (i.e. the position of the cerebellar fossa) of the two temporo-mandibular joints and the mandibular dental arch depend on these late embryonic kinetics. The future occlusion between the maxillar and the mandibular dental arches requires coherent dynamics between the three sphenoidal synchondroses. **Materials and Methods:** These correlations were analyzed by using a metric methodology applied to x-rays or CT scan images of extant and fossil skulls. **Results and conclusions:** This approach presents major interests for the study of occluso-postural balances in fossil hominids as well as for the analysis of the evolutionary mode, tempo and phylogenetic association, in particular when dealing with the emergence of the contemporary occlusion at about 7,000 years BP. A better knowledge of this transition can be useful to understand the increasing ageneses and occluso-postural dysharmonies in modern populations.

Key words: occlusion, posture, biodynamics, ontogeny, hominids, phylogeny, evolution.

Introduction

Understanding the relationships between the skull base and both the lower and mid-faces is the specific field of study at a few schools of Dento-maxillo-facial Orthopaedics dealing with growth disorders in children before the age of six, when the sphenoccipital synchondrosis (SSO) is still patent. The synchondroses joining the ethmoid, sphenoid and basi-occipital anlagen (the planum basale) are in the same alignment during the first weeks of the embryonic period. The basi-occipital anlage belongs to the metameric axial skeleton (petrous pyramids, exoccipital, vertebral column and sacrum), both the sphenoid and ethmoid bones belong to the prechordal territories. The simiiforms are the only mammals in which the embryonic kinetics breaks this alignment by a flexure at the chordal-prechordal limit, the SSO, because of a prolonged neurulation. The degree of verticality of both facial and axial skeletons, i.e. the position of the cerebellar fossa, of the two temporomandibular joints and of the mandibular dental arch depends on the rate of this late embryonic kinetics. The future occlusion with the maxillary dental arch requires the deployment of coherent dynamics between the three sphenoidal synchondroses before the first synostoses occur.

This paper lays the groundwork for a future 3D modelling of the occluso-postural transition between Mesolithic and Neolithic peoples. As we will see, a modelling of this kinetics is possible for fossil hominoids and hominid species, their comparative studies and their phylogenetic relationships bring suggestions to understand the evolution of the occlusion from the most ancient hominid species up to modern *Homo sapiens* after 9000 years BP. It would be premature to link the modern occluso-postural imbalance to the Neolithic revolution since this occlusal change (from end-to-end to crossed incisor-canine arches) is observed on contemporary hunters-gatherers. It became first necessary to carry out a palaeontological investigation in order to search for the parameters inherited from possible phylogenetic determinism. The relationships between the skull base and the jaws are, without any doubt, the most complex ones in the entire morphogenetic process; paleoanthropologists regularly attempt to approach them in the fossil hominid record.

For 50 years, a few French scholars, among which former PhD students like Haddad (1991), Rame (2000), Maitre Robert (2001), Guichard (2002), Guichard *et al.* (2002), Millet (2003), Cho (2005), Korpál (2005) have followed the steps of Gudin (1951), Delattre and Fenart (1960), Fenart (2008), Deshayes (1986, 1997, 1998). This anthropological school is traditionally associated with Dentomaxillofacial Orthopaedics, Osteopathy and Posturology bringing a large corpus of knowledge established on the dynamical interaction during growth between the skull base and the sacrum (Andrieux, Hadjouis, Dambricourt Malassé 2000). This school can be found in North Africa with Hadjouis, attached Professor at the National Centre for Prehistoric, Anthropological and Historic Researches in Algeria, and completes Anglo-Saxon paleoanthropological approaches (Rak and Clark Howell 1978, Ross and Ravosa 1993, Collum Mc 1994, Ross and Henneberg 1995, May and Sheffer 1999, Spoor, O' Higgins, Dean and Lieberman 1999, Hardt 2008).

Materials and Methods

The aim of this study is to identify the correlations between the occlusion and the dynamics of the sphenoidal synchondroses during the growth of the skull base in fossil hominids. By hominids I mean all species in which the metamerized axial skeleton (from the basi-occipital to the sacrum) acquired a degree of verticality which does not allow any more the quadrupedal stance on the ground. This stage of axial verticality originates from the cephalic pole by preserving the cranio-palatine equilibrium, a key point of reference for orthodontic treatments (Deshayes 1993a, b, 1996). The orientation of the foramen magnum does not bring enough information on this verticalization, especially in human palaeontology (Zolliköfer *et al.* 2005, Guy *et al.* 2005); it is therefore necessary to complete the analysis by observing the conformation of the cerebellar fossa with the posterior slope of petrous pyramids and the clivus (caused by the flexion of the speno-occipital synchondrosis). Two particularly illustrative examples are given by the skull and the mandibles of *Sahelanthropus tchadensis*, as well as by the composite skull and the mandibles of *Ardipithecus* (Ethiopia 5, 5-4, 4 Ma).

There are no 3D metrical studies on the endocranial surface of fossil hominoid skull base, although it is the only way to understand the ontogenetic processes of 1) the verticalization of the metamerized axial skeleton and 2) the equilibration between occlusion and posture in a permanent bipedal equilibrium. This field of exploration is facilitated by the development of the medical imaging. However these data would be hardly understandable without taking into consideration the knowledge, based on dentomaxillofacial radiology, from half a century of Orthopaedics and Posturology studies. They describe the kinetics taking place between the dynamics of the sphenoccipital synchondrosis and the face in a three-dimensional space (Gudin 1951, 2002, Gudin and Godard 1973, Björk and Keiller 1984, Deshayes 1986, Couly 1991, Loreille *et al.* 1992).

Identifying the correlations between occlusion and basicranial flexure in fossil hominids implies to develop three-dimensional protocols applied to different series of radiographs of dry skulls then to CT scans. Their applications require however the presence of both the mid and lower faces as well as that of the three floors of the braincase including the clivus and the petrous pyramids, criteria rarely met in the fossil record. In this case, their study will require the reconstruction of the missing parts of the skull base, using mobile 3D scanner laser or spiral helical CT scan. This programme is currently in development at the Department of Biomechanics and Bioengineering at the University of Technology of Compiègne (Luft 2010).

The fossil record suitable for this analysis is however particularly well supplied. Along with *Sahelanthropus tchadensis*, there are also several Australopithecines, such as the child of Dikika (Ethiopia), the complete skull of Sterkfontein Stw 573 (South Africa), the skulls of Dmanissi (*Homo georgicus*), Atapuerca (*Homo heidelbergensis*) in Southern Europe, Dali in China, Hathnora in India (Narmada valley), Sangiran 17, Ngawi 1, *Homo floresiensis* in Indonesia, Bouri, KNM ER 42700, Kabwe (Broken Hill) or even Bodo whose base is crushed but can be reconstructed, and Herto in East Africa. This list is of course not exhaustive. A first approach may be achieved independently of this program. This is the aim of this paper: the type of occlusion is defined and then put into a corpus of anatomical and metric data about the mandible, gathered since 1987 (Dambricourt Malassé 1987), and the skull base.

These metric and angular data were already collected through a protocol applied to x-rays taken in the three planes of the skull, following conventional orthodontic standard. This protocol compares endo and exocranial measures and was applied to different series of dry skulls from the collections of both the Department of Comparative Anatomy and Department of Prehistory of the National Museum of Natural History (NMNH) and the Institute of Human Paleontology of Paris (IPH). These series included extant Hominoid species (66 paninae and ponginae), 120 skulls of recent Anatomically Modern Human and some original fossils of the early upper Pleistocene (Qafzeh 6, 95 ka, Cro-Magnon, 30 ka and La Chapelle-aux-Saints, 28 ka) completed by *Australopithecus africanus* (Stw 505, Sts 5, MLD37 / 38, Taung, Witwatersrand University of Johannesburg) (Dambricourt Malassé 2005). The collection of human skulls is considered as for any primates species, at the level of the genus without ethnic distinction, or without distinction of the different cranio-palatine balances observed between geographic groups as known in Orthodontics (the variability within the sapiens species).

Furthermore, a biodynamical cephalometric analysis used in Dentomaxillofacial Orthopaedic was applied to an ontogenetic series including: 1) gorilla, chimpanzee and orang-utang (Deshayes and Dambricourt Malassé 1990, Deshayes 1991), 2) historic populations from the Paris Basin (Val-de-Marne) (Hadjouis 1998, 2000a, 2000b, Cho and Hadjouis, 2005), 3) prehistoric Iberomaurusian and Mechtoid groups from North Africa (Hadjouis *et al.* 2000a, b, c, 2002, 2003a,b). This cephalometric analysis was based on the study of living *Homo sapiens* by Jean Delaire (University of Nantes) and was completed by Marie Josèphe Deshayes (Delaire 1961, 1980, 1988, 1993, Delaire *et al.* 1992, Deshayes 1986, 1988, 1991, 1993a, b, 1996, 1997, 1998), with the identification of an important statement and concept, the cranio-palatine balance.

The cranio-facial equilibrium is assessed by tracing cephalometric lines directly on the radiographs (figure 1). They are a) C3 (the sphenoidal line): from the intersection between the frontal and the nasal bones (M) to the anterior clinoid apophysis, b) C1: from M to the posterior edge of the mandibular condyle and going on until its perpendicular line crosses the contact of the sphenoidal line with the occipital bone.

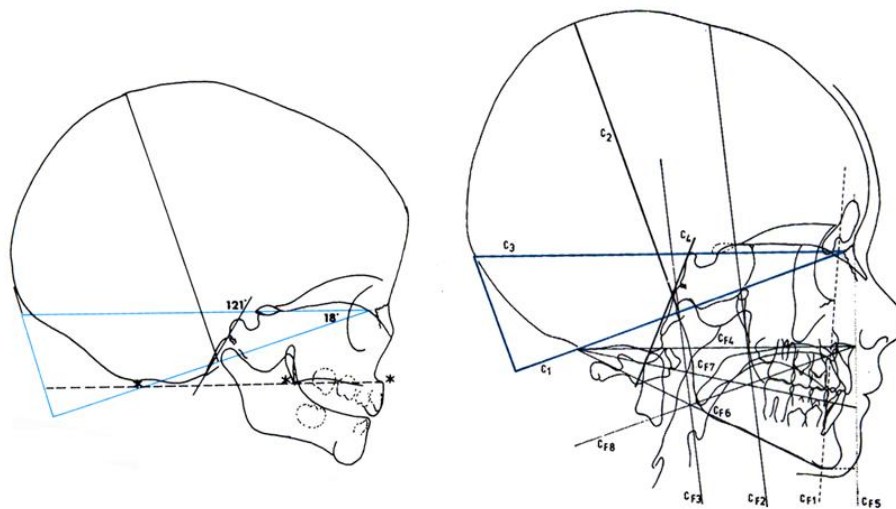


Figure 1

Cranio-palatine balance, modern *Homo sapiens* at foetal and adulte stages. This equilibrium is given by the alignment of the nasal spine, the contact of the pterygoid apophysis with the palate, and the summit of the odontoid apophysis (the three stars in the foetus) (according to M.J. Deshayes 1991) (scale variable).

The cranio-palatine equilibrium (i.e.CF4) is shown by a straight line connecting the anterior nasal spine to the inferior point of the pterygo-maxillary fissure (contact point between the pterygoid wing and the palate), prolonged until it reaches the tip of the odontoid apophysis of the axis vertebra. CF4 is parallel to C3. On a “well-balanced skull”, the median of C1 divides the skull into two areas of equal proportions: the cranio-facial and the cranio-rachidian areas; C1 and CF4 cross at the lowest section of the occipital bone. Comparison between *Homo sapiens* and extant hominoids showed that the cranio-palatine balance is an orthodontic reference which does not exist in other living primates after birth. This is a constituent feature of the human architectonics acquired at the end of the embryonic period and linked to the sphenoidal kinetics (Deshayes and Dambricourt Malassé 1990, Dambricourt Malassé 2006a).

The cranio-palatine balance is established during the intra-uterine development, before the emergence of the dentition, so it is not induced by occlusion. The origin of this balance is precisely the coordination between the kinetics of the sphenoid bone rotation which splits into three territories, 1) the post-sphenoidal territory with the basi-occipital isolated by the sphenoid-occipital synchondrosis (SSO), 2) the presphenoidal territory with the ethmoid isolated by the sphenoid-ethmoidal synchondrosis and 3) the sphenoid bone divided by the intra-sphenoidal synchondrosis (figure 2).

The latter fuses before the age of two, the speno-ethmoidal around the age of ten and the speno-occipital around the age of 23. These cartilaginous sutures can be compared to the joints around which the growth vectors are organized; in this case, they can be called “vorticity” vectors. These vectors are coordinated through biomechanics that some experts compare to a cogwheel system. However, these vortices can vary depending on the kinetics speed and conflict situations can arise between the territories, resulting in growth disharmonies between the base, the lower and mid-faces.

The present study completes the data through the observation of the occlusion of human fossils, original skulls and mandibles from 1) the late upper Pleistocene in North Africa (Afalou-Bou-Rhummel in Algeria and Taforalt in Morocco), in France (Isturitz), completed by 11 casts of European and South African, 2) the Mesolithic in France (Atlantic facade, Hoedic, Teviec) and in South-East Asia (Tam-Pong, Laos), all from the Department of Prehistory and the Institute of Human Paleontology (table 1). A synthesis gives a first identification of the constraints of equilibration between the occlusion and the kinetics of the basicranial synchondroses in hominoids and fossil hominids.

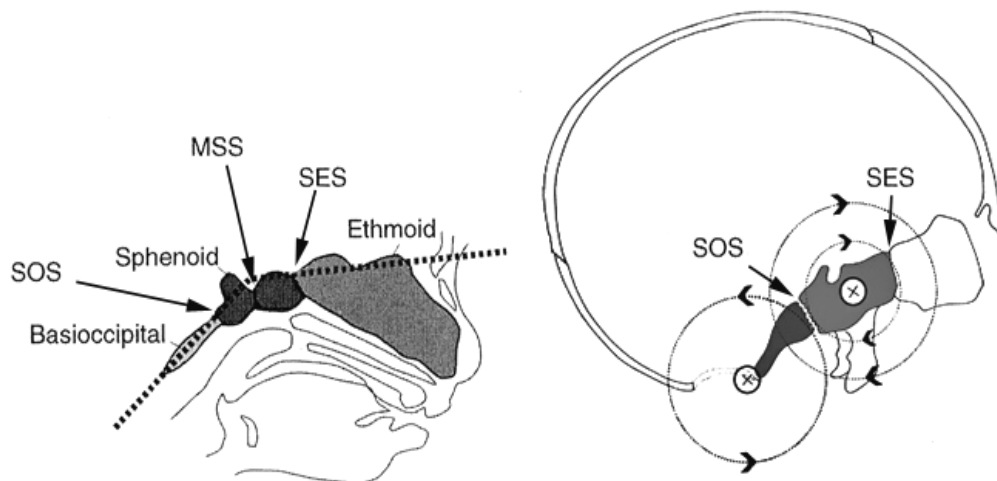


Figure 2

The sphenoidal synchondroses : during foetal growth (D.E. Lieberman, 1998) and after birth according to M.J. Deshayes (1988). MSS: midsphenoidal or intrasphenoidal synchondrosis, SES: sphenoethmoidal synchondrosis, SOS : spheno-occipital synchondrosis.

Table 1 : List of skulls and isolated mandibles

Taxa	Specimen	Mode of acquisition
Gorilla	NMNH - IPH	x-rays
Pan	NMNH - IPH	x-rays et CT scan
Pongo	NMNH - IPH	x-rays
Recent Homo sapiens	IPH	x-rays
Australopithecus	Sts 5	CT scan
	Stw 505	CT scan
	MLD 37/38	CT scan
	Taung	CT scan
	TM1517	cast
	Sts 71	cast
	KNM WT 17000	cast
Paranthropus	KNM WT 17400	cast
	OH 5	cast
	KNM ER 13750	cast
	KNM ER 406	cast
Homo neanderthalensis	La Chapelle-aux- Sts	x-rays
Homo sapiens Middle Pleistocene	Qafzeh 6	x-rays and CT scan
	Qafzeh 7	mandible original
Homo sapiens Upper Pleistocene	Cro magnon 1	x-rays
	Isturitz	mandible original
	Predmost ♂	cast
	Predmost ♀	cast
	Brno III	cast
	Dolin Vestonice III	cast
	Ofnet K 1802	cast
	Ofnet K 1806	cast
	Ofnet K 1818	cast
	Combe Capelle	cast
	Zhoukoudian CKT1	cast
	Fish Hoek	cast
	Florisbad	cast
	Cape Flats	cast
Homo sapiens Late Upper Pleistocene	Afalou (n= 50)	original
	Taforalt (n=27)	original
Homo sapiens Mesolithic	Hoëdic (n=11)	original
	Teviec (n=7)	original
	Tam Pong (Laos)	original
	Tam Hang (Laos)	original

The embryonic origin of the cranio-palatine balance: the speno-occipital rotation or the reduced field of embryonic anteroposterior polarity.

The mammalian embryo distinguishes itself by an anterior-posterior polarity, noticeable along the notochord and by a dorsal-ventral polarity. In quadrupedal mammals, antero-posterior polarity is preserved until the adult stage. In humans, however, it disappears well before birth, reduced by the distance between the prosthion and the opistocranium, and it merges with the dorsal-ventral polarity, entirely redistributed along the vertical axis.

This reduction of the antero-posterior polarity in humans is related to the verticalization of the cephalic termination of the metamerized axial skeleton (Dambricourt Malassé 1988, 2006, 2009a, b). Until the sixth week of the embryonic development, the cephalic skeleton is formed only by the future base, the cartilaginous blastema with the body of the sphenoid and the basi-occipital in the same alignment (Figure 3). We showed that the breaking of this plane (the planum basale) takes place during the closure of the neural groove at the apex of the notochord and is caused by the interaction of cellular tensions occurring between the cells of the neural plate, just above the discontinuity between the notochord and the pre-chordal plate (Dambricourt Malassé 1987, 1988, 1993, 2006, 2009).

The neural groove does not close in this area where specific constraints develop, taking place between the segmented axial skeleton (metamerized) and the pre-chordal head skeleton, i.e. between the body of the sphenoid and the basi-occipital. This neural kinetics, located in front of the notochord and centred on its apex, follows an antero-posterior rotation which straightens the head of the embryo. The vector expands beyond a vertical line passing through the apex of the notochord. The neural groove continues with a reverse rotation forward and downward. The underlying planum basale formed by the cartilaginous blastema initiates two kinetics “mirroring each other”. The posterior sphenoid initiates a rotation in the direction of the neural kinetics at the speno-occipital synchondrosis causing the downward and forward bending of the basioccipital and of the future cerebellar fossa. The anterior sphenoid (pre-sphenoid) initiates a reversed kinetics.

The Meckel cartilage of the mandibular arch (first branchial arch), in connexion with the chondrocranium via its distal termination, tracks the topographic changes; the future TMJ connected with the skull base tilts forward and downward, while a retraction (backward movement) straightens the Meckel arch in its facial anlage, caused by the spheno-ethmoïdo-maxillar retraction (Dambricourt Malassé 2006a).

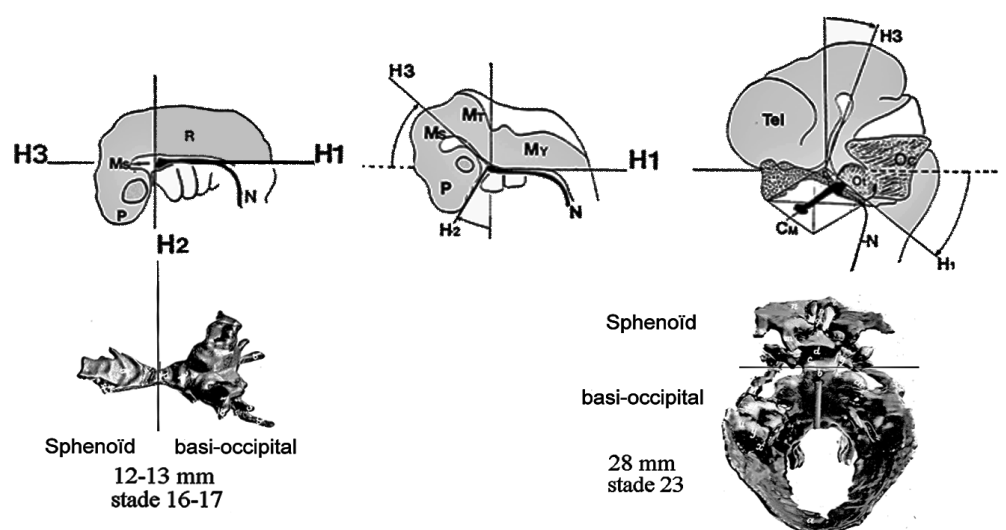


Figure 3

The neurocephalic rotation during neurulation centred on the chordal apex (above) and the chondrocranial flexure acquired during the 8th week (Carnegie stage 23) (below pictures from Levi 1900 in Dambricourt Malassé 1988, 1993, 2006a). H1: horizontal axis or the cephalic segment of the notochord, H2 vertical axis crossing the chordal apex, H3: pre-chordal horizontal axis. Cm: Meckel's cartilaginous, Ms: mesencephalon, Met: metencephalon, My: myelencephalon, N: notochorde, P: prosencephalon, R: rhombencephalon, Tel: telencephalon.

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In other mammals, such as chiropters (bats) or three-toed sloth (Bradypus), for example, these kinetics start from the apex of the notochord, but they are fast and short, they do not exceed the pre-chordal field (Figure 4). In Prosimians such as Lemurs, Tarsius, or Lorises there is no real bending; the segmented basicranial skeleton keeps its embryonic antero-posterior polarity and the cerebellum is aligned with the brain. The cerebral hemispheres are more or less complex according to their way of life (diurnal or nocturnal species) but they never exceed this vertical line through the apex of the chord. Therefore their face develops in front of the braincase, their mandible is long and narrow, with a short ascending ramus.

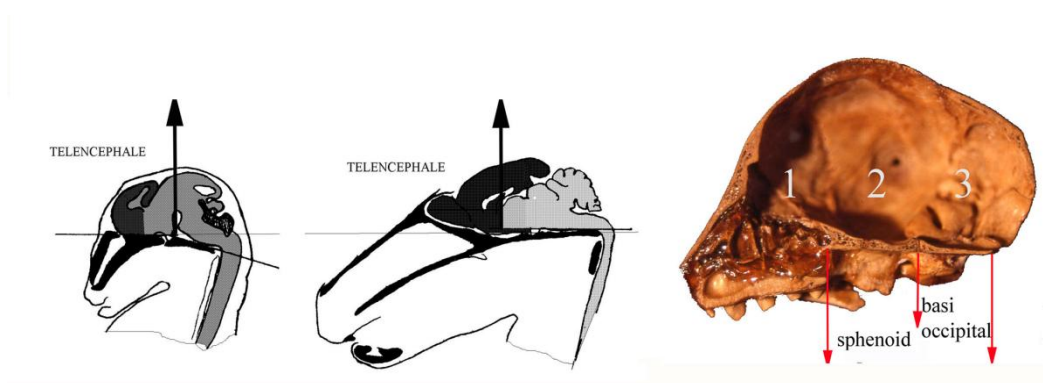


Figure 4

The skull base, the neural tube, the brain and the cerebellum in foetus and adult flying Mammal (bats) and a foetus of the arboreal Bradypus. 1, 2, 3: the three cranial fossae.

So, the base, initially flat in humans as in all mammals, flexes in its centre, the cerebellar fossa migrates forward and downward, the anterior-posterior polarity becomes extremely reduced, reversed kinetics start from the presphenoid, ethmoid and septum nasi territories dragging the future upper face downward and backward. The whole chondro-splanchno-cranium contracts, the territories therefore shorten and a vertical polarization emerges. The internal constraints around the sphenoidal flexure balance each other between the face and the cerebellar fossa through complex kinetics, like in a mirror, between the post and the presphenoid territories; the conditions of the cranio-palatine balance are acquired at the end of the embryonic period. These sagittal movements come along with identifiable kinetics in the transversal plane, namely the frontalization, not only with the petrous pyramids (Dean and Wood 1981, 1982) but also with the incisivo-canine arch (Björk and Keiller 1984). The mandible keeps the innovations of every ontogenetic phase until the adult stage (figure 5).

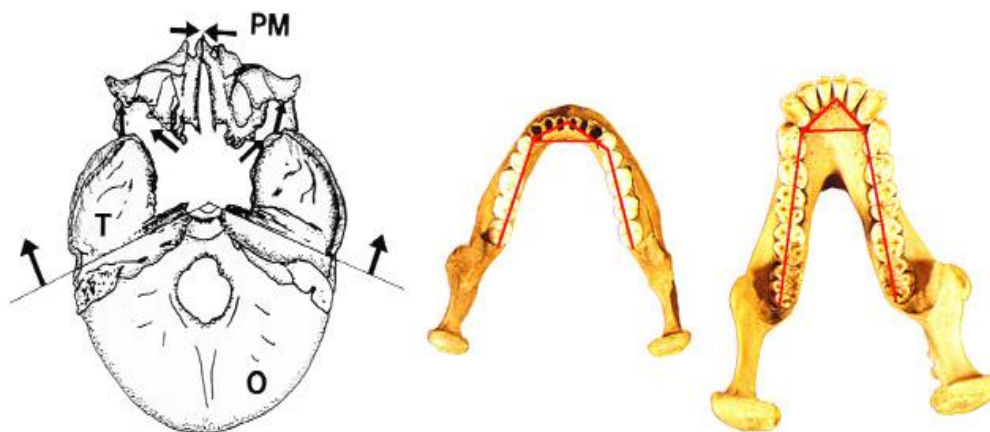


Figure 5

Growth vectors during the spheno-occipital synchondrosis activity in modern human (endocranial view according to Bjork) and alveolo-dental angular differences at the adult stage between *Homo sapiens* and Gorilla (note the incisor-canine frontalisation)

It is important, in human palaeontology, to know the precocity of these embryonic equilibrations and that it is impossible on a biomechanical point of view, for the primate cerebral fossa, to be moved forward, without a prior straightening of the clivus which contracts the anterior base and the upper face. At the end of the human embryonic period the three cerebral fossae are verticalized, resulting in the smallest antero-posterior polarity in the entire primate lineage. The cranio-palatine balance is preserved until the adult stage, according to equilibrium of internal tensions acting right from the neurulation stage.

The cranio-palatine balance and the occlusion

The dental occlusion in modern *Homo sapiens* (AMH) is said to be in equilibrium or in dental Class I, when the first lower molar lays half a cusp ahead of the first superior molar. The dental Class II shows the first lower molar behind the first superior molar (retromandibular position). The dental Class III corresponds to the first lower molar being situated ahead of the first superior molar, the incisors and canine are then positioned ahead of the maxillary incisivo-canine arch (promandibular position). Occlusal diseases reveal that conflicts between both cranio-facial and cranio-rachidian fields occurred during the intra-uterine growth between the synchondroses. Orthodontists distinguish numerous combinations between the different components of the basicranial flexion and the facial kyphosis (I unified the kinetics in single embryonic process called cranio-facial contraction see Chaline 1999-2007, Nottale *and al.* 2009, Chaline and Marchand 2010).

Let's take two very simple cases: 1) a child in promandibular position for whom the occlusion is Class III; the sphenoidal angle is closed, the occipital bone is low, the cranio-palatine balance is disturbed, 2) a child in retromandibular position for whom the occlusion is Class II; the sphenoidal angle is opened and the occipital scale above the CF4 line. In dental Class II, the rachidian field is more significant, whereas in dental Class III, the facial field is dominant (Deshayes 1986, 1998). The disorders are more complex and show a wide variability of diseases with different type of discordances between the synchondroses, and function of the growth rate and the stage of cephalic growth at which the disorder is detected (Hadjouis 2000a,b, Cho 2005, Cho and Hadjouis 2005).

The orthodontic practice aims to correct the malocclusion between the arches; Deshayes advocates taking into account the sphenoid kinetics before the age of six, because the treatments are based on the use of extra-oral forces supported by the cranial vault, revealing interaction with the SSO according to slowing-down or accelerations. An ordered dynamic plasticity was progressively revealed in the three planes, identified by vectors, the most significant one showing correlations between the posture of the head (the craniospinal field) and the occlusion (craniofacial field) (Delaire 1980, Hadjouis 1998, Amat 2008, Tecco *et al.* 2010).

Hominoid

The Linnaean nomenclature defined by a fixist paradigm during the eighteenth century then introduced in the gradual evolutionist paradigm during the nineteenth century, is not suitable to classify the increasing levels of embryonic body plan emerging from saltationist processes as observed in twentieth and twenty first centuries. For example, a simian is not a prosimian; it derives from this ancient embryonic body plan still living inside many species, but it cannot fit into the pattern from which they derive. Nowadays, classifying fossil species only by fitting implies a single evolutionary model of gradualism which maintains confusion regarding the internal mechanisms, as with the mosaic model for instance. Therefore, in order to be consistent with the biological data and to keep their intelligibility, the distinction between embryonic categories will not follow here the classification by hierarchical fitting.

Many fossil hominoids are classified within the Hominidae, i.e. in the same phylogenetic level as *Australopithecus* and *Homo*, because of the Linnean system; Hominidae is automatically at the same level as the oldest fossil families of Hominoid such as *Dryopithecidae* or *Proconsulidae*. However different evolutions by dichotomy occurred from the common ancestor, gradually without change of the embryonic pattern (*Dryopithecidae*, *Proconsulidae*), but also by punctuated equilibrium with a complete change of this common pattern shared from the common ancestor (Hominidae). This creates confusion when *Pongo*, *Gorilla* and *Pan* are classified along with *Australopithecus* and *Homo* in the same category, the Hominidae (Cameron 2004) while *Australopithecus* is not a genus from the hominoid embryonic body plan.

Macro-evolutionary processes occurred at their respective level of embryonic pattern (Dambricourt Malassé 1988, 1993, 2006b, 2009b, Nottale *et al.* 2009). As we will see, basicranio-facial contraction associated to permanent bipedalism and new dental occlusion cannot be the result of a mosaic evolution after gradual selection caused by environmental changes (Chaline *et al.* 2000, Dambricourt Malassé 2009a).

Since 2009, a huge pillar of the gradual paradigm has collapsed; as a matter of fact the oldest species classified as vertical hominids were arboreal and lived in moist and wooded environments (White *et al.* 2009). The paradigm stands for a global warming leading to the significant regression of the forest areas as a cause for the emergence of permanent bipedalism; this is because one single point of view focusing on the postnatal skeleton. Since embryogenesis is still rarely taken into account, the gradualist and mosaic models are still the dominant vision that led to the creation of composite taxa (association of fossils separated in time and space) hardly compatible with the knowledge of occluso-postural Orthopedics (Dambricourt Malassé 2006b). Human palaeontology is unfamiliar with the new "evo-devo" paradigm (evolutionary embryology), but it is very likely that, within a few years, this interpretation will be the most acknowledged one. Indeed, the abandonment of the palaeo-environmental paradigm (White *et al.*, *ib.*) requires searching for internal causes, especially since the use of CT scanners becomes systematic for the study of the dynamic relationships between the skull base and the brain (Roelfsema *et al.* 2007), and more specifically for the semicircular canals (Jeffery and Spoor 2002, 2004, Spoor 2003, Spoor *et al.* 2003).

We have shown that the differences between Australopithecine and Homo semicircular canals, well enlightened in Spoor's work, precede the bending of the base and necessary imply a change within the homeodomain genes (Dambricourt Malassé and Lallouet 2009) that exclude any transitional species because of the high degree of their pleiotropy (Spitz and Duboule 2008). Such changes deal with the coordination of the homeodomains and can not be the result of random mutations (abortive) nor that of environmental changes (Duboule 2007) because the level of information is embedded into the genetic memory of the embryonic body plan, its own complexity and its internal organization. New hypotheses take into account the dynamical properties of self-organized systems (Kauffman 1993).

Deshayes's cephalometric analysis applied to extant hominoids (Pongo, Gorilla, Pan) brings to light what puts them into a specific category clearly apart from *Homo sapiens*. Any great ape species remains in dental Class I, none of the species develops occlusal imbalance. The homologous landmarks occupy various positions from the intra-uterine development with growth vectors much less involved with the neural rotation, interrupted much earlier. The differences can be spotted from the end of the embryogenesis: the basi-cranio-facial anlage of *Homo sapiens* is more contracted from the beginning of the fetal growth period, the palate and the premaxillars are placed below the sphenoidal planum, while during the very same weeks only the most distal part is directly below the sphenothmoidal anlage in the great ape (figure 6).

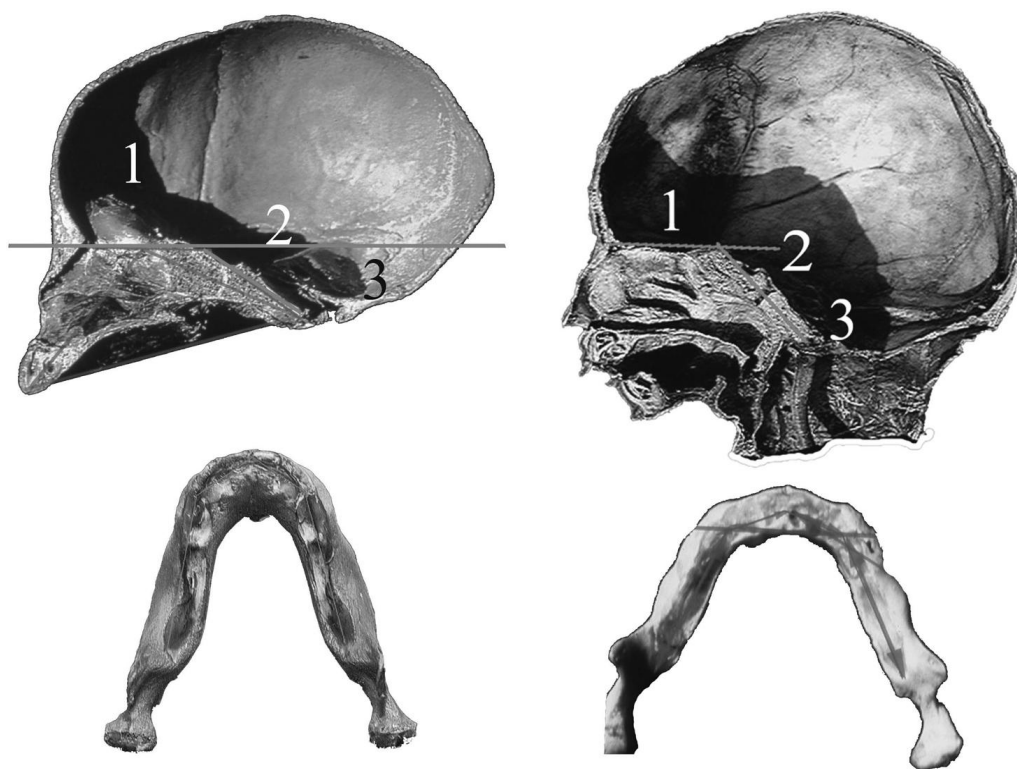


Figure 6

Comparison between Gorilla and *Homo sapiens* at the term of the foetal growth, in sagittal and transversal view. Note with *Homo sapiens* the verticalization of the three cranial fossae (1, 2, 3), the straightening of the sphenoidal body, the mid and low face below the ethmosphenoidal territories, the frontalisation of the incisor-canine alveolar arch, an enlarged post-canine arch and a straightening of the mandibular symphysis.

The extant Hominoid species share the same embryonic spheno-occipital bending, thus a beginning of verticalization emerges in the topographic organization of the three cranial fossae, but the cephalic kinetics of the neurulation stop earlier. The development of the nervous system is shorter than in Modern Man not only since the onset of the fetal period but since the antero-posterior patterning of the neural plate.

The hominoid morphotype, or the basi-cranio-facial embryonic pattern, leads to a cranio-palatine balance, but with a less contracted position, below the planum sphenoidal. This is because the cerebellar fossa does not tilt forward and downward with the same amplitude as in the human embryo. The two cranio-facial and cranio-rachidian fields remain equal until the deciduous dentition erupts. The occlusion sets up but, unlike in man, the post-sphenoidal kinetics stops. Then the sphenoidal angle opens, the base grows following a dynamic of extension, the cranio-palatine balance disappears (Figure 7). In the transversal plane the angles of frontalisiation, still less pronounced during the fetal growth, close (incisivo-canine arches and petrous pyramids)

The occluso-postural balance gives the ability to develop a bipedal equilibrium during the first years after birth, but the mixed dentition since the emergence of the first molar, the reversed constraints of equilibration between the face and the skull base tend toward a quadrupedal gait with a loss of vertical polarity for the benefit of the original antero-posterior polarity. Any great ape species shows a bipedal ability all the more easily as it remains close to the constraints of equilibration maintained during the foetal development. The further the trajectories separates from it as the adult stage gets closer, the more energy this balance requires to walk on the ground; on the other hand chimpanzees walk easily in water over long distances. The male gorillas are the ones that stand most remotely from the infantile balance, with an opened sphenoidal angle, a huge prognathism, tall canine teeth (roots and crowns). The dental variabilities are clear between Gorilla and Pan from the eruption of their deciduous dentition; the canine and premolar cusps are more protruding and sharper in gorillas. The endocrine modalities are also different. A late ontogenetic dichotomy occurred between Ponginae (Pongo) and Paninae (Gorilla and Pan) namely the airorhynch. The cranio-palatine balance in Pongo disappeared but became parallel to the sphenoidal planum (Deshayes 1991) because the face grows as a whole in a ventral-dorsal trajectory (Delattre and Fenart 1960).

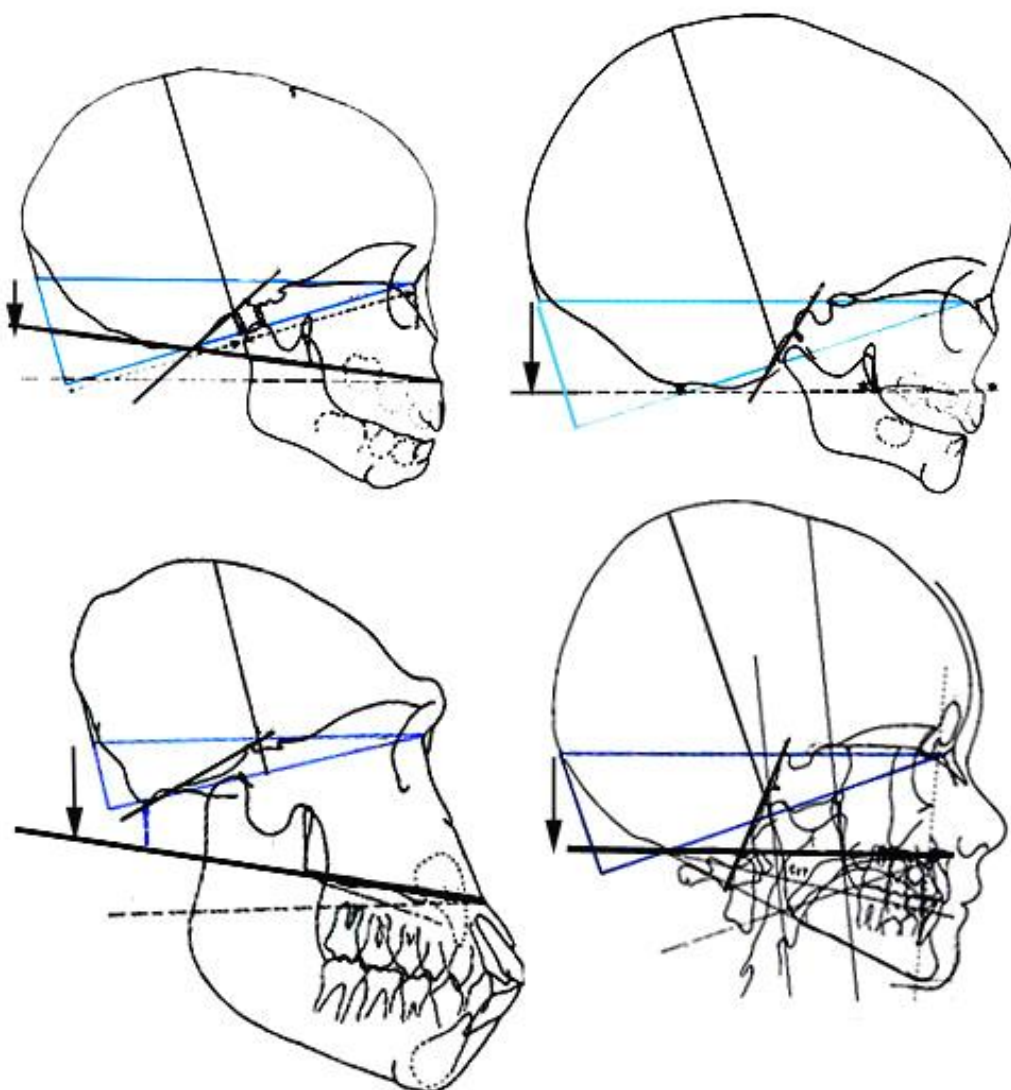


Figure 7

Comparison between the cranio-palatine balance of Gorilla and *Homo sapiens* at the late foetal and adult stages; the arrows compare the cranio-palatine balance (according to M.J. Deshayes 1991).

This divergence between the facial kinetics can be explained by the premature ossification of the intra-sphenoidal synchondrosis while it remains patent after birth in Paninae (Deshayes ib.). This phenomenon has already been observed on two Asian fossils, namely *Sivapithecus* in the Himalayan foothills (Siwaliks) and *Lufengpithecus* in Tibetan plateau foothills (Yunnan). Nevertheless, palaeontologists do not consider those fossil species as ancestor of orang-utans. This dichotomy would thus be registered in the genetic memory of the embryonic development of all the Asian fossil great apes since at least 12.5 million years, the geologic age of *Sivapithecus indicus*.

The equilibration of the constraints were organized differently because the synostosis of the intrasphenoidal synchondroses did not follow the same growth rates; however, a primary constraint dominates the overall architectural balance, caused by the limits of the amplitude of embryonic contraction, inherited from a common ancestor, the mandibles of both Pongo and Gorilla are much more less distinguishable than between Sivapithecus and Pongo.

The three extant genera have developed the same pattern of dental occlusion issued from the constraints emerging from the cephalic neurulation, dominating the spheno-occipital kinetics and fixing the topological configuration of the three cranial fossae (i.e. the maximal limit of the vertical polarity). The occlusion stabilises the face while the growth of the spheno-occipital synchondrosis determining the position of the TMJ, generates new constraints through its reversed growth vectors. The deciduous (or temporary), mixed and permanent dentition stabilizes the basicraniofacial architectonics in constant remodelling, with different growth rates between the species of the three genera, but with a common and unchanged spheno-occipital dynamics (same range of rotation). An isolated mandible does not reflect the variety of intrasphenoidal kinetics, but it gives the morphogenetic pattern of the basicraniofacial pattern that I call, for convenience, "hominoid type".

The hominoid type is characterized by 1) a U-shaped arch of the deciduous, mixed and permanent dentition, 2) a neonate angle of 90 ° at the base of the mandibular symphysis between the two mandibular bodies, going down to 68 ° at the adult stage, instead of 60 ° in Hylobatidae and monkeys. This value is a primate conformation observed at the beginning of the fetal period which increases when encephalisation starts. The post natal value of this angle is phylogenetically discriminant between monkeys and Hylobatidae, on one hand, and Hominoid sensu Great Ape, on the other. To this basic morphogenesis one can add the Y5 pattern, or Dryopithecus cusp pattern, of the lower molars and a huge dental lock, not only with the C-P3 complex but with the entire incisor-canine arch; I call the "I-C-P3 complex". This lock is due to the protusion of the two lower canines ahead of the upper canines and laterally wedged by the incisors, while the upper canines are wedged by the "sectorialization" (development of proximal cusp) of the first lower premolars (deciduous and permanent). The growth of the lower canine provokes a diastema between the upper canine and lateral incisor.

This complex stops any lateral movement and prevents any retromandibular condition that could be caused by the caudal growth of the base, pushing the TMJ toward the caudal pole of the axial skeleton. The symphyseal angle opens with the growth thus contributing to facial prognathism. The mandibular symphysis is sagittal, and often results into a simian plate in gorilla and the orang-utan, giving attachments for both the digastric muscles.

The anterior dental lock (I-C-P3 complex) is still present with the deciduous dentition because the first morphogenetic determinism is not the mastication but the basicraniofacial balance. Consecutively the absolute size of the canine crown is phylogenetically no significant, it is necessary to add the type of occlusion which reflects the cranio-palatine balance. The adult dentition is widely variable, depending on the weight and size of individuals and it is common to mention the presence of huge canines in male gorillas, but it is not systematic; canine crowns may have a very strong apical wear and a medium size. What must be analysed is the dental complex system which stabilizes the face when the skull base and the cervical spine growth vectors tend to develop the primitive antero-posterior polarity.

By choosing the intercuspidation between the lower and superior M1 as the ancestral benchmark, it is evident that the incisor and canine roots, crowns and alveolar arches are reduced in *Homo sapiens*. As we see, such changes can not be reduced to masticator consideration neither to endocrine influences. A true backward motion of the bones occurred not only during embryogeny, but during phylogeny as Delattre and Fenart concluded. Indeed, the M1 intercuspidation is located below the sphenoidal planum in *Homo sapiens*, while it just begins to get out of the endocranial perimeter when M1 eruption starts in Hominoids. In monkeys and Apes, the neural deflection is shorter than in *Homo sapiens* (AMH) where the dynamics are more pronounced. The way of life and ecosystems differ between the three genera and between species of the same genus with sexual dimorphism, growth rate (Millet *et al.* 2001), different diets, but these variations does not go beyond the topological limits fixed during the neurulation, identified at the facial pole by an invariant type of occlusion : "*In pongids, there is a high stability in the facial and occlusal balance, they always stay in Class I, while major cranial changes occur during their development*" (M.J. Deshayes, 1991).

Modern Humans follow the same trajectories but over a longer period, that does not imply a mere continuation of the sphenoidal kinetics. These are not the same when the planum basale flexes; new kinetics appear from the neurulation stage so that the base begins to differ in a different context of kinetics and chordal induction. All the embryonic rostro-caudal axis changes, a greater inflexion of neurulation causes the embryonic cranio-facial contraction and the verticalization of the metamerized cephalic axial skeleton. But these kinetics, the acquisition of cervico-cephalic verticality, are a late epigenetic effects, an embryonic epiphenomenon which does not occur if the neural groove does not close (Dambricourt Malassé 1987, Dambricourt Malassé and Lallouet 2009). Other changes are under the control of homeobox genes, such as teeth (Sharpe 1995) and the semi-circular canals (Merlo 2002).

The various occluso-postural balances since Proconsulidae

Fossil species illustrate important morphological differences; nevertheless the morphogenetic pattern is distinguishable while all of them share the common cartilaginous flat base at the beginning of their embryogenesis. The more the sphenoccipital flexion is great, the more the facial anlage is retracted below the sphenomethmoidal anlage. So the dental occlusion helps to balance the constraints between the face and the skull base. The diversity is as widened as the morphotype is ancient. As explained above, the criterion of this study is the cranio-facial background which is confused with the verticalization degree of the metamerized axial skeleton. Dietary adaptations, heterochronies or range of locomotion mode (more quadrupedal than bipedal, terrestrial than arboreal) are not the aim of this research. Thus the question is not to know if *Sahelanthropus tchadensis*, *Orrorin tugenensis*, *Ardipithecus ramidus* are ancestors or not, the finality is to identify their basi-cranio-facial embryonic patterns.

The comparison of fossil and living species since the common ancestor of Paninae (Gorilla, Pan) and Ponginae (Pongo), shows six types of occlusion for the deciduous, mixed and permanent dentitions; they match the successive changes of the sphenoidal kinetics from the fastest (the smallest bending) to the longest (the most verticalized one), in accordance with the duration of the neurulation stage (Dambricourt Malassé 1987, 1988, 1993, 2004, 2005, 2006a, 2009a,b, Dambricourt and Deshayes 1992a, Dambricourt Malassé *et al.* 1999, Dambricourt and Lallouet 2009, Caro 2004, Chaline *et al.* 1996, 1998, 2000).

Type I common to paninae, ponginae and fossil species of Hominoids

Type II common to the species of Australopithecus (including Praeanthropus)

Type III common to the species of Paranthropus

Type IV common to the fossil species of the genus Homo, with subgroups (Neanderthals)

Type V common to the fossil populations of robust Sapiens

Type VI common to the living and prehistoric populations of gracile Sapiens after 9000 years BP

The Hominoid type. The last living species are Pongo, Gorilla and Pan. The oldest species developed their common morphogenesis is *Dryopithecus (Proconsul) africanus* (R106 Rusinga Island, 20 Ma., Miocene, Kenya), a small hominoid female with a reconstructed skull base and a well preserved-face featuring the U-shaped dental arch, the 68° angular distance between the base of the two hemi-mandibles, a sagittal symphysis, the Y5 molar pattern, and the protruding incisor canine lock. The 68° are in accordance with a brain relatively larger than that of extant monkeys of similar body size (Walker *et al.* 1983). The fossil species are mainly known through mandibles and maxillary bones, the base is exceptionally preserved (*Sahelanthropus tchadensis* in Central Africa, some fossils of *Lufengpithecus* in the Southwest of China, particularly flattened).

The fossil species of the Hominoid type are Proconsul, Dryopithecus, Kenyapithecus, Nakalipithecus, Chororapithecus Sahelanthropus, Ardipithecus in Africa, Hispanopithecus, Pierolapithecus, Anoiapithecus, Dryopithecus, Hungaropithecus, Rudapithecus, Ouranopithecus, Graecopithecus and Ankarapithecus in Southern Europe, Sivapithecus, Gigantopithecus, Lufengpithecus and Khoralopithecus in Asia. The size of the canine crown is variable, for example the canines of *Lufengpithecus* (Yunna, China), *Proconsul major* and *Proconsul africanus* (East Africa); that of *Gigantopithecus* shows an extreme apical wear, resulting from coarse vegetable fibres (like bamboo). Nevertheless, the U-shaped arch, the inclination of the symphysis, the I-C-P3 complex are systematically present, which prevented the antero-posterior and lateral movements of the lower jaw, the diastema, on the other hand, is not systematic, and is even absent in particular from the most ancient species *Proconsul africanus*.



Figure 8
Proconsul africanus

The skull of *Sahelanthropus tchadensis* enables to know the position of the cerebellar fossa and assess the cranio-palatine balance, its endocranial study is currently the subject of a PhD at the University of Poitiers. In the absence of these data, an analysis remains possible through its occlusion, the position of the inion and the orientation of the foramen magnum. The geologic level is subject to controversy (10 Ma rather than 7 Ma, Beauvillain 2008) and the matter of the acquisition of a bipedal balance closer to that of Hominidae than that of Paninae brings important controversial issues (Wolpoff *et al.* 2002, 2006, Pickford 2005, Dambricourt Malassé 2006a,b). The CT scan reconstruction of the fossil (Zöllikofer *et al.* 2005) proposes an estimation of the foramen magnum orientation. The ability for bipedal equilibrium was established on an approximate position of the foramen magnum in exocranial view, compared with the x-ray image of a chimpanzee. The anatomical comparison is indeed truncated for three reasons. The first one is because the line drawn on the radiograph joins the opisthion at the tip of the mastoid apophysis and not the basion; consequently the foramen magnum seems excessively vertical.

The second reason is because it is impossible to locate the opisthion on the virtual reconstruction in exocranial view and place it at the lowest level of the cerebellar fossa. The opisthion is slightly situated above the lowest point. After all, the orientation of the foramen magnum is not horizontal but oblique toward the back and fits into the great apes' growth trajectory. The third is the absence of ontogenetic references which would enable to notice that the plane is in a less horizontal orientation than at the juvenile stage of the Paninae, meaning that the kinetics of the neurulation did not exceed the topological limits of the ancestors common to Ponginae and Paninae (Dambricourt Malassé 2006a,b, 2009) (figure 9).

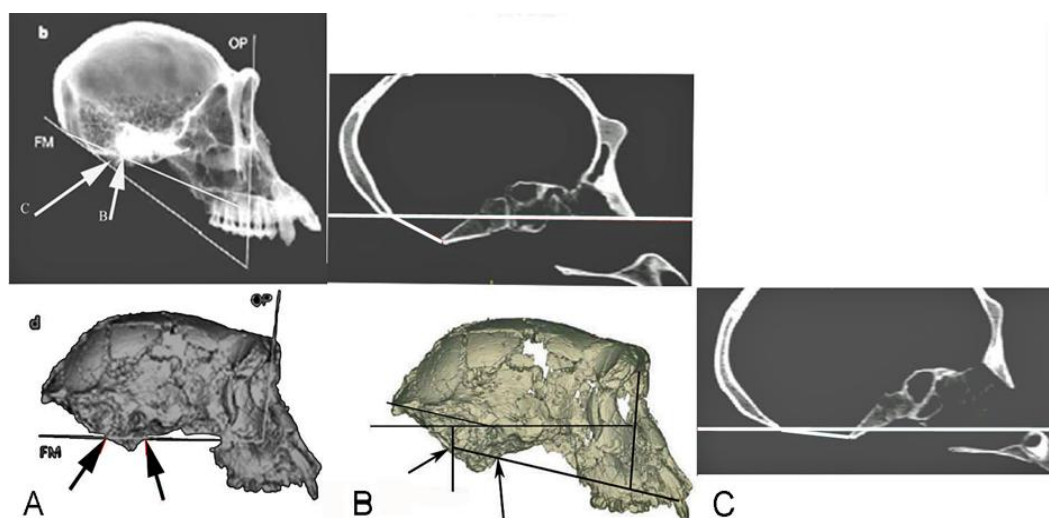


Figure 9

Sahelanthropus tchadensis (virtual restitution) A: official cephalometric analysis (Zollikofer *et al.* 2005) and location of the basion (B, right arrow), B: the inion position above the Frankfurt plane (FP), a highest position of the opisthion, the foramen magnum inclination between the two arrows compared with adult Chimpanzee (CT scanner, sagittal view), C : foramen magnum inclination of a juvenile Chimpanzee (CT scanner, sagittal view). Both CT scans of chimpanzee are parallel to FP(scale variable).

This basi-cranio-facial conformation is consistent with the position of the inion, as high at the deciduous stage of the Paninae, while in Hominidae, it goes down during growth by following the speno-occipital kinetics, which maintains the cranio-palatine balance (see below). As for the occlusion, the canine root is tall, the crown is not complete because the apex is broken, a reconstruction shows a significant overtaking of the molar and premolar occlusal surfaces (figure 10).

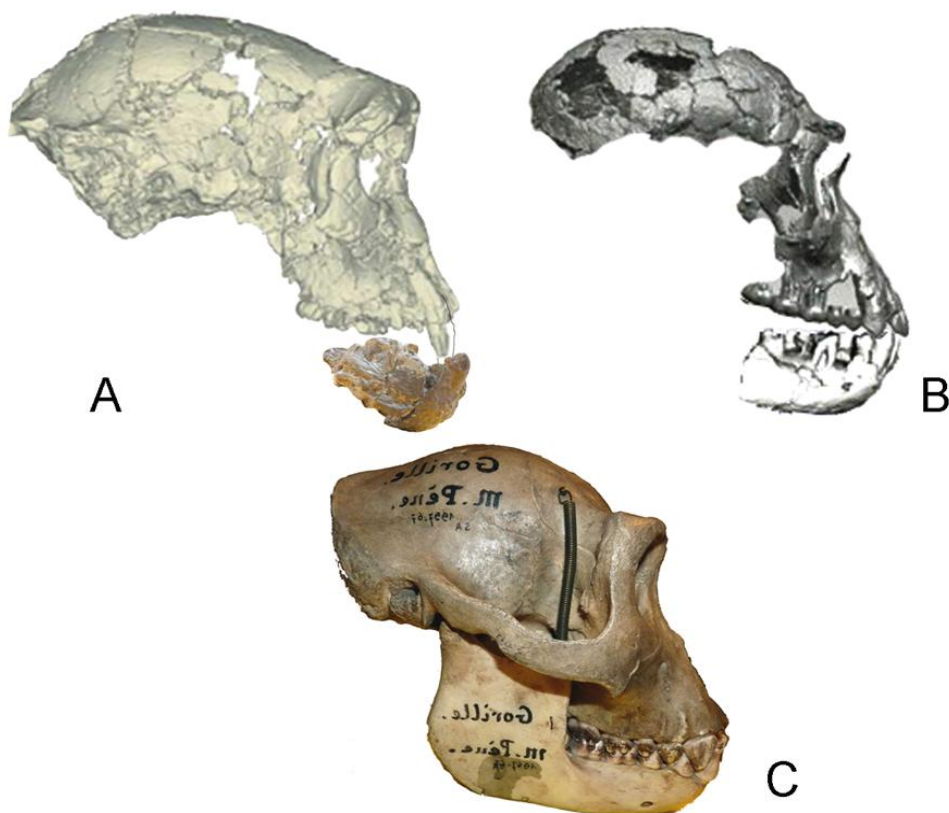


Figure 10

The incisor-canine lock in Sahelanthropus, Ardipithecus and Gorilla

The upper canine created a wear on the lower canine, typical of the I-C-P3 lock. Finally the skull and the associated mandibles show a coherent architectonic pattern which has lost his cranio-palatine balance as in any species of the Hominoid type. Other matters such as prognathism and little canine have no meaning outside the variability of growth. The size of the upper canine is not sufficiently reduced to allow lateral movements that are possible in Hominidae whose axial skeleton is in permanent bipedal balance with a verticalization of the three cerebral fossae. So the I-C-P3 lock is typical of a postural equilibration in basicranial extension with the ability to walk in quadrupedal equilibrium, no more possible in Hominidae. *Sahelanthropus tchadensis* therefore had the ability to be in bipedal balance, according to the constraints that normally occur in Ponginae and Paninae during growth, in other words which occurs in any Hominoid species. The bipedality of Sahelanthropus was no more evolved than during the growth of *Proconsul africanus*, Ponginae and Paninae.

Other experts have concluded that Sahelanthropus was not an Hominidae (Wolpoff, Pickford, Hawks, Senut, Ahern). Paninae could derive from this genus through processes of hypermorphose.

The second debatable fossil is *Ardipithecus ramidus*, Ethiopia, 4.4 Ma (White *et al.* 2009), its metamerized skeleton (from the basi-occipital to the sacrum) was not preserved (figure 10). The cephalic skeleton ARA-VP-6 / 500 contains only a part of the vault, the upper and mid-face. The occlusion is that of a dynamics which lost its cranio-palatine balance; it is coherent with what was deduced from the hip, namely a capacity for quadrumanal movements in trees. On other hand, the basicranial fragments ARA-VP-1 / 500 found on the ground surface at another site about one kilometre away and visibly more recent (Woldgabriel *et al.* 1994) gives evidence for a clear shortening of the base with frontalization of the petrous bones, that is possible if and only if, a change in the sphenoidal kinetics occurred with increasing rotation rates, i.e. after a change in the neurulation process, along with new inductions of the homeotic genes with their cascade effects all along the antero-posterior polarity of the embryo (Dambricourt Malassé 2009a,b). This shortening of the antero-posterior polarity is associated with the permanent bipedal balance as in any *Australopithecus* species and a new occlusion. Thus taking the sphenoidal kinetics constraints into consideration it is unlikely that this isolated base be associated with the mandibles of *Ardipithecus kadabba* and *Ardipithecus ramidus*, i.e. the ARA-VP-6 / 500 skeleton as in the official statement. The first nomination *Australopithecus ramidus* (White *et al.* 1994) can be kept for ARA-VP-1 / 500, this individual was indeed erected and could not adopt a quadrupedal stance. However, the set of teeth of ARA-VP-6 / 500 belonged to a specimen which axial skeleton showed an architectonics in extension and able to walk in a quadrupedal equilibrium.

During the International Conference of the Academy of Sciences at the Institut de France in Paris and a debate with Tim White, Michel Brunet, Brigitte Senut and Yves Coppens, I proposed to abandon the environmental paradigm because of the isolated base of ARA-VP-1 / 500 and concluded that for the first time in North East Africa, arboreal Hominoids coexisted with arboreal Hominidae (Dambricourt Malassé 2006a).

The coexistence of the two groups is not in contradiction with the evolutionary mechanisms and can be admit without the necessity to create a gradual missing link, i.e. an hominoid face with an hominid base.

In conclusion, the protruding incisor-canine lock (I-C-P3 complex) of Sahelanthropus and Ardipithecus is characteristic of an axial skeleton in extension with a dominant antero-posterior polarity, reduced vertical polarity and quadrupedal ability, with a bipedality no more evolved than that in the Paninae ontogeny. A bipedal balance is visible with the femoral neck of *Orrorin tugenensis* as well as with *Ardipithecus ramidus*. These recent palaeontological discoveries converge to draw a morphogenetic background of the upper Miocene Hominoid that goes beyond the mere observation of diversity; whatever the African Hominoid fossil and living species, they develop a bipedal balance as a result from the tensions of the neurulation acquired from their oldest common ancestor *Proconsul africanus*. At the pelvic gurdle the coherence with the skull base can be interpreted as the consequence of cascade effects of the homeotic genes controlling the organogenesis from the cephalic to the caudal poles. The common morphogenetic background shared by Sahelanthropus, Orrorin and Ardipithecus is the genetic substratum, or the common ancestor, from which more verticalized axial skeletons could and will emerge.

Hominidae

From the middle Pliocene, many fossils species cannot be integrated into the Hominoid morphogenesis; all these species and those which will derive from them, have in common the preservation of the cranio-palatine balance until the grown-up stage, for the first time in the primate lineage. The permanent bipedal equilibrium is *in fine* the occluso-postural balance which keeps the cranio-palatine balance. These punctuated emergences are significant of a macro-evolution arising from the deepest level of the species, that is to say, its internal organization programmed from the onset of the embryonic development and placed under the control of the homeotic genes. This threshold defines the Hominidae; Large Primates have to be excluded, regardless of their bipedal stance, for they do not maintain the cranio-palatine balance with the threshold acquired at end of the neurulation stage and thanks to which the specimens cannot return to a quadrupedal stance.

Numerous studies were dedicated to the comparative and metric anatomy of fossilised teeth in a functional perspective, reflecting dietary patterns and of growth rates. The intercuspidation on the other hand was not studied in a systematic way; the scarcity of maxillary bones associated with mandibles from the oldest fossil record can justify this. However the large number of specimens allows a first estimation of the various types of occluso-postural balance. Several types have emerged from the most primitive one, the *Australopithecus* genus, to the most recent, that of Modern Man appeared after the Mesolithic. Two grades are divided: that of the hominines with two morphogeneses, *Australopithecus* and *Paranthropus*, and that of *Homo* with also two morphogeneses, *Homo* and *Sapiens*.

Hominines

The australopithecine morphogenesis: the oldest fossil is the base ref. ARA-VP-1 / 500, initially called *Australopithecus ramidus* (White *et al.* 1994) appeared ca 4.4 Ma ago. *Kenyanthropus* (KNM WT 40000), dated 3.5 Ma belongs to the morphotype. The lower incisor-canine arch always stands ahead of the superior arch, but the intercuspidation is totally remodelled. On the lower arch, the deciduous molars have five cusps, like the molars, instead of two in Hominoids; the permanent premolars develop two cusps, nevertheless the sectorialisation of the proximal one (caniniform) is just slightly marked or absent. Also, the canine apex exceeds slightly the occlusal surface of other teeth, its diameter is more reduced, so is the root, the diastema is scarcely found and its crown does not form a canine lock, the contact surface with the lateral incisor and the first premolar is reduced. The I-C-P3 complex does prevent neither the lateral movements nor the antero-posterior movements of the mandible. The proportions of the mandibular arch give a relatively parabolic profile, with a frontalization of the incisor-canine row, visible at the deciduous stage and kept with the premolars at the adult stage. The mandibular prognathism is reduced, the symphyseal angle is more closed and shows no simian plate. The parabolic shape decreases due to a longitudinal growth at a rate faster than in the transversal plane, limited for architectural reasons which depends on the position of the temporomandibular joints, varying with the transversal development of the brain and cerebellum. The basal angle between the two hemi-mandibles closes as quickly as in the Hominoids (68°).

These morphological differences result in a face substantially shortened and broadened, which implies a change in the sphenoidal kinetics, due to an increasing rotation of the neurulation around the chordal apex, corroborated by the endocranial surface of the sphenoid (Figure 11).

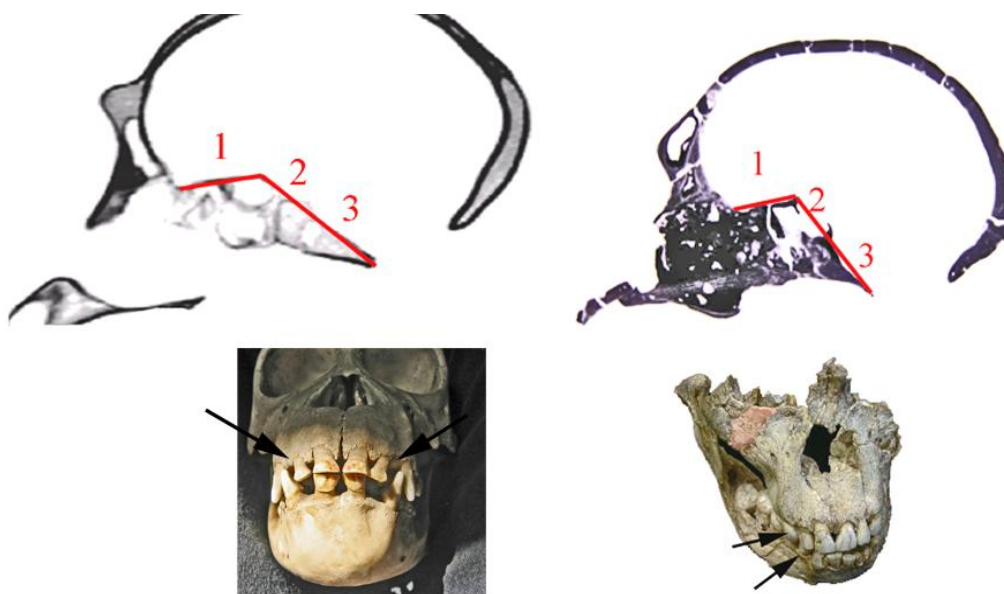


Figure 11

Sagittal Ct scan of adult Chimpanzee and *Australopithecus africanus* Sts5 with the verticalisation of the three cranial fossae and the largest sphenoidal rotation. Incisor-canine arches: the lock of the mandible still the deciduous dentition in Chimpanzee, no more lock for the adult dentition of *Australopithecus africanus* Sts 52 (scale variable).

The sphenoidal kinetics amplified their trajectories, the sphenothmoidal unit pulls the facial tissues toward the clivus, markedly verticalized, the cerebellar fossa is lowered forward, the foramen magnum cuts the line joining the two TMJ, the petrous pyramids frontalize (figure 12). All result from increased tensions in the fascia, attached to the posterior clinoid apophyses, the edges of the cerebellar fossa and continuing to the sacrum, as predicted by osteopathic principles Any *Australopithecus* species developed a neurulation different from that of the Hominoids, and derived from an evolution necessarily located at the homeotic genes level, a network which effects act like a time lag, spread to the whole system development and its internal dynamics. Tooth bud development depends on the neural crest cells, their differentiation is thus sensitive to the changes affecting the duration of the neurulation; cusps take more time to form.

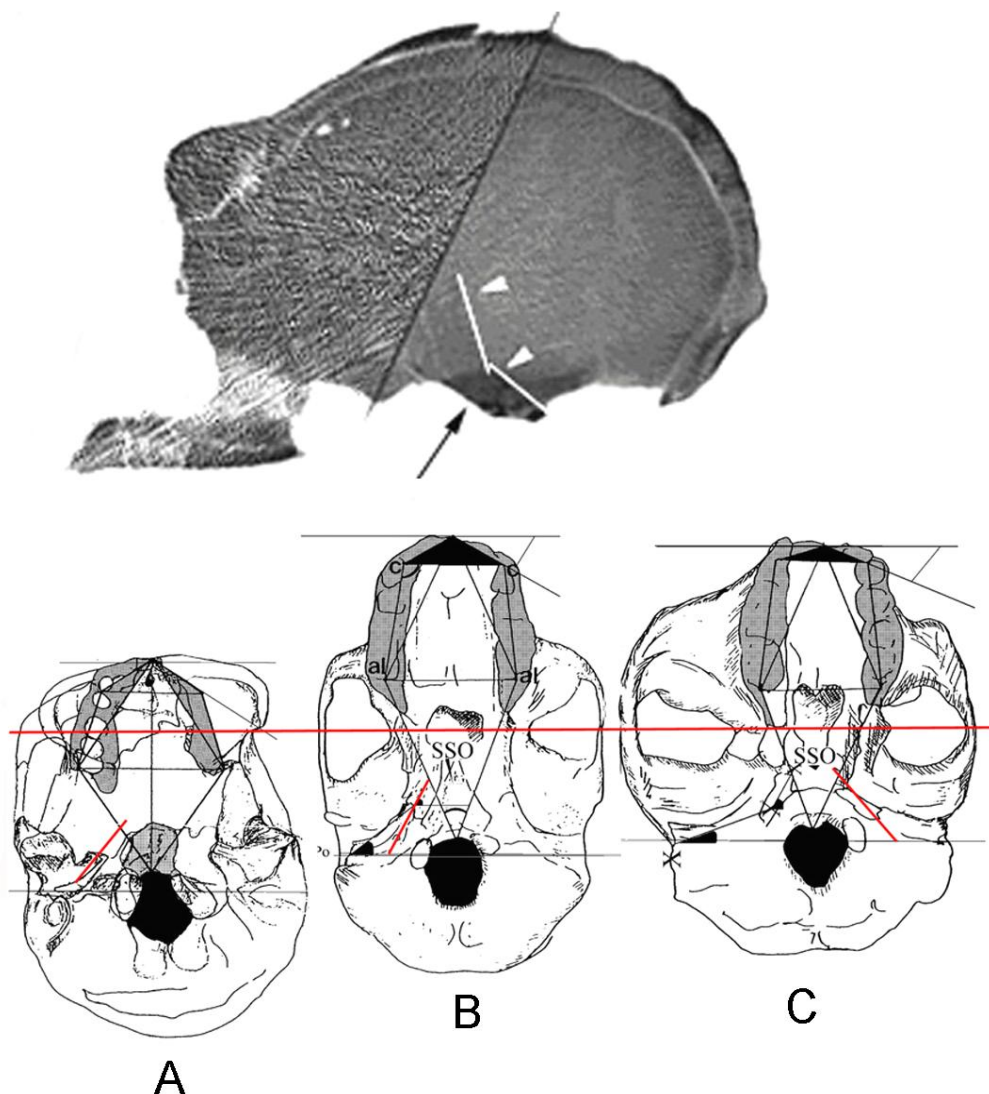


Figure 12

Above: CT scan of *Paranthropus boisei* (in Korpál 2005), white arrows: the straightening of the sphenoidal body and the less flexed basi-occipital, black arrow: the broken pharyngeal face. Below: basal view of *Homo*, *Australopithecus* and *Paranthropus*, aligned on the post-orbital constriction in the Frankfurt plane.

This is not a question of heterochronies (Macho and Wood, 1995) but a matter of consistent and coordinated regulation regarding the whole animal organizational plan. The equilibration of the constraints between the face and the base is specific and corresponds to a metamerized axial skeleton verticalized in its cephalic pole with a more reduced bending angle, hence the shortened longitudinal proportions.

An analysis of *Australopithecus* skulls from Sterkfontein, Sts 5 and Sts 505 (original CT scanners) shows a standing of the three cranial fossae marked for the first time, by the conservation of the cranio-palatine balance, quite parallel with the sphenoidal planum as in Anatomically Modern Humans (figure 13).

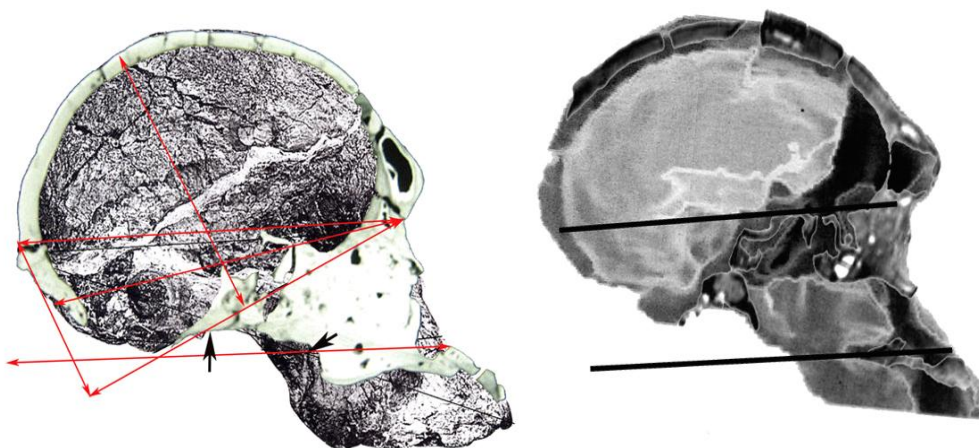


Figure 13

The approximate cranio-palatine balance in *Australopithecus africanus* Sts 5 and Sts 505 (sagittal CT scanners superposed on the exocranial view).

The antero-posterior polarity is clearly reduced to the cephalic pole that can be realized only after an increasing speno-occipital rotation during neurulation; the pelvis, the vertebral column, the hip, the knee and the podal skeleton have no homology with great apes. This discontinuity matches what we know about the modalities of homeotic gene regulation when genes are modified at the cephalic pole, with a cascade of coordinated activation up to the caudal pole, independently from arboreal adaptation which can be preserved for it is not about constraints generated by organogenesis. Thus consistent differences emerge between the hips of *Ardipithecus ramidus* and *Australopithecus*, two postures, resulting from two neurulations: one in which cephalic tensions and morphogenetic inductions are sufficient to generate a verticalized orientation of the three cranial fossae but with a standing axial skeleton able to walk with a quadrupedal equilibrium, and another one, more advanced in its amplitude, which no longer makes quadrupedal stance possible. The occlusion in *Australopithecus* is gracile, the I-C-P3 lock disappears with the deciduous dentition, and the base is not in extension any more. This pattern includes a wide variety of species from Chad, South Africa and Pliocene formations of the East African Rift.

The Paranthropus morphogenesis includes the species boisei, crassidens and robustus from the lower Pleistocene (lower limit 2.5 millions years). The I-C-P3 lock does not exist and is no more protruding, canines become confused with incisors, occlusal surfaces are end-to-end and abraded, the arch is wide and strongly frontalized, the basal angle between the two mandibular bodies is 68° , the longitudinal facial growth rate remains faster. The mandibular symphysis is straightened and presents a trigone mentale, an ossified triangular space located at the base of the symphysis which separates the two extremities of each mandibular body. Also shown in *Homo sapiens*, this space is formed gradually during the fetal period in relation with the differential growth rate between the basal and the alveolaris pars of the symphysis (Dambricourt Malassé 1987). The sphenoid body is more straightened than in *Australopithecus* and *Homo* (figure 12), with inevitable repercussions on the petrous pyramids more frontalized, as well as for the speno-ethmoidal territories which move closer to the skull base. These occlusal and architectonic alterations mean a change in the sphenoidal kinetics and, consequently, in the duration of the neurulation process.

The face of *Paranthropus* is isolated from the braincase by a strong post-orbital constriction in association with large fossa temporale, large post-canine teeth with abraded occlusal surfaces. The development of the temporal muscle causes the frontal orientation of the malar bone and flattens the face transversely; however the malar root is placed above the P4 alveolus and not of M1. This difference between *Paranthropus* and *Australopithecus* can not be reduced to the adult masticatory systems; this specialization is superimposed on a previous architectural reorganization which affects the skeletal structure from the beginning of the embryonic kinetics of the sphenoidal synchondroses. These kinetics are different from those of *Australopithecines*, the verticalization of the postsphenoid is more pronounced and provoked probably an inevitably reversed kinetics of the speno-ethmoidal territories. The canine tooth is extremely reduced, the lower incisor-canine row is aligned below the superior arch, and there is no more I-C-P3 lock. Such a significant reduction started with the tooth buds that imply an important change in the neural crests induction, i.e. in the prechordal plate during the neurulation process. These kinetics are also different from those of the *Homo* genus because the basi-occipital remained flat, breaking the pharyngeal plane.

The equilibration of the constraints is that of a permanent bipedal equilibrium, but the occluso-postural balance is different from that of *Homo* and it is probably at the end of the embryonic period between the sixth and eighth weeks that the differences occurred. A noticeable encephalization took place as a logical consequence of the time lag, to the advantage of the nervous system since the onset of the neural plate dynamics, not only the brain but also the cerebellum. Rarely taken into consideration, this latter plays an important role in each macro-evolutionary change because of the more verticalized position of the cerebellum itself, within an axial skeleton in an increasing instability.

Humans

The *Homo* morphogenesis includes the first species known as *habilis*, from 2.3 Ma in Ethiopia (Hadar) with a short and wide palate such as A.L. 666-1 (Kimbel 2009) with more space for the tongue. The occlusion is scarcely known on the most ancient specimens; the best preservation condition is illustrated by the Nariokotome adolescent (KNM WT 15000) (figure 14). The I-C-P3 complex is still protruding, ahead of the maxillary arch, but the row is more rounded, more frontalized. The mandibular arch is widened, parabolic, because the angular distance between the two mandibular bodies is more opened by 10° ; Modern Man and extant Hominoids have the same angular value at birth, but the angle closes according to the longitudinal growth rate.

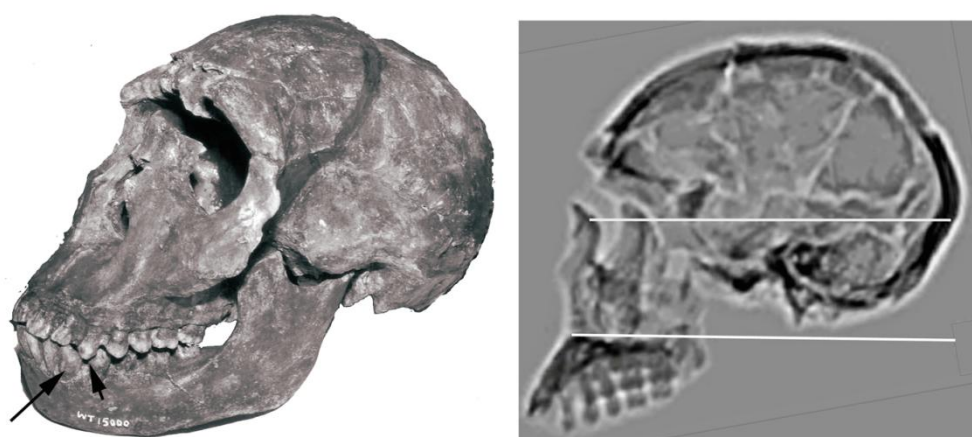


Figure 14

The approximate cranio-palatine balance of *Homo ergaster* (KNM WT 15 000) and the occlusion of the incisor-canine arches, the arrows indicate the upper and lower canines (X-rays in Korpál 2005).

An adult mandible is doubtless human if the angular value between the two mandibular bodies is 78° , giving evidence for a longitudinal growth slower than those of the hominine. The fetal triangular symphyseal notch is well noticeable with the tuber symphyseos (not to be confused with the mentum osseum), the symphysis still results in a prognathism with a symphyseal angle greater than 90° except in Neanderthals where it does not exceed this neonate value. Consequently no mandible forms a mentum osseum. The temporal fossa is particularly reduced; the manducatory apparatus and teeth get more gracile. Those differences match a longer nervous system development in comparison with *Australopithecus* (440-450 ml), as shown by a marked encephalization leading to an increasing cranial capacity from the most ancient species (600 ml, *Homo habilis*, 800 ml *Homo georgicus* 1.8 Ma), gradually increasing until the late upper Pleistocene with Neanderthals in Europe (*Homo neanderthalensis* 1,700-1,900 ml, 28 ka) and Ngandong Man in Indonesia (Solo Man, *Homo erectus soloensis*, 1,300 ml, 40 ka).

This extension of the neural growth is found again in the proportions of the base, with the verticalized cerebellar fossa and clivus as in *Australopithecus* but with the face mostly directly below the planum sphenoidal. Nevertheless the sphenoidal angle is not significant because the Sts 5 value falls into the Modern Man variability (Dambricourt Malassé 2005). The sphenoidal synchondroses must be considered as a whole since the neurulation and the chordal inductions. Unfortunately, the endocranial base of *Homo georgicus* or the remarkably preserved *Homo erectus* KNM ER 47200 have not yet been described.

A comparative analysis of the oldest *Homo* species with *Australopithecus* is a major keypoint to understand their relationships. From our point of view, this evolution is that of the neurulation (Dambricourt Malassé 1988, 1993, 2006), i.e. the entire nervous system and especially the cerebellum; it is not so much the rubicon of cranial capacity that will make the distinction possible, but the cranio-palatine balance and an unstable posture requiring the complexification of the cerebellum and its connections with the brain. The question is whether *Homo* organogenesis which is, at least, 3 million years old, emerged from the Hominoid morphogenesis such as *Ardipithecus ramidus*. Indeed, *Australopithecus* and *Homo* organogeneses are alike by the increase of the Hominoid kinetics and the closure of their sphenoidal angle.

It is likely that the neurulation of the Homo genus resulted from a parallel and quasi synchronous macroevolution from the Hominoid body pattern. An evolution of the Australopithecus neurulation results in a Paranthropus with a strong antero-posterior reduction of the speno-occipito-temporal territories; the oral cavity would not have enough space if the face was not projected outside of the neurocranial perimeter.

The latent problems in modern Human Palaeontology is the persistence of the gradual model and the conviction that the bipedal balance is the result of a micro-evolution of the post-natal locomotion similar to the arboreal adaptation, while it results from an other evolutionary determinism, that of the homeogenes. The arboreal locomotion of *Ardipithecus ramidus* was not an adaptive barrier for the success of a permanent bipedality which depends on the macroevolutionary potential of its genome; it can be the ancestor of the oldest Australopithecus species as well as of the oldest Homo species, with their very close ontogeny and anatomy, the struggles for life were the same.

Some cranial radiographs completed by exocranial cephalometric analyses enable to assess the oldest human kinetics (figure 15) already giving a good indication of the position and proportions between the upper face and the third floor of the cranial cavity. Oriented in the Frankfurt plane and centred on the porion, the analysis compares the position of the cerebellar fossa in KNM-ER 3733, KNM-WT 15000 (1.8 Ma), Kabwe and *Homo sapiens*. The cerebellar fossa stands above the prosthion in the three fossil skulls, whereas in Modern Man the occipital condyle stays close to the L4 line connecting the prosthion to the vertical line crossing the basion (Figure 15).

All these fossil species have a cerebellar fossa in a heightened position with regards to the occluso-postural balance of the modern man, *Homo sapiens*, and they give evidence of a variability included, however, within the same amplitude of the neurulation. The variability of the kinetics is visible by antero-posterior extensions, in Indonesia with Sangiran 17 (*Pithecanthropus VIII*), as well as in Europe with the late Neanderthal). In both cases, the mandibles grow with a retromolar space, i.e. the face (alveolo-dental arches) and the base (TMJ) in two opposite dynamics. All the neural growth is prolonged with a delayed hormonal development which systematically, and independently of the sexual dimorphism, provokes a pneumatization of the frontal sinus (the supra-orbital torus).

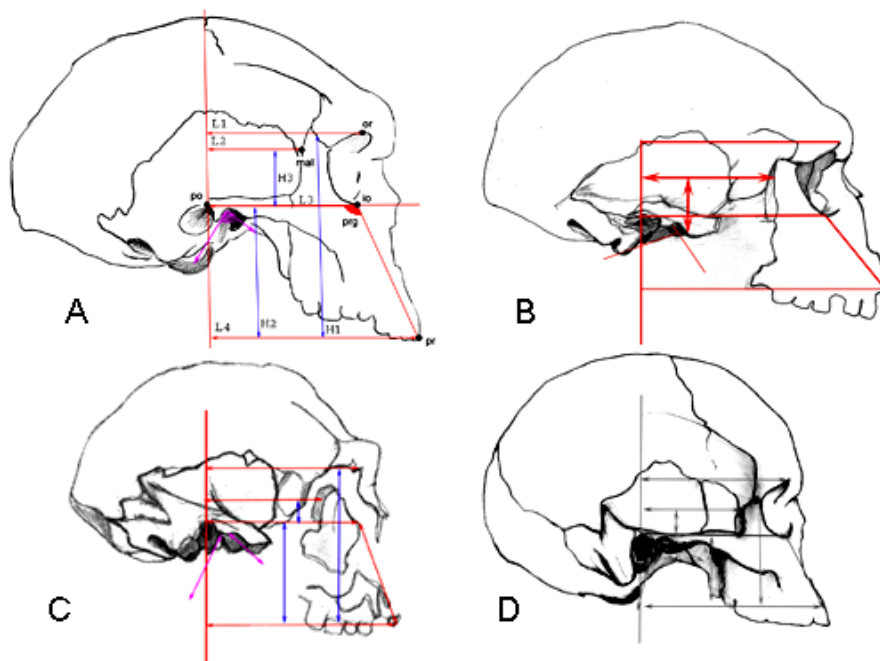


Figure 15

Exocranial protocole, A : Kabwe, B : Sangiran 17, C : KNM ER 3733, D : modern *Homo sapiens* (scale variable).

Thus the upper face keeps its longitudinal growth which separates it from the braincase, and the mandible follows, with an alveolo-dental arch mainly placed ahead of the neurocranial perimeter. The constraints of equilibration between the face and the base are not comparable yet to that of Modern Man. The occluso-postural equilibration in Neanderthal is original, and quite different from that of *Homo sapiens*, the cranio-palatine balance is preserved but it is not parallel to the sphenoidal plane like in the oldest species. The neck is higher and the base is in extension, the neurulation does not exceed the limit of the most ancient species, which is coherent with an axial and appendicular skeleton also different in its morphogenetic modalities. A comparison between the cranio-palatine balance of La Chapelle-aux-Saints (*Homo neanderthalensis*) and Cro-Magnon 1 (*Homo sapiens*) confirms these differences between the sphenoidal kinetics (Dambricourt and Deshayes 1993) (figure 16).

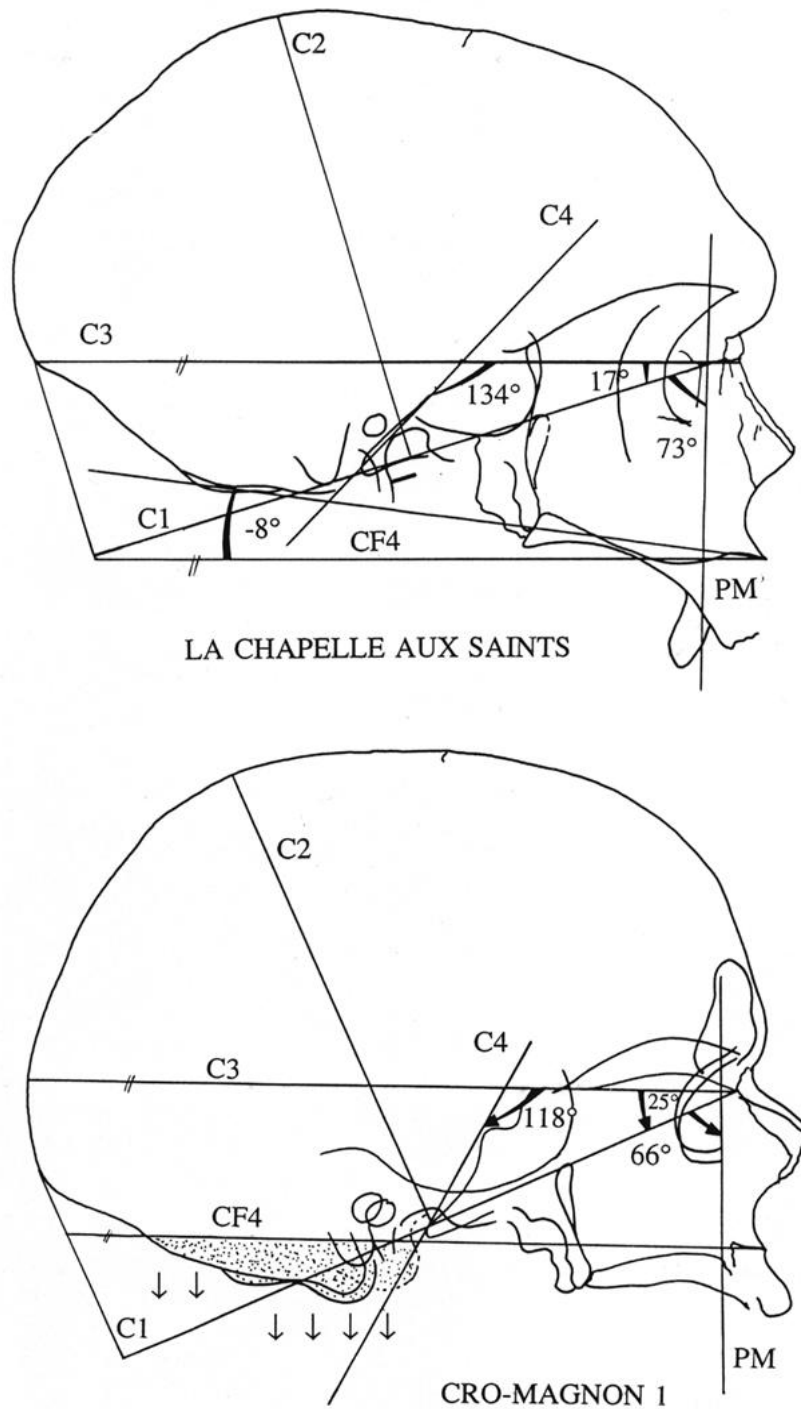


Figure 16

Cranio-palatine balance (CF4) of Neanderthal (La Chapelle-aux-Saints) and Cro Magnon 1. Neanderthal CF4 is not parallel to the sphenoidal planum. The verticalization of the three cranial fossae is clearly advanced in *Sapiens* (Dambricourt and Deshayes 1995).

The occlusion of its incisor-canine arch is end-to-end, and no longer stands ahead of the upper arch, the canine is in the alignment with the incisors. This remodelling is associated with the oncognathism, due to a third maxillary sinus which “blows” the face forwardly so that the maxillary incisor-canine arch meets over the mandibular arch. All the morphogenetic data put Neanderthal into the range of the kinetics of neurulation established from the first species of the genus *Homo*. An almost complete Neanderthal neonate (Le Moustier 2) with the sphenoid could give precious information, but the reconstitution and its biometrical comparison with *Homo sapiens* are still unpublished (Maureille 2002).

The differences between Sapiens and all these oldest species stand at the level of the genus. As a result, the Sapiens embryonic data remain far from those of Neanderthal or from any oldest species. There is no more gradualism between the Sapiens and *Homo* embryonic neurulations than between Hominoids and the two *Australopithecus* and *Homo* neurulations. The hybridization deduced from a very small percentage of genes common to Sapiens and Neanderthals (Green *et al.* 2010) is matter of strong criticism (Heyer, Escoffier) and does not sufficiently take into account the genes inherited from their common ancestors. On the other hand, the evolutionary modalities of the homeotic genes from the cephalic to the caudal pole are unknown, and hybridization seems unlikely between the ancient regulatory network and its macroevolution.

The skull of Flores (Flores Island, Indonesia), although dated from only 18 to 12 ka, relates to this first human species with the absence of chin, the supra-orbital torus and a high cerebellar fossa, a frontalization of the petrous pyramids comparable to *Homo erectus*, carpal and tarsal bones with embryonic development resembling neither that of Neanderthals, nor that of modern humans. A first approximation makes possible the assessment of the kinetics of neurulation unchanged from the first *Homo* species (figure 17).

The cranial capacity of Kabwe (Broken Hill 1, E 686, *Homo heidelbergensis*, Rhodesia, uncertain age between 130 and 300 ka) is comparable to modern *Homo sapiens* (1,280 ml), but stating that this specimen belongs the same species implies the existence of a community of embryonic neural kinetics from the emergence of the neural plate.

This implies the same ontogenetic changes for the neural development as for the cranio-sacral skeleton; nevertheless the upper face still develops ahead of the braincase with pneumatized frontal sinus (supra-orbital torus) while it would be premature to assimilate the sphenio-occipital kinetics to that of the *Homo sapiens* one (figure 15).

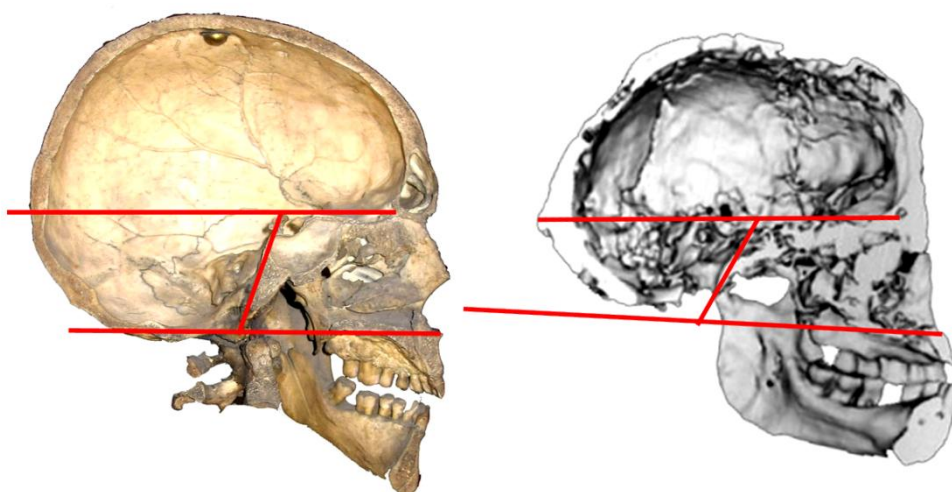


Figure 17

Homo floresiensis (right) (Brown et al. 2004) : evaluation of the cranio-palatine balance and comparison with modern *Homo sapiens*. The cerebellar fossa is highest, the sphenoid less flexed, the CF4 line is not parallel to the sphenoidal plane, the incisor-canine arches are in end to end, the mandibular symphysis is prognath (without chin). The occluso-postural balance is typical of early Homo species (scale variable).

The encephalisation thus evolved in all the inhabited territories in Africa, Europe and Asia without increasing the sphenoidal kinetics; beyond the wide geographic variety and evolutionary trends by telencephalization and cerebellization, fossils share a common morphogenetic pool, set up since embryogenesis and genetically programmed until puberty. This morphogenetic pool is independent from the species and subspecies differentiated by dichotomy and endemism and defines the genus Homo (Dambricourt Malassé 1993, Chaline et al. 2000).

The Sapiens morphogenesis: a comparison between *Homo georgicus* and Herto (Ethiopia 160 ka) centred on the porion in the Frankfurt plane, shows the pterygoid wings and the palate with a more retruded position towards the pharyngeal face of the clivus, the absence of the premaxillary (sub-nasal) prognathism, a backward movement of the dental arch relatively to the infra-orbital point which overhangs M1 in *Homo georgicus* and the interalveolar margin P3 / P4 in Herto (figure 18). These differences cannot be explained by a simple increase of the cerebellum growth, the cerebellar cortex is complicated and related to a change of the postural balance and, therefore, the occlusion.

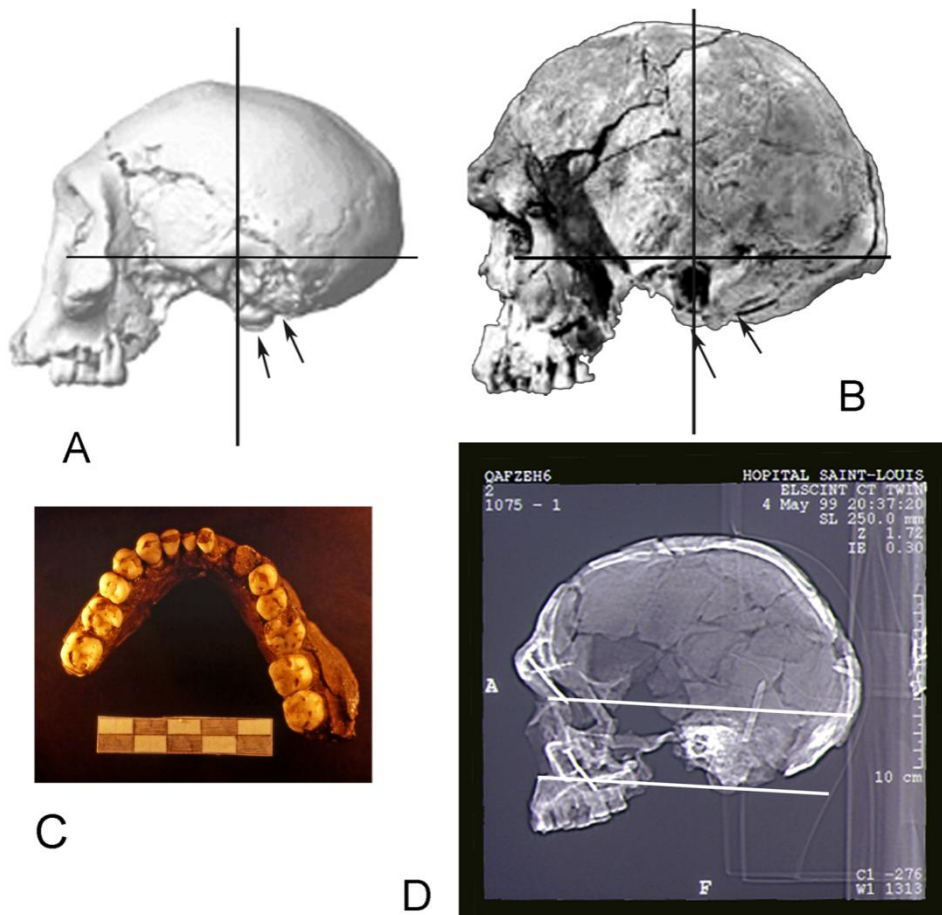


Figure 18

Comparison between *Homo georgicus* (A), Herto (B), Qafzeh 7 (C) and Qafzeh 6 (D) (scale variable) (Sources: *Homo georgicus* Vekua et al. 2002, Herto from White et al. 2003. Qafzeh: originals from A. Dambricourt Malassé D.R.).

The cerebellar fossa moves again forward only if the sphenoidal kinetics is induced by a reprogramming of the neurulation. But precisely this rebalancing of the posture observed from the middle Pleistocene, comes along with a release of the tuber symphyseos forming the mentum osseum, a differential growth between the basilar and the alveolo-dental pars of the mandible. The adult wear of the incisor-canine complex is significant because the occlusion is end-to-end. This differential growth corresponds to a slowing down of the dental growth; however, this applies to the whole body including the pars basilaris.

When the maxillary anlage moves backward during embryogenesis it pulls the mandibular arch toward the clivus. Thus the reduced subnasal prognathism, the mentum osseum, and the downward and forward bascule of the cerebellar fossa would show an increasing rotation of the spheno-occipital kinetics. The constraints of equilibration between the base and the face match a change in the duration of Homo neurulation kinetics and the nervous system development with consequences on the endocrinal functions. Indeed, the encephalization is sharply marked by the frontal lobes, a curvature of the frontal bone, more stressed at the adult stage, since the facial growth is no longer projected by the generalized pneumatization of frontal sinus. The endocrinal functions are more efficient than in Modern Man, the pneumatization is significant but limited to the eyebrow and does not form a supra-orbital torus, it becomes a secondary sexual character. In other words, the nervous system, once again, gains complexity through the elongation of its growth, a delay in the endocrinal functions and the necessity to control a more verticalized and more unstable axial skeleton.

The oldest specimens, sufficiently well preserved to observe these changes (i.e. those with the mandible) are from Omo Kibish 1 in Ethiopia (the alveolodental arch is absent but the chin is present), the protocromagnoids from the Middle East (Qafzeh 6 and the mandible Qafzeh 7, Qafzeh 9, Skuhl V) then slightly more gracile European populations with Cro-magnon 1, Combe Capelle, Predmost I and II, Isturitz, Brno III, Dolni Vestonice III, Ofnet K 1802, K 1806 with K1818 more gracile, the Chinese specimen from Zoukoudian Upper Cave CKT1, Iberomaurusians from North Africa, Fish Hoek, Cape Flats and Florisbad in South Africa and the Mesolithic populations Hoedic and Teviec (Atlantic façade, France), Tam Pong in Laos and, according to the work of Détroit (2002), the two skulls from Moh Kiew (MKC91 B1, B2) in Thailand, Song Terus 1, Song Keplek 5 in East Java (figure 19).

The modern *Homo sapiens* is well known with the incisor-canine complex seating back from the upper arch and a reduced pneumatization of the frontal sinus. The standard hypothesis explaining the skeletal gracilization and the new type of dental wear (Smith 1994) is related to the transition from the hunter-gatherer groups to agropastoralist societies around 7,000-8,000 years B.P. However, the new retraction of the mandibular arch (Guichard *et al.* 2003) is also visible in contemporary hunter-gatherers.

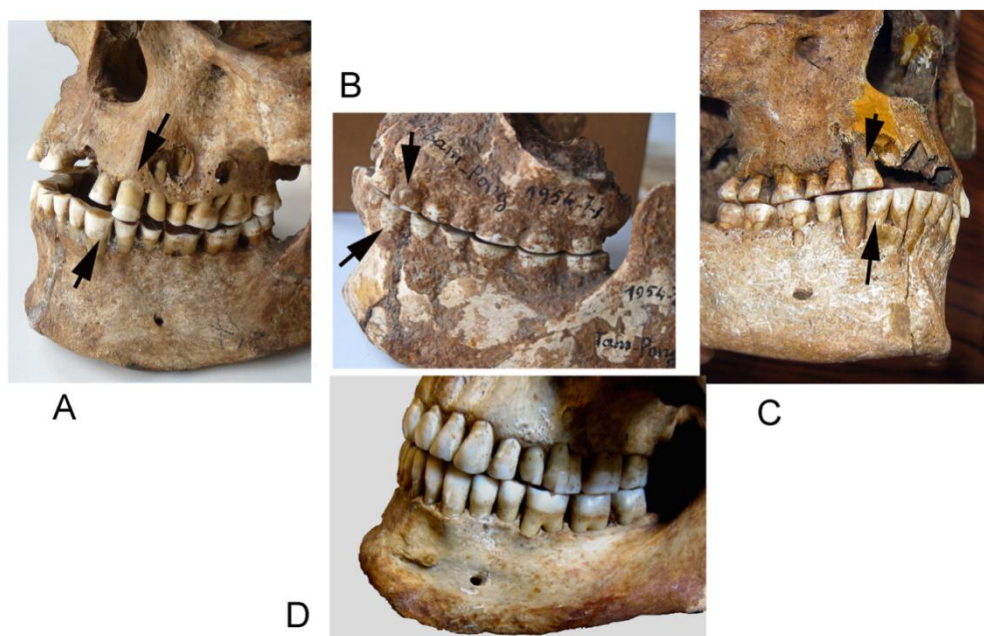


Figure 19

Comparison of the incisor-canine occlusion between the fossils Afalou-Bou- Rhummel (A), Tam Pong (B), Teviec (C) in end-to-end and modern *Homo sapiens* (D). The arrows indicate the superior and inferior canine tooth (pictures A. Dambricourt Malassé).

The growth rate of Epipaleolithic peoples is still unknown, we do not know if the evulsion of the incisors in Iberomaurusians occurred in same conditions than in modern *Homo sapiens*, since the occlusion was an end-to-end type, nevertheless change occurred in the hormonal growth factors during Middle Holocene and consecutively on the growth tempo of the synostoses.

Hadjouis (2002, 2003a,b) was the first to apply the biodynamical concept to the fossil populations and shown that during growth, the evulsion generated a reorganisation of the middle and lower faces, but in no case, he wrongly concluded apparent promandibulia (or retromaxilla) as a result from the sphenoidal flexion (Balzeau 2005). So the gracilization of the face and postcranial structures can be included in the diagnosis of the “Sapiens type of organogenesis” since the first fossils, nevertheless to understand the origins of the evolutionary process 200 ka ago and the latest change of the occlusion during Middle Holocene, we need not only the convergence of multifactorial approaches but also the development of a 3D cephalometric analysis from which the parameters are representative of the kinetics and the growth rate of each synchondrosis.

As we have seen this approach is not new in human paleontology, but its application to sub-fossil and fossil populations of Sapiens needs time and progress in medical imaging; the most important works are to come with a new generation of paleoanthropologists and palaeontologists educated with the emergent concept of Evo-Devo, the biodynamics and a global look on the organism from the cephalic to the caudal pole.

With the discovery of a macroevolutionary process acting exponentially and irreversibly in the same architectonic direction (Chaline *et al.* 2000, Chaline and Marchand 2010), we cannot exclude a phylogenetic determinism sensible to various and still unknown parameters. This protocol will first be applied to the Mesolithic skulls in order to determine what parameters changed in the past and if such data could help the understanding of the present and global troubles, especially the increase of dental malocclusions over several decades, with lack of space, frequency of dental Class II and agenesis of I2, upper P4 and M3 (lack of embryonic formation of the end of dental series).

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