

Jean Chaline  
Université de Bourgogne, Dijon

## A new view of hominid evolution

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The diversification of the common ancestor into gorillas, chimpanzees and humans can be explained through two alternative models. Both are based on the pattern of chromosomal rearrangements in extant species and entail a reappraisal of the influence of climate. The tiny genetic difference between chimpanzees and humankind is greatly amplified at the morphological level, thereby giving rise to the 'human paradox'. The answer to the paradox lies in the economical and flexible evolutionary mechanism of mutations in regulator genes and the heterochronies they control. These are the true internal clocks of evolution. Changes in cranial morphology are quantified and utilised to analyse and explain the stages in the transition from great ape to human morphology. It is suggested that numerous heterochronies punctuate the comparative development of great apes and modern humans (hypermorphosis, hypomorphosis and post-displacements). It was once thought that bipedal gait might result from climate change, but revised assessment of the role of climate shows that it has nothing like the effect once ascribed to it, although climate does bring about prior differentiation between ecological niches. The appearance of bipedalism in australopithecines was certainly not the outcome of any gradual adaptation to an increasingly dry climate; it was rather mutations of regulator genes that instantly imposed permanent bipedal gait, thereby allowing colonisation of the savannahs.

Correspondence: Prof. dr J. Chaline, Laboratoire de Biogéosciences (UMR CNRS 5561) and Laboratoire de Paléobiodiversité et Préhistoire de l'EPHE, Centre des Sciences de la Terre, Université de Bourgogne, 6 Bd. Gabriel, 21000 Dijon, France

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### INTRODUCTION

Human evolution is an area of research that requires a multidisciplinary approach.

Although palaeontology comes up with fossil finds like so many occasional snapshots from which hominid history can be reconstructed within a time frame that is being constantly refined by physical dating, it fails to provide any insight into the underlying evolutionary mechanisms. These are the realms of biology, genetics and developmental biology. It is in this perspective that a new overview is presented here covering three topics:

- (1) diversification of the common ancestor of great apes and humans with reconsideration of the role of climate,
- (2) resolution of the human paradox by the internal clocks of life. Human evolution is

a prime example of this new key to understanding biological evolution,

- (3) discussion of the origins of bipedalism.

Palaeontology is constantly contributing new information to the history of apes and humankind, as for example with the finds of *Australopithecus bahrelghazali* in Chad, known as Abel (Brunet *et al.* 1995, 1996), and the fossilised remains of neonate australopithecines and *Homo* by A. Keyser at Drimolen (South Africa). Such traces of past biological events allow family trees to be constructed within a time frame made relatively precise by means of physical dating. However, palaeontology does not yield any answers about the mechanisms behind species change. Coppens

(1986) was one of the first investigators to broaden the palaeontological approach by introducing data about tectonics and climate. A multidisciplinary approach can produce a more comprehensive view of the evolution of the apes and humankind, encompassing biology and palaeontology. The much acclaimed advances in genetics (King & Wilson 1975; Smouse & Li 1987; Miyamoto *et al.* 1987, 1988; Caccone & Powell 1989; Sibley *et al.* 1990; Pruvolo *et al.* 1991; Bailey *et al.* 1991, 1992; Perrin-Pecontal *et al.* 1992; Goodman *et al.* 1994; Goldberg & Ruvolo 1997), blood serology (Socha & Moor-Jankovski 1986) and in reading chromosomal formulas (Dutrillaux & Couturier 1986; Dutrillaux & Richard 1997; Stanyon & Chiarelli 1981, 1982, 1983; Yunish & Prakash 1982; Marks 1985, 1993; Matera & Marks 1993) mean we can now evaluate genetic distances and put forward hypotheses about the diversification of the common ancestor (Chaline *et al.* 1991, 1996). Finally a new area of research has arisen, that of developmental biology, linking the genetic programme to changes in form acquired by species in the course of geological time. The implementation of a new approach in comparative embryology (Dambricourt Malassé 1987, 1988, 1993, 1996; Deshayes & Dambricourt Malassé 1990; Millet 1997) and evidence of alterations in the timing and tempo of development (Chaline *et al.* 1986; Shea 1988, 1989; Reilly *et al.* 1997; Tardieu 1997; Penin 1997; Chaline *et al.* 1998; Chaline 1998), provide fresh insight into the evolution of the apes and humankind (Chaline 1994, 1996; Chaline & Marchand 1999).

#### **HIERARCHICAL ARRANGEMENT AND UNCOUPLING OF THE LEVELS OF INTEGRATION OF THE LIVING WORLD**

This global approach involves a first essential concept for understanding the phenomenon of evolution: that of a hierarchy in the organisation of the living world and of the uncoupling of the different levels.

#### **The echelons of the living world**

The initial biological level is that of the genetic programme (genes and chromosomes) controlling molecular synthesis. These form another level of integration, that of the cells. The cells in turn are arranged at a higher level still, that of the organs, the assembly of which, in accordance with sometimes very stringent, sometimes more flexible rules of development, leads to the level of the individual organism. Individuals constitute populations, which collectively form a given species. Species develop various patterns of behaviour (ethology) with respect to other organisms and are distributed in ecological niches characterised by physical features, in particular climatic and biological features (ecology). A new species is distinguished from other related species by discontinuity which ensures the essential reproductive isolation, but which may occur at any level of organisation of life. The changes occurring at different levels of organisation are often muted or amplified from one level to another (Chaline 1996), giving rise to genetic/morphological uncoupling phenomena (Courant *et al.* 1997).

#### **The human paradox: uncoupling between genetics and morphology**

The evolution of apes and humans is one of the striking examples of uncoupling between genetic and morphological divergence (King & Wilson 1975). The genetic divergence between humankind and the chimpanzee, as calculated from a  $\omega\eta$ -globin gene sequence, is 1.61%. The corresponding figures are 1.84% for the gorilla and 3.46% for the orang-utan (Miyamoto *et al.* 1987). The human-chimpanzee grouping is corroborated in many DNA sequences concerning epsilon and alpha immunoglobulin pseudogenes (Ueda *et al.* 1989), 12S (Hixson & Brown 1986) and 28S ribosomal genes (Gonzalez *et al.* 1990), part of the tRNA<sup>His</sup>, tRNA<sup>Ser</sup>, tRNA<sup>Leu</sup> genes, part of the ND4 et ND5 genes (Hayasaka *et al.* 1988) and finally oxydase II of mitochondrial gene cytochrome (Horai *et*

*al.* 1992; Pruvolo *et al.* 1993). The genetic proximity of the chimpanzee, gorilla and humankind results from their sharing a common ancestor from which their genetic make-up was inherited. Divergences in form (phenetic) are much greater, in the order of 50%, although they have not yet been completely quantified. This uncoupling between divergences at both levels of organisation constitutes what I call the human paradox.

### RECONSIDERATION OF CLIMATES OF AFRICA AND THEIR ROLE IN HOMINID EVOLUTION

Climate has occasionally been considered to be the driving force behind human evolution. For example, Coppens (1986, 1994) argued that the relief associated with the East African Rift Valley, by creating a N-S climatic barrier, engendered bipedalism and the split between apes and humankind. He asser-

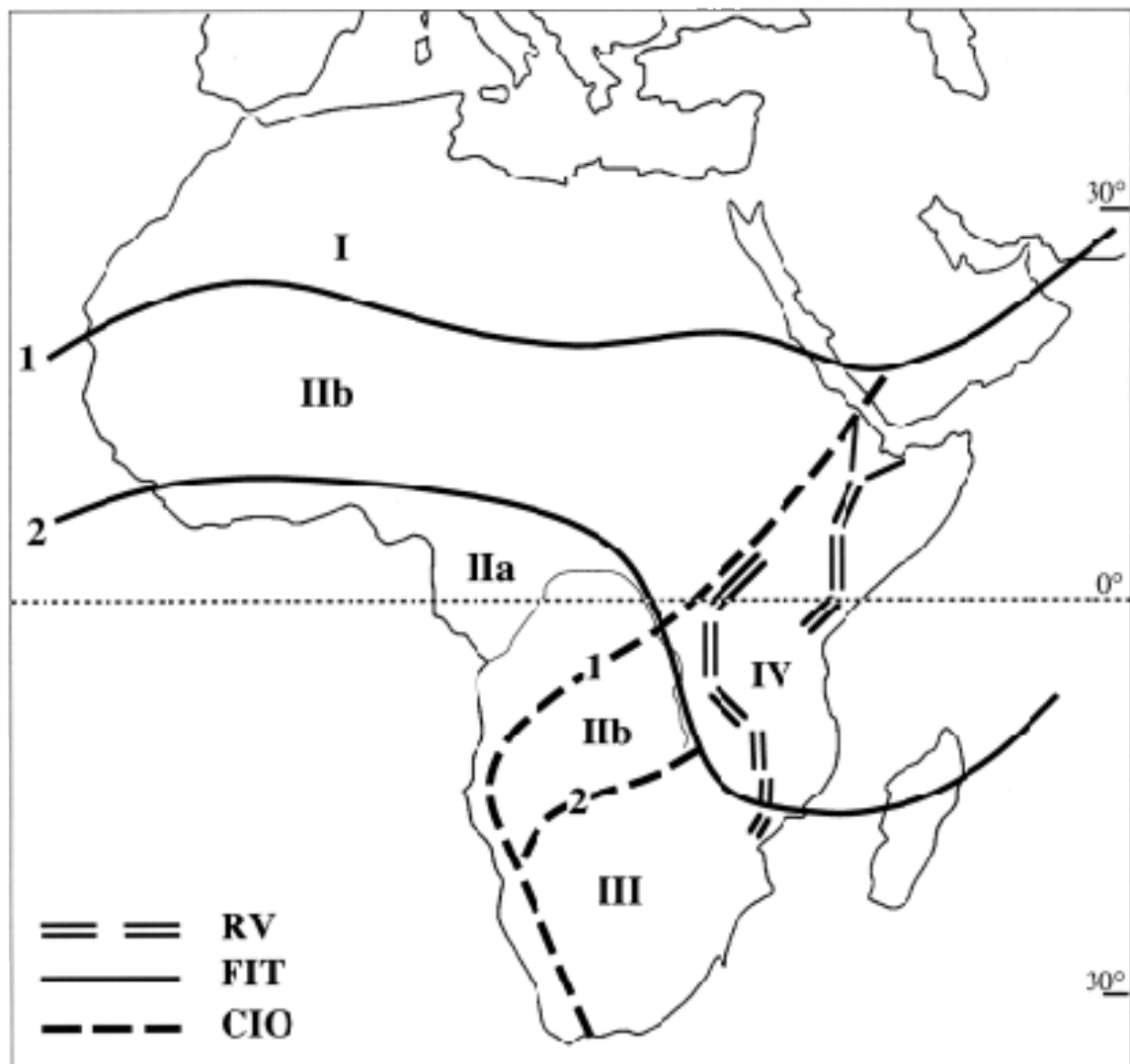


Figure 1 Presumed, general geographical distribution of climates and environments in Africa between 23 My and the Present. **FIT** Inter-Tropical Front; **CIO** Inter-Oceanic Confluence; **1** summer; **2** winter; **I** area of continental trade-wind; **II** area of Atlantic monsoon; **IIa** area of permanent Atlantic monsoon; **IIb** area of seasonal Atlantic monsoon; **III** area of Indian Ocean trade wind; **IV** area of East African monsoon; **RV** rift valley (after Scotese *et al.* 1988, completed by Durand 1995).

ted that australopithecines became bipedal because of the need to stand upright to spot their predators in savannah environments. This Lamarckian conception is now completely outdated (Chaline 1998). In fact, the major climatic domains of Africa are governed by atmospheric dynamics (Chudeau 1921, Leroux 1975, Sarnthein *et al.* 1982, Ruddiman & Raymo 1988, DeMenocal 1995, Durand 1995) and are dependent on:

- (1) the position of Africa relative to the geographical equator (where rising air allows cloud formation) and
- (2) the oceans surrounding the continent and supplying the water vapour necessary for cloud formation in the form of monsoons.

The boundaries of the climatic zones are therefore determined primarily by the annual oscillation of the E-W meteorological equator which cuts the inter-oceanic confluence perpendicularly (junction of the Atlantic and Indian Ocean monsoons) running N-S in the northern part and veering S-W in the southern part (Fig. 1). It is because the northern part of the inter-oceanic confluence roughly coincides with the position of the Rift Valley that some observers came to believe that the tectonic zone could account for the climates and the diversification of hominids. In fact, the present-day climatic situation came about very gradually ever since the South Atlantic Ocean opened up some 130 million years ago and Africa pivoted and drifted northwards by more than 3,000 km (Scotese *et al.* 1988). The geographical equator lay a mere 600-km further north by about 23 My. The distribution of the different environments associated with the main climatic domains seems to have become comparable with the present-day pattern by about 15 My (Bonnefille 1987, Maley 1987, Takashi & Jux 1989, Retallack *et al.* 1990, Kingston *et al.* 1994). It was therefore not the Rift Valley, formed a mere 8 million years ago, that dictated environmental changes but the position of the continent relative to the equator; and it was not the tectonic valley that was responsible for the appearan-

ce of bipedalism in hominids. Climate exerts a significant influence and was instrumental: (1) in the prior establishment of ecological niches allowing the common ancestor to become differentiated into three subspecies heralding the three present-day genera; (2) in dividing up the area of distribution of species, resulting in the present-day subspecies of gorillas and chimpanzees; (3) in facilitating relative fluctuations of the geographical areas of distribution of the various species, particularly the spread of australopithecines across the African savannah from north (Chad, Ethiopia) to south (South Africa), (4) in determining adaptive geographical differentiation among australopithecines, *Homo erectus* and *Homo sapiens*.

### THE COMMON ANCESTOR

The existence of an ancestor common to chimpanzees, gorillas and hominids is also demonstrated by comparison of chromosomal formulas characteristic of the various extant species. The history of the common ancestor can be broken down into three distinct major stages.

#### The early days of the common ancestor: a homogeneous species

Comparison of the chromosomal formulas of gorillas, chimpanzees and modern humans (Fig. 2) brings to light a remarkable fact. All three share seven identically reworked chromosomes, which are not found in the orangutan (Dutrillaux & Couturier 1986). These chromosomal re-arrangements must therefore have come about after the Asian branch of orang-utans broke away, and they are the clearest evidence of the existence of the common ancestor, which passed them down to the three genera (gorilla, chimpanzee and humans). The simplest explanation for the occurrence of these seven re-arranged chromosomes is to accept that the mutations appeared in the common ancestor. This first homogeneous stage of the common ancestor (phase 1) probably lasted a comparatively

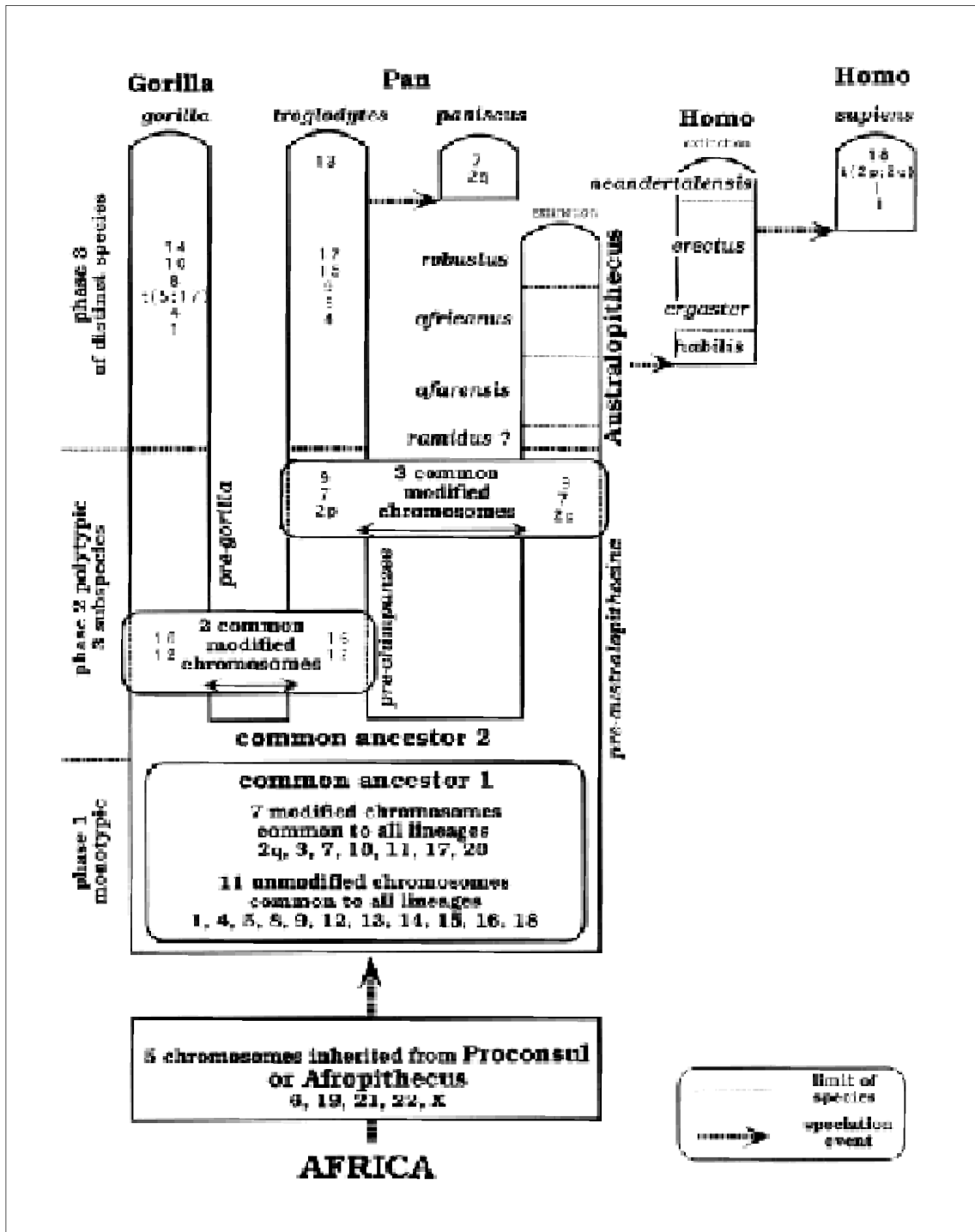


Figure 2 Trichotomous chromosomal model incorporating palaeontological and ontogenic data. After a monotypic stage accounting for chromosomal apomorphies 2, 3, 7, 10, 11, 17 and 20, the common ancestor must have become polytypic and divided into three subspecies: pre-gorilla, pre-chimpanzee and pre-australopithecine. Some five million years ago the three subspecies produced the extant and fossil genera: *Gorilla*, *Pan* and *Australopithecus*. About 2 My ago the *Homo* lineage derived from *Australopithecus* to give primitive man (*Homo*) and around 0.18 My modern humans (*Homo sapiens*) (after Chaline *et al.* 1996 modified).

long time (3 - 4 My) to enable the seven chromosomal re-arrangements to accumulate (Chaline *et al.* 1991, 1996).

### **Diversification of the common ancestor into two or three subspecies**

There are two further paradoxical observations (Fig. 2). The first is the occurrence of two identical re-arrangements on corresponding chromosomes in the gorilla and chimpanzee. The second is that of three identical re-arrangements shared by chimpanzees and humans, but not found in gorillas. To describe this highly paradoxical situation, Dutrillaux & Couturier (1986) proposed the existence of an undetermined populational phenomenon. Two models of diversification of the common ancestor can be considered, the trichotomous and dichotomous models, which must integrate an essential palaeontological component, the bipedal ape *Australopithecus*.

**The trichotomous model.** In order to explain the unequal distribution of re-arranged chromosomes in the three extant genera, it must be accepted that at some time in its existence, the 'homogeneous common ancestral' species subdivided into three subspecies; this was the heterogeneous second phase. This division of the common ancestor into three interbreeding subspecies, forerunners of the three extant genera, which we shall term pre-chimpanzee, pre-gorilla and pre-australopithecine, occurred interactively with differentiation of the climatic environment. Observation of the contact of the three main climatic zones in Africa, whose distribution in the mid Miocene must have been pretty similar to the present-day situation, shows (Fig. 1):

- (1) in the West, equatorial rain forest related to the permanent Atlantic monsoon, where gorillas are still found today on the right bank of the River Congo;
- (2) to the north, a zone affected by the Atlantic summer monsoon; this is the zone where some of the chimpanzees are still found today;
- (3) to the east, bounded by the inter-oceanic

confluence, the zone of influence of the trade winds and monsoons of the Indian Ocean where most of the remains of australopithecine bipedal apes have been unearthed, except for Abel, discovered in Chad 2500 km west of the Rift Valley (Brunet *et al.* 1995).

This seems to explain how two identical re-arranged chromosomes came to be shared by pre-gorillas and pre-chimpanzees and three re-arranged chromosomes by pre-chimpanzees and pre-australopithecines. The absence of common re-arrangements between pre-gorillas and pre-australopithecines implies geographical separation. Given that the earliest remains attributable to the great apes are located in the region of Lake Victoria, hypotheses can be proposed for the diversification of the common ancestor from this zone, as set out in Figure 3. This trichotomous model cannot readily explain why the three re-arrangements in pre-chimpanzees and pre-australopithecines were not passed on to pre-gorillas and vice-versa. The dichotomous model resolves this dilemma neatly.

**The dichotomous model** implies that the common ancestor, in its heterogeneous second phase, first split into two geographically isolated subspecies, the pre-gorilla (to the west) and the pre-australopithecine (to the east), each sub-species having acquired the two and three identified re-arranged chromosomes respectively. Then two populations of pre-gorilla and pre-australopithecine met and interbred, with the resulting hybrid form giving a third subspecies, the pre-chimpanzees, with the five re-arrangements observed. This is the most parsimonious explanation.

Both models involve a third phase of transformation of the three subspecies into three separate species. Proof of this ancient genetic isolation is provided by comparing the chromosomal formulas of the three groups, where it can be seen that each group acquired unique and independent chromosomal re-arran-

gements (Dutrillaux & Couturier 1986): six in chimpanzees, six others in gorillas and four others in the course of the history from pre-australopithecines to their present-day human descendants (Fig. 2). Palaeontological data for australopithecines dates this isolation to at least 5 My. But the phenomenon did not stop there, because since that time the species have subdivided. Three subspecies of chim-

panzees appeared successively by derivation, from west to east, *Pan troglodytes verus*, *P. t. troglodytes* and *P. t. schweinfurthii*; (Goldberg & Ruvolo 1997). An analogous intraspecific subdivision is found in gorillas with *Gorilla gorilla gorilla*, *G. g. graueri* and *G. g. beringei*.

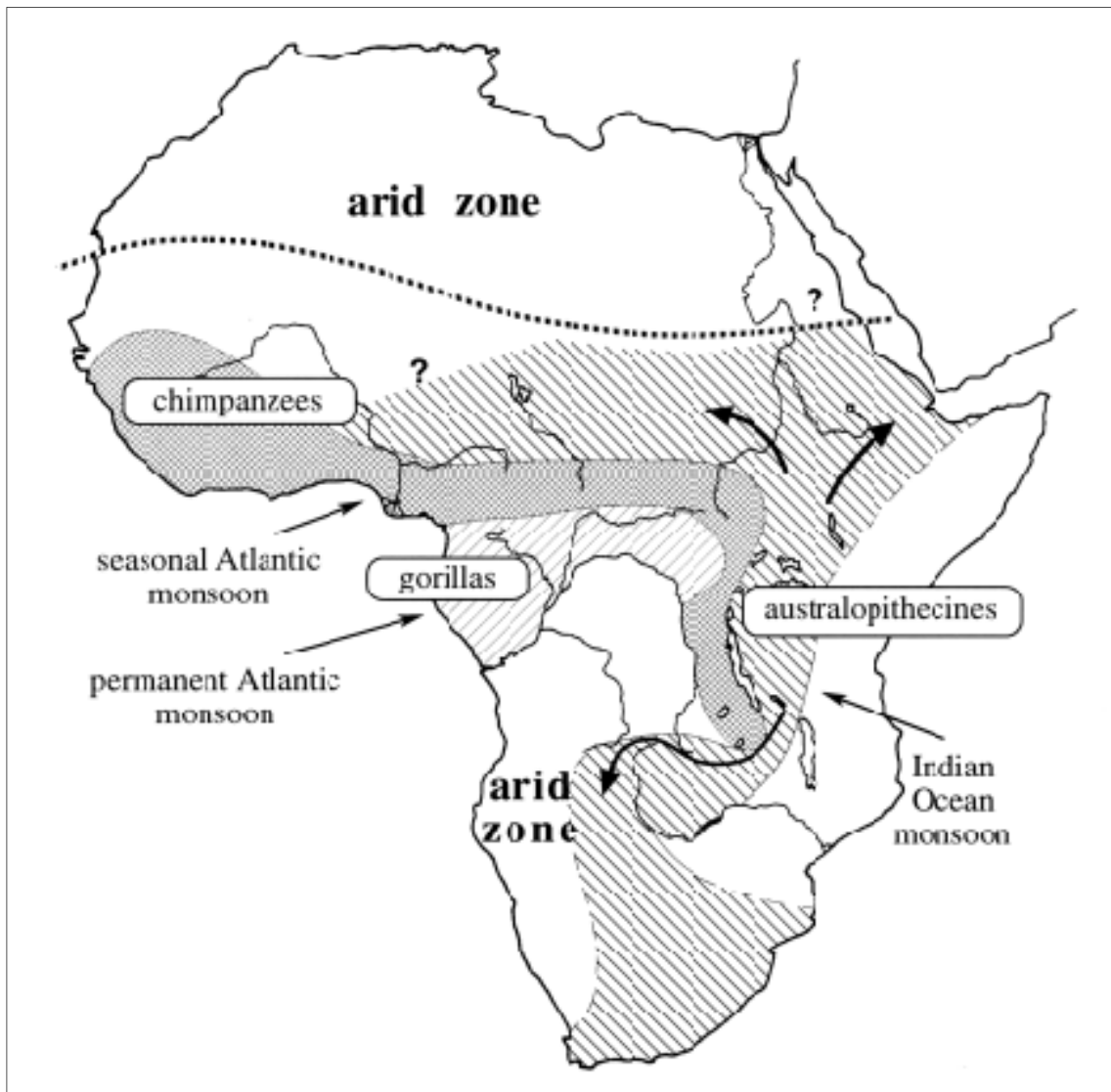


Figure 3 Distribution of gorillas, chimpanzees and *Australopithecus*. Chimpanzees spread across NW Africa, north of the Zaire River (ex. Congo River), in a mosaic of forest-savannah habitats as far as Guinea. Gorillas must have been confined to the west in the tropical rain forests north of the Zaire River. The australopithecine group separated from the two other genera around 5 My and invaded the savannahs of eastern Africa to the north and from there the western savannahs as far as Chad (Koro Toro), and southwards they reached South Africa by skirting round the Zambezi River which probably formed a geographical barrier.

## MORPHOLOGICAL CHANGES FROM APES TO HUMANS

Comparison of the morphologies of apes and humans shows, if we confine ourselves to modifications of the skull alone, that primate evolution is characterised by a major phenomenon: increased cranial capacity and cranio-facial contraction accompanied by broadening of the mandible. Deniker (1886) was the first observer to notice the importance of flexure at the base of the skull, which was later taken up by Anthony (1952) with particular emphasis on the forward shift of the *foramen magnum*, and then by Biegert (1936, 1957), Schultz (1926, 1936, 1955, 1960), Delattre (1952, 1958) and Delattre & Fenart (1954, 1956, 1960). The latter two workers showed that cranial ontogenesis of apes and humans is characterised by varying degrees of cranio-facial contraction depending on the genera in question. This dynamic phenomenon, inherent to the entire group of primates and to mammals generally, was taken up by Dambricourt Malassé (1987, 1988, 1993, 1996) who distinguished six separate organisation plans of cranial morphology in primates, identifiable from the varying intensity of cranio-facial contraction.

New developments in geometric morphometry, in particular the Procrustes programmes using the homologous point method (Sneath 1967, Rohlf & Bookstein 1990, David & Laurin 1992, Penin 1997), now enable us to quantify morphological differences between skulls independently of size differences (Chaline *et al.* 1998):

- (1) Intense cranio-facial contraction and expansion of the cranial vault mark the transition from an ape skull to that of an australopithecine. Despite the more intense cranio-facial contraction than in gorillas, the skull still features the superorbital ridge, the constriction behind the eye sockets, and a sagittal crest in males. This is what earns australopithecines the name of bipedal apes, because the skull retains

an ape-like structure despite the acquisition of bipedal gait, albeit of a different type from ours (Deloison 1991, 1995).

- (2) The transition from australopithecine to primitive man is reflected by occipital rotation with an anterior shift and tilting of the *foramen magnum*, posterior extension of the skull and broadening of the frontal bone with increased cranial capacity.
- (3) Finally the transition from *Homo erectus* to modern humans (*Homo sapiens*) is marked by occipital rotation, marked elevation of the cranial vault and lowering of the skull base, thereby increasing cranial capacity, and by shortening of the face which becomes vertical; to this is added the disappearance of the simian characteristics such as the brow ridge.

These data suggest the occurrence of three separate cranial organisation plans: the 'great ape', 'australopithecine' and 'Homo' plans, including both primitive and modern humans; this latter conclusion is confirmed by the works of Penin (1997). Figure 4 recapitulates these transformations, emphasising the overall trends of cranio-facial contraction which occur in stages modifying the shortening and verticalisation of the face, the contraction of the skull, the tilting of the *foramen magnum* and the increase in cranial capacity.

## THE SOLUTION TO THE HUMAN PARADOX THROUGH THE INTERNAL CLOCKS OF LIVING ORGANISMS

An explanation of the substantial morphological change accompanying the slight genetic divergence between apes and humans can be proposed on the basis of data of evolutionary and comparative developmental biology.

### Development heterochronies

The development of characters of a species can be modified in its descendants in terms of duration (shortened: hypomorphosis; exten-



ded: hypermorphosis), tempo (deceleration; acceleration) or of the time signal for its emplacement (pre- or post-displacement) (Gould 1977; Alberch *et al.* 1979; Shea 1988, 1989; Reilly *et al.* 1997). These shifts determine two types of heterochronic pattern: paedomorphosis which maintains ancestral juvenile characters in the adult descendant and peramorphosis which, on the contrary, gives rise to new characters.

**Genetic control of heterochronies**

These changes in the timing of development are well known in the animal world where their genetic and hormonal mechanisms have been elucidated in some cases, as with the retention of the 'premetamorphic' morphology of the axolotl *A. mexicanum* (hypomorphosis after Reilly *et al.* 1997) determined by one or more genes (Voss 1995) triggering or inhibiting the production of a growth hormone. It is the regulator genes that are involved

in the development of a species and these can produce mutations modifying the timing of their action. Their identification has been underway for several years now; these are the *Hox* genes (Gehring 1985, McGinnis & Kuziora 1997. De Robertis & Sasai 1996, Carroll 1995, Raff 1996, Pennisi & Roush 1997, Hérault & Duboule 1998, Meyer 1998). A minor change in the genetic programme can therefore induce considerably amplified consequences through the mechanism of changes in the timing of development.

This explains, for example, how digits were formed since the appearance of tetrapods in the late Devonian (around 370 My). We know that *Hox* genes are closely involved in the evolution of homologous series and that in all tetrapods they are indispensable for limb formation (Hérault & Duboule 1998). Limbs are invariably constructed in three successive stages:

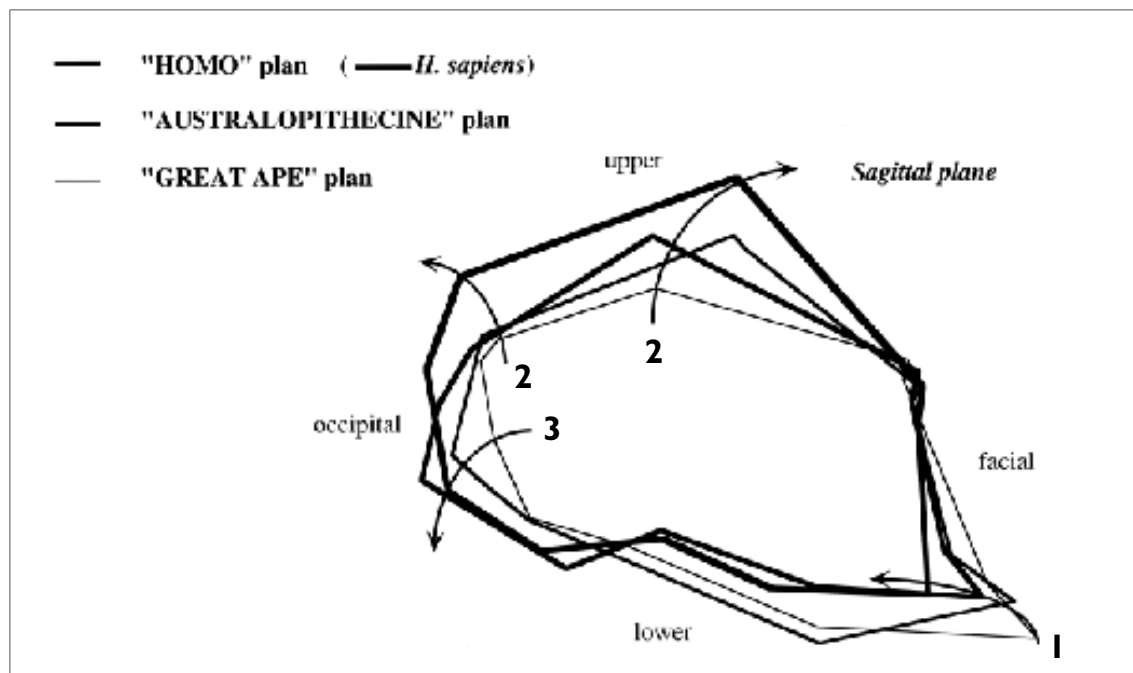


Figure 4 Recapitulation of the stages of morphological change in the evolution of hominid skulls between the three plans: 'Great Ape', 'Australopithecine', 'Homo' and *Homo sapiens* (simplified outline of vector field in sagittal plane). (1) retreat and verticalisation of face, (2) contraction of skull and increase in cranial capacity, (3) tilting of *foramen magnum* (the direction of tilt relative to the horizontal being reversed between *Australopithecus* and *Homo erectus*) (after Chaline *et al.* 1998).

- (I) the humerus and femur appear first,
- (II) the radius and cubitus, and tibia and fibula appear second, and
- (III) the hand and foot last.

In zebra fish stages I and II of development of paired limbs are similar to those occurring in tetrapods; however, stage III does not occur. It can therefore be considered that the third stage, i.e. the appearance of the hand and foot is a fundamental morphological innovation in tetrapods. Knowledge of developmental biology acquired in recent years allows us to propose an embryological solution to the transition from fin to foot (Dollé *et al.* 1993, Hérault & Duboule 1998, Chaline & Marchand 1999). In sarcopterygian (fleshy finned) fish, the paired limbs are articulated by a single bone on the scapular and pelvic girdles; these limbs also have a segmented endoskeletal axis. Study of fossil forms and of the Coelacanth, as the only extant representative, shows that it is the femur and humerus that appear first, probably around the late Silurian, followed by stage II and finally stage III in the late Devonian.

Embryological studies have shown that the following series of events is controlled by the regulator genes *Hoxd-9/13* (Hérault & Duboule 1998). In stage I, it is the *Hoxd-9* and *10* genes that are expressed in the totality of the limb bud until the first component of the limb is formed. Stage II is initiated by *Hoxd-11* and *12* genes. Stage III begins eventually when the *Hoxd-13* gene acts in the terminal bud. In this instance, the ontogenetic and the historic series concord: ontogeny really does recapitulate phylogeny. As regards limbs, the transition from fish to tetrapods is reflected by the acquisition of stage III, allowing the development of feet and hands. Palaeontological history seems to show that this potential has been expressed once only, but that it was sustained and amplified. In this case it is the organ that allows the function to be acquired!

It is also known that a simple mutation of the

*Hoxd-13* gene governing limb morphogenesis induces a local heterochrony giving a mouse with neotenic limbs (deceleration), with loss of phalanges, shortening and fusion of the bones, or even total disappearance of the digits (Dollé *et al.* 1993, Hérault & Duboule 1998); there are therefore probably close ties between heterochronies and regulator gene mutations. This mechanism of the 'internal clocks of living matter' provides new insight into the morphological changes of evolution.

#### APPLICATIONS OF HETERO-CHRONIES TO HOMINIDS

The rationale of heterochronies has already been applied to hominids in general terms (Gould 1977; Chaline *et al.* 1986; Shea 1988, 1989; Penin 1997; Chaline *et al.* 1998; Chaline & Marchand 1999), but the phenomenon can be analysed in more detail in the light of the review by Reilly *et al.* (1997). Comparison of the different stages of development of apes and humans (Dambricourt Malassé 1987, Millet 1997) suggests that cranio-facial contraction and human characteristics are related in part to changes in the timing and the tempo of development of characters through the different stages of the individual's life: embryonic, foetal, lacteal (milk teeth) or substitution (replacement of milk teeth by permanent teeth) (Chaline *et al.* 1998).

The embryonic phase, which lasts for two weeks in chimpanzees, is extended to eight weeks in humans and it is during this phase that nerve cells multiply by 5000 neurons per second, resulting in humans having some 100 billion neurons. The extension of this period and cellular multiplication in humans is therefore of the hypermorphic type and entails hypertrophy of the brain.

The foetal phase lasts just one month longer in humans than in chimpanzees, whereas Portmann (1941) argues it should last 21 months; this means therefore that it has been shortened by the action of bipedalism that

entails earlier parturition than expected. Development of cerebral growth is slowed between the 30<sup>th</sup> and 40<sup>th</sup> weeks; therefore deceleration occurs (Lazar 1986). Human parturition can be thought of as the outcome of greatly truncated post-displacement giving an image of paedomorphosis, as human babies are less mature than chimpanzee offspring at birth, but can still pass through the birth canal.

The lacteal phase, lasting three to four years in chimpanzees and six to seven years in humans, terminates with the eruption of M1. The doubling of the duration of this phase is due to post-displacement of the appearance of this character. At the beginning of this period, the *foramen magnum* is located inferiorly in the young chimpanzee, which explains why they are often bipedal up to 18 months of age, but the tilting of the *foramen magnum* to the rear during this period brings about the

quadruped gait of the adult chimpanzee. The position of the *foramen magnum* and the general rounded and juvenile shape of the young chimpanzee skull are maintained in human adults (Fig. 5) (Millet 1997, Chaline *et al.* 1998), implying a process of hypomorphosis, as the posterior tilting of the *foramen magnum* does not occur in humans. This blocked position of the *foramen magnum* imposes permanent bipedal gait. It is this observation that was interpreted as foetalisation by Bolk (1926), and as retardation of human development by Gould (1977) and Verhulst (1993).

In the substitution phase, the same process of hypomorphosis prevents the appearance of simian characters (superorbital ridge and fang-like canines). This phase ends with the onset of sexual maturity marking the beginning of adulthood at about six to seven years in chimpanzees and about 14 years in

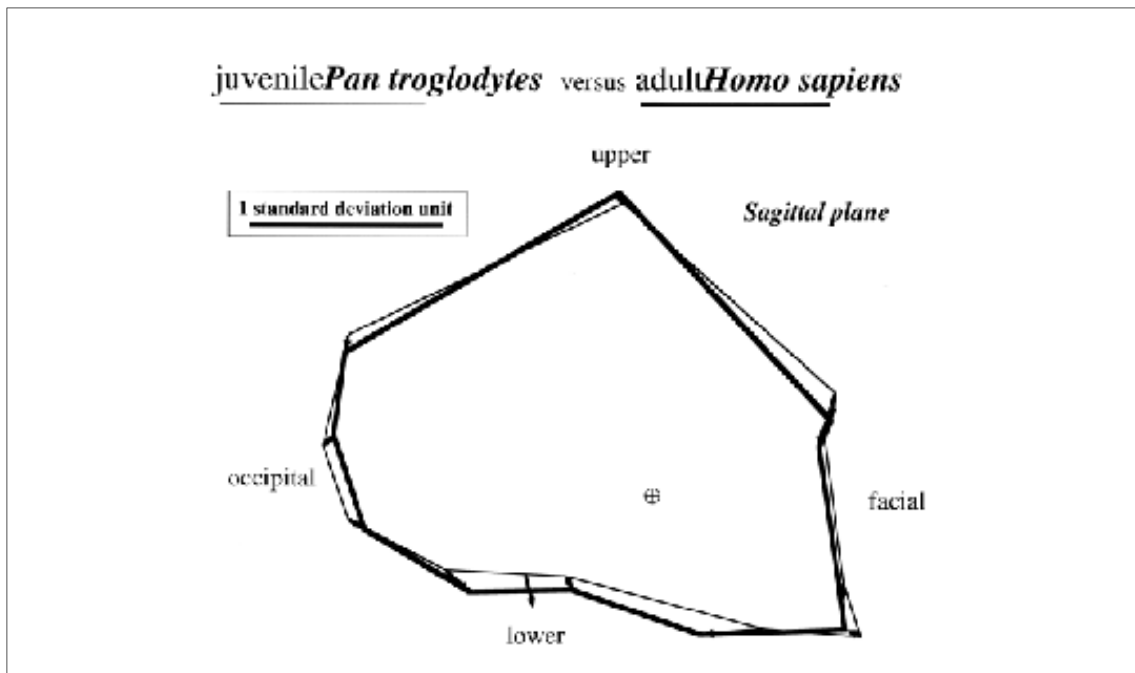


Figure 5 Comparison of a juvenile *Pan troglodytes* skull (Great Ape) and an adult *Homo sapiens* skull in the sagittal plane. Points with no vectors indicate zero or negligible morphological variation. The vectors, on the contrary, indicate significant variation: vector direction and length specify the orientation and intensity of the morphological differences. The ringed cross marks the barycentre (after Chaline *et al.* 1998).

humans. This postponement, which is a post-displacement, doubles the duration of the phase. It is during this phase that innovations arise affecting the femur (modification of the epiphysis) and this extended growth period means these bones are much longer than in apes and australopithecines (Tardieu 1997). It is during this phase again that the capacity for abstract thought is acquired, enabling the transmission of culture.

The transition from ape to human morphology therefore involves complex phenomena of heterochronies. Hypomorphosis of general skull shape imposes permanent bipedalism and prevents the appearance of simian characters, giving humans a juvenile paedomorphic appearance. In contrast, hypermorphosis of the nervous system increases brain size and post-displacements of several characters extend the lacteal and substitution phases (peramorphosis).

### CONCLUSION

The 98% genetic identity between chimpanzees and humans together with the seven identical re-arranged chromosomes are indelible marks of the existence of a common ancestor which must have lived in Africa between 10 My and 5 My. Three major changes attested by palaeontology occurred after the common ancestor episode:

- (1) the acquisition of bipedalism in *Australopithecus*,
- (2) the increase in cranial capacity and the improvement of bipedalism in primitive humans, and finally
- (3) a new increase in cranial capacity associated with the non-appearance of the later simian characters in modern humans.

The externalist approach (Eastside story of Coppens), with its claim that climate was responsible for the gradual appearance of bipedalism, now seems to be ruled out by biological, palaeogeographical and palaeontological data, and by the palaeoclimatic data

on which it was based. The pattern of different environments in relation to the main climatic domains (permanent or seasonal Atlantic monsoons and Indian Ocean monsoons and trade winds) seems to have been comparable with the present-day situation since about 15 My, i.e. well before the formation of the Rift Valley (8 My). Biological data, however, support the embryonic origin of cranio-facial contraction which determined the increase in cranial capacity and, through the position of the *foramen magnum*, brought about bipedalism. Mutations occurring probably in regulator genes (*Hox* or others) seem to lie behind the genetic/morphological uncoupling and explain human morphological characteristics through the bias of a mosaic of heterochronies of development.

It appears increasingly clearly that the evolution of species in general and of humankind in particular is related to an internal driving force, that of the saltatory, economical and flexible mechanism of the clocks of life, and that the environment, of which climate is an important component, plays only a secondary external role, affecting populations and the diversification of subspecies. It was not climate and the environment that determined permanent bipedalism through gradual adaptation but the permanent support of the cranial structure of juvenile apes with the *foramen magnum* at the base of the skull that imposed bipedal gait. It is obvious that the maintenance of permanent bipedalism in ancestral apes, which were previously quadrupeds in the adult stage but probably temporarily bipeds during the lacteal stage, corresponds to true saltation, i.e. adaptation brought about initially by a sudden leap at the level of the regulator genes (Chaline 1999), which allowed them to colonise the ecological niche of the savannahs at an opportune moment.

This conception challenges many postulates of the neo-Darwinian, synthetic theory of

evolution, which claimed that thousands of mutations were sorted by natural selection in a process where gradual adaptation was considered to be the driving force behind evolution. The internal clocks of life offer a new answer and a fully revised, all-round vision both in terms of the basic mechanism and of adaptation. Adaptation, or rather aptation, seems to be the result of compatibility (saltaptation) and environmental constraints. At the very least, the environment because of their neutrality tolerates the new structures, at best they provide an immediate advantage allowing their geographical extension within populations.

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