

Hominidae and *Homo* - discontinuity and continuity, "environnementalisme et comportementalisme" +

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Abstract

The family Hominidae, starting with the split of the Panidae from the common ancestors Hominoidea, are comprising the two subfamilies Australopithecinae and Homininae. Because of the geographic division of their ancestors into a western and into an eastern group, the Panidae and Hominidae were never together. The eastern solution was the adaptation to an open habitat and the story of this adaptation is the story of the Hominidae - I have called it East Side Story, it is a cladogenesis, a discontinuity. The Australopithecinae with three possible genera (*Motopithecus*, *Pre-Australopithecus*, *Australopithecus*) and six possible species is more complex than it was thought.

The origin of *Homo* is a product of discontinuity and "environnementalisme" again. Their oldest remains could be 2.5 to 3 m.y. old. The evolution of this genus is passing through 3 main steps: *Homo habilis*, *Homo erectus*, *Homo sapiens*, which are more looking like grades than true species and the evolution of *Homo* is looking like a continuum, an anagenesis, a phyletic gradualism. Tool-making activity preceded *Homo*. With *Homo*, the cultural evolution which is also a continuity, is going successively, shown than biology, first, and then faster. The speeds of the biological and of the technological evolution are different and reverse.

Key words: Hominidae, continuity, discontinuity, "environnementalisme", "comportementalisme"

I use, in the long title of my paper, the words Hominidae and *Homo*. In this communication, at least, the family Hominidae is understood as starting from the split with the African Apes, the family Panidae: I mean that it is a 7.5 to 8 million years family, comprising two subfamilies.

- the Australopithecinae (from 7.5 to 8 to 1 million years about) and
- the Homininae (from around 3 m.y. to the present) and the genus *Homo* is, of course, understood as the only genus of the subfamily Homininae, appearing in Eastern Africa (around 3 m.y.) and characterized in particular, by a brain quantitatively developed and by an omnivorous type of dentition and diet.

I will try, in my paper, to develop some aspects of four points:

1. the origin of the Hominidae;
2. the evolution of their first subfamily, the Australopithecinae;

3. the origin of *Homo*;
4. the evolution of the second subfamily, the Homininae.

The origin of the Hominidae. Discontinuity and "environnementalisme"

The crucial event of this period (I mean the last 8 m.y.) is the emergence of the family Hominidae (and not at all the emergence of the genus *Homo*). All the features which make the human being what he is, us what we are, bipedalism, development of the brain and its consequences, organization of the society and, even, discovery of this strange phenomenon called culture, seem to appear before man, before the genus *Homo*, with the Hominidae.

When one tries to understand why and how the Hominidae emerged, one finds oneself in front of a contradiction:

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1 - All disciplines today (comparative anatomy, embryology, physiology, molecular biology, cytogenetics, ethology) are claiming that Hominidae and Panidae, the African Apes, are very close cousins (share common ancestors not very far - geologically speaking - in the past),

2 - and when palaeontologists questioned the fossil record as they have done (I was one of them) during the past 25 years in Eastern Africa, they are unable to find any remains of Panidae among thousands of remains of Hominidae, nor any remains of early Hominidae in the geographical area of extant Panidae.

And this geographical distribution (of the Hominidae and of the Panidae) must be precisely the answer.

I will tell you an hypothesis for the origin of the Hominidae that I proposed in a congress in Rome in 1982 (Coppens 1983a). Let us imagine the common ancestors of the Hominidae and of the Panidae, around the end of the Miocene, in the mosaic of forests and wooded savannahs which existed at that time from the Atlantic Ocean to the Indian Ocean (Andrews & van Couvering 1975; Axelrod & Raven 1978). The geologists tell us that the process of rifting had, in the Upper Miocene, a period of reactivation in Eastern Africa; intense volcanism happened, as well as uplifting of the Rift shores and of the whole eastern province, between the Rift and the Indian Ocean. The palaeoclimatologists conform that, because of the modification of the topography, rains, formed in the Gulf of Guinea and pushed to the east by the winds from the Atlantic, were then stopped by the

walls of the Western Rift and by the altitude of the East African Plateau. The west remained moisty, the east became increasingly dry, under the recently fixed seasonal system of monsoons. We, the vertebrate palaeontologists, describe, at the same time, the appearance of endemic faunas adapted to open landscapes between the Rifts and the Indian Ocean (since about 10 m.y.; it is what we call the Protoethiopian and the Ethiopian faunas) and the palaeobotanists say that the trees decreased dramatically in the east, showing, in number of taxa and in density, a retreat of the forest to the west.

The population of Hominidae which was to become the common ancestors of both the Hominidae and the Panidae, was, then, divided by chance into two parts, a western one and an eastern one by this tectonic accident, becoming an ecological barrier, and their descendants continued to evolve just where they were, the western in the west, in the area which had kept the humidity and the woody environment, the eastern in the east, in the area which became dryer and dryer, offering an open environment looking like an open savannah, a grassland and sometimes even a steppe. There was no movement of the first from the savannah to the forest (as for instance Kortlandt 1972 is saying), no movement of the second from the forest to the savannah (as most of the authors are saying - Laporte & Zihlman 1983 for instance). The forest remained around the first and disappeared from around the second. The first, the western group became the Panidae; the second, the eastern group, the Hominidae.

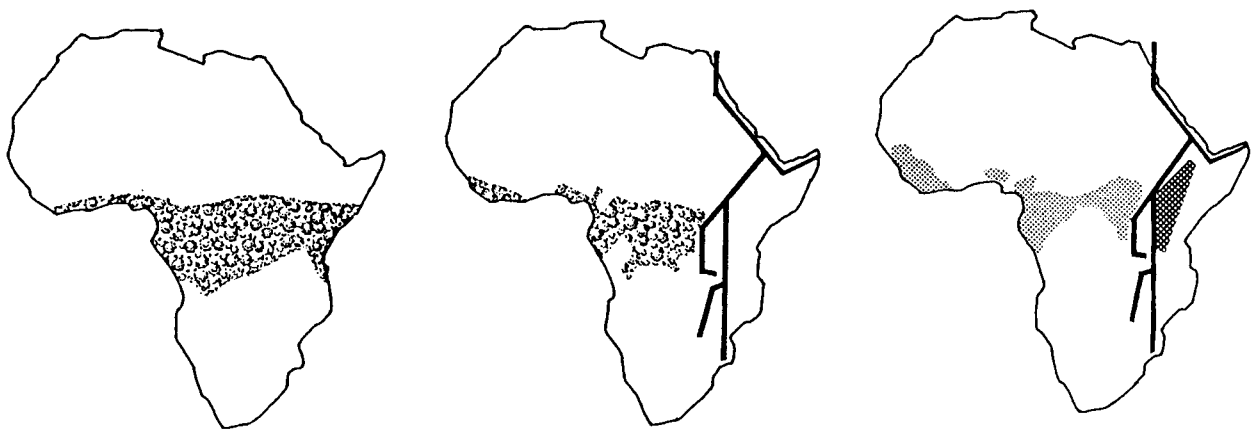


Fig. 1. "The East Side Story" hypothesis (Coppens 1982).

From left to right: 1 - Africa and its equatorial belt, 10 m.y. ago; 2 - the reduction of the forest after the refitting, 8 m.y. ago; 3 - the distribution of the Panidae (west) and the Hominidae (east), on both sides of the Rift system.

If my model (Fig. 1), that I called the East Side Story (Coppens 1983a,c; 1984; 1986; 1988a,b) is true (and I am proud of it), it is a particularly good example of a speciation by geographic peripatric isolation; it is a cladogenesis, a discontinuity. The Panidae and the Hominidae were never together; it is because of the geographic division of their ancestors that they derived.

The western solution was the adaptation to a woody environment. We know with the living chimpanzees and gorillas the result of this selection: limbs of quadruped, knuckle walker, as well as arboreal, climber and semibrachiator, a pelvis with an ilium in tension and a dentition for a frugivorous and folivorous diet, mostly.

The eastern solution was the adaptation to an open habitat and the story of this adaptation is the story of the Hominidae, the Australopithecinae, first, and then the Homininae: limbs of a biped, somewhat arboreal in the beginning, a pelvis with an ilium in compression and a dentition for a vegetarian diet becoming more and more omnivorous.

It is an extraordinary story which may mean, if it is the way it happened, that, without this uplifting and this consecutive drying out of Eastern Africa, neither the family Hominidae nor the genus *Homo*, would have existed.

The evolution of the first subfamily of the Hominidae, the Australopithecinae. Discontinuity and "environnementalisme".

The first subfamily of the family Hominidae, the Australopithecinae, seem to be more important and more complex than it was thought. I am counting today three possible genera and six possible species of Australopithecinae.

The very first one could be what Ishida (1984) is sometimes calling *Motopithecus*. The type and the only specimen attributable to this genus is a part of a maxilla with its 2 premolars and its 3 molars that he found in the Suguta area of the Samburu Hills in north Kenya, in a locality which dated at 7 m.y. The teeth of this maxilla are very low, the enamel thick, the premolars enlarged bucco-lingually as in the more evolved australopithecines. It will obviously be particularly important to learn more about this odd-looking hominid (Ishida 1984). *Motopithecus* is only East African.

The second genus is what I am calling, informally, *Pre-Australopithecus* (Coppens 1981b). It is partly what Johanson, White and myself

named *Australopithecus afarensis* in 1978 (Johanson et al. 1978). I gave to *Australopithecus afarensis* this name because it is obviously more archaic than *Australopithecus* sensu stricto, because it is composed of a certain number of ancestral characters but also of many derived ones and because it is partly contemporaneous with *Australopithecus* (*Australopithecus africanus* from Makapansgat and Sterkfontein is 3 m.y. old, "Lucy" is 3 m.y. old as well) and cannot, consequently, be its direct ancestor.

Pre-Australopithecus is a hominid of small size (1.10 - 1.20 meters high). It is a biped but with the capacity of climbing trees remaining. Among the plesiomorphic characters, we can mention, for instance, the big size of the first upper incisors, the presence of a diastema between the second incisor and the upper canine and between the lower canine and the lower first premolar, the U-shape of the dental arcade, the shallowness of the palate, the strong post-orbital constriction, the cranial orientation of the glenoid cavity of the scapula, the deep and narrow sulcus intertubercularis of the humerus, the antero-posterior flattening of the humeral epicondyle, the development of the epitrochlea of the humerus, the curvature of the phalanges of the hands and of the feet, the mediolateral enlargement of the distal epiphysis of the femur, the amplitude for the movement of rotation of the knee-joint, even the shape of the section of the ribs leading to an idea of a thorax chest in funnel shape (Senut 1981, 1983; Stern & Susman 1983; Tardieu 1983 a,b). Among the apomorphic features, we can mention, the strong entoglenoid process of the temporo-mandibular joint, the one cusp but not sectorial first lower premolar, the double trochlea of the distal epiphysis of the humerus (Coppens 1977; Picq 1985; Senut 1981, 1983). *Pre-Australopithecus*, known from more than 6 m.y. (Lukeino) to about 2.7 m.y. (Omo), is, as *Motopithecus*, only East African.

The third genus, *Australopithecus*, is well known from a large number of remains that come from Eastern and Southern Africa, from levels dated from 3 m.y. to 1 m.y. about. *Australopithecus* tells beautifully the story of a specialisation as well as the story of a parallel evolution, from a species called "gracile" to a species called "robust": and I personally think that this gracile-robust evolution, parallel but discontinuous (the last gracile are contemporaneous with the early robust) happened at about the same time in Eastern Africa and in Southern Africa and that

there is enough distance between these two provinces to think that the species were different in the east and in the south.

The East African gracile species, successively described and cancelled for many years, is probably well documented now by the Olduvai Hominid 62 found by Johanson & White and not yet fully described (Johanson et al. 1987). They call it a *Homo habilis* (because it is not robust) with *afarensis* features. This gracile species, if it is a new species, does not have a name yet.

The East African robust species is composed of two subspecies: *Australopithecus boisei aethiopicus* that Arambourg and myself described in 1967 from a level 2.5 m.y. old from the Omo Basin in Ethiopia (Arambourg & Coppens 1967, 1968) and which was rediscovered by R. Leakey & Walker in West Turkana in Kenya in 1987 (the black skull) (Walker et al. 1986) and *Australopithecus boisei boisei*, 2 to 1 m.y. old described by L. Leakey in 1959 from Olduvai under the generic name of *Zinjanthropus* (L.S.B. Leakey 1959; Tobias 1967).

The South African gracile species is, of course, *Australopithecus africanus*, described from Sterkfontein, Makapansgat and Taung, 3 to 2.2 m.y. old.

The South African robust species is *Australopithecus robustus* from Swartkrans and Kromdraai, 2 to 1 m.y. old.

The picture of *Australopithecus* is then the one of a hominid of an increasing size, 1.25 to 1.50 meters high, of a bipedalism closer to ours than was the Pre-*Australopithecus* one, and not climbing any more, and of a complex of unbelievable adaptive features in the teeth, in the jaws and, consequently, in the whole face and skull, for finding hard food; superstructures such as a sagittal crest and a nuchal crest, developed for the muscular attachment of the masticatory apparatus; a face wider because of the enlargement of the zygomatic arches which had to leave space for powerful masseter muscles; a dentition organised in three parts, a front one, made of incisors and canines small, straight, tight, vertically inserted and two lateral ones, made of molarised premolars, enlarged bucco-lingually and enormous molars, with thick enamel, numerous cusps and interstitial wear facets, formed by the very close contact between the teeth. The type of evolution and diversification of the Australopithecinae is looking like a cladogenesis, a punctuated equilibrium, a

discontinuity and like a movement from the cradle, from East to South Africa. And as we will see further, it is an evolution which happened under a strong environmental pressure: we are still here in the realm of "environnementalisme".

The origin of *Homo*. Discontinuity and "environnementalisme" again.

I studied, personally, in the Omo Valley in Ethiopia, a climatic crises which happened between 3 and 2 m.y. It is not this time a simple hypothesis like for the one of the origin of the Hominidae, it is a data, of demonstration, recently confirmed by the study of deep sea cores and oxygen 18 (Coppens 1975 a,b).

If we look for instance at the transformation of the macrofauna during this time span, it is easy to describe the spectacular evolution of *Elephas recki* (development of the height of the teeth relatively to their width, increasing number of plates, increasing quantity of cement, decreasing thickness of enamel), to describe the evolution of *Hipparion* (development of the height and of the volume of the incisors and of the cheek teeth, increasing frequency of an extra stylid called ectostylid on the lower cheek teeth, development of its height and of its mesio-distal length, decreasing number of folds of enamel in the upper cheek teeth - 20 to 24 at 3 m.y., 6 to 17 at 2 m.y.), to describe the evolution of the rhinos, the white rhino of open countries more and more abundant, the black rhino of the bush, less and less and the evolution of the white rhino itself (increasing hypsodonty again), to describe the evolution of several species of suids (increasing length and number of tubercles of the last lower molar in 4 phylums: *Kolpochoerus limnetes* - *Kolpochoerus olduvaiensis*; *Nyanzachoerus pattersoni*; - *Nyanzachoerus jaegeri*; *Notochoerus euilus* - *Notochoerus scotti*; *Metridiochoerus jacksoni* - *Metridiochoerus andrewsi*).

It is interesting to notice the first appearance of the genus *Equus*, the true horse, adapted to run and to eat hard grass, and of the genera *Phacochoerus* and *Stylochoerus*, characterized by their very high crowned teeth for eating grass, to notice the importance of the bovids, *Tragelaphini*, *Bovini*, *Reduncini*, browsers, living in thick bush close to the water in the levels 3 m.y. old and the development of the bovids *Alcelaphini* (*Megalotragus*, *Connochaetes*, *Parmularius*, *Beatragus*),

Antilopini (*Antidorcas*, *Gazella*), *Hippotragini* (*Oryx*), grazers, living in open grasslands and adapted to run, in levels 2 m.y. old.

If we look at the primates (except hominids), we can see their frequency decreasing beautifully as decreases the frequency of the trees; 367 remains by square kilometer at 3 m.y., 39 at 2 m.y.

The demonstration given by the micro-mammals is as good as the previous ones: 3 species of *Galago*; 2 genera of *Chiroptera*, *Eidolon* and *Taphozous*, a great development of the Muridae (*Mastomys*) and of *Grammomys*, *Paraxerus*, *Thryonomys*, *Golunda* characteristics of thick savannah, tall grass, water in levels 3 m. y. old. No more *Galago*, 2 different genera of *Chiroptera*, *Coleura* and *Hipposideros*, 5 specimens of Muridae instead of 85 and abundance of *Aethomys*, *Thallomys*, *Gerbillurus*, *Heterocephalus*, characteristics of dry savannah acacias, steppes, even half desert, in levels 2 m.y. old.

The flora is as explicite as the fauna, 22 to 24 taxa of trees of wooded savannah at 3 m.y. (like *Garcinia*, *Combretum*, *Berlinia*); 11 taxa of trees of open gallery forest at 2 m.y. (like *Ficus* or *Myrianthoxylon*). The ratio of pollens of trees on pollens of grass is passing from 0.4 at 3 m.y. to 0.01 at 2 m.y. The good indicators of humidity, *Olea* and *Typha* are evolving as follows: *Olea* 23 % of the pollens of the trees at 3 m.y., 3,2 % at 2 m.y.; *Typha* 15.6% at 3 m.y., 1.6 % at 2 m.y. The frequency of allochthonous pollens, indicative of humidity in meaning a greater capacity of transportation of the river Omo, passing from 21 % at 3 m.y. to 2 % at 2 m.y. (Coppens 1985).

And it is at this moment (this geological moment) that two hominids appeared; our family had found two solutions to the crisis; the powerful *Australopithecus boisei* with its small brain but its robustness and its jaw to crush the hardest plants, roots, nuts remaining after the drought and the tiny *Homo habilis*, the first *Homo*, with its small size but its big brain and its jaw to eat anything, including meat.

It was in the Omo Valley, because this period between 3 and 2 m.y. is very well documented there and is documented only there (Hadar is earlier, Olduvai later, and Turkana has a sedimentary gap at that time), that I could point out for the first time the existence of this climatic change. I gave the demonstration of the correlation between this evolution of the environment and the

evolution of the hominids, in other words, between a drought and the emergence of the robust *Australopithecus* and of the first *Homo*, in 1974 in London and was followed, 10 years later, by Vrba in South Africa (Coppens 1975b, 1978; Vrba 1985).

This again is an example of discontinuity under powerful environmental selective pressure.

The evolution of the second subfamily, the Homininae. Biological continuity, technological continuity and "comportementalisme"

The oldest remains of the genus *Homo* could be 2.5 to 3 m.y. old; they are coming from Kanapoi in Kenya, Hadar and Omo in Ethiopia (Coppens 1987; Senut 1981, 1983; Tardieu 1983 a,b).

The evolution of the genus *Homo*, according to the fossil record, is passing through three main steps which received the status of species: *Homo habilis*, *Homo erectus*, *Homo sapiens*. As many intermediate specimens do exist between these three species, they are more looking like grades and the evolution of *Homo*, like a continuum, an anagenesis, a phyletic gradualism. For the first time we meet continuity (Coppens 1981a; Hublin 1985).

Why this change in the mechanism of evolution when passing from the Australopithecinae to the Homininae? May be because this is the time of the extraordinary development of culture and society and of the room they take in man's life, interfering more and more in his biological evolution. Culture and society, products of the biological evolution, are having a sort of feedback action on the biological evolution itself. Culture and society are man's ecological niche (Facchini 1988).

And to finish, a few words on the phenomenon called culture. I think that tool making activity preceded *Homo*.

Seven important excavations and many surveys done in the lower Omo Valley gave thousands of artefacts and several remains of Australopithecinae associated in levels dated from 2 to 3 m.y. (Chavaillon 1976; Merrick & Merrick 1976). These artefacts, mainly flakes, are in majority in quartz and of very small size and 5 to 6 % of them have marks of use and even true retouches; they are real stone tools. It is obviously an unexpected assemblage in so early levels. Their age as well as their association with Australopithecinae remains, makes me thinking that it is the austra-

lopithecines the authors of these very first true made tools (Coppens 1983).

Personally, I think that it is not difficult to admit that the use of hands, made free by bipedalism, is very ancient and that, a long time before *Homo*, the hominids must have used pieces of wood, of stone, of bone and, one day, had knocked on one of them with another one to make the first one more efficient. With *Homo*, the cultural evolution which is also a continuity, is going faster. The variety of tools is increasing with the development and diversification of man activities, but every new technique is using the experience of the past ones. Culture is becoming permanent and abundant and it is evolving like a snowball. But this progress is amazingly working in a particular way.

Homo habilis seems for instance to make what we call Oldowan culture. In Melka Kunturé in Ethiopia, I found that the very first *Homo erectus* (documented by a humerus and a jaw) were making Oldowan culture as well (Chavaillon et al. 1977). Most of the *Homo erectus* are making what we call Acheulean culture, hand axes. In Melka Kunturé I found early *Homo sapiens* (pieces of a skull), making Acheulean culture, hand axes, as well (Chavaillon et al. 1987).

Biology seems to change first, then technology, at least in these very ancient times.

But if you add to our scheme the recent data obtained in Europe with *Homo sapiens neanderthalensis* and *Homo sapiens sapiens*, you get the contrary. *Homo sapiens neanderthalensis* made what we call the Mousterian. But in some places (in France, in Croatia), it seems that it is *Homo sapiens neanderthalensis* which is starting the Upper Palaeolithic industries, Chatelperonian and possibly Aurignacian (Fig. 2).

Then comes *Homo sapiens sapiens*; he makes the Solutrean, the Magdalénian but also the Mesolithic, the Neolithic, the Bronze Age, the Iron Age and the Plastic Ages...

Everything is happening as if there was an inversion in the speed of biology and culture around 100.000 years. It is this increasing influence of culture that I am calling "comportementalisme".

Conclusions

In summary, whatever could have been the reason of evolution, it is clear that for the Hominidae, as for the other vertebrates, the selective importance of the environment has been crucial. The most im-

100.000 years	Homo sapiens sapiens	Upper Paleolithic
	Homo sapiens	Upper Paleolithic
	Homo sapiens	Middle Paleolithic
	Homo sapiens	Acheulean
	Homo erectus	Acheulean
2.500.000 years	Homo erectus	Oldowan
	Homo habilis	Oldowan

Fig. 2. The different species in the biological and technological evolution.

portant reason for the selection of the Hominidae, 8 m.y. ago, as well as for the selection of *Homo*, 3 m.y. ago, was, each time, a climatic change, a discontinuity.

This is what I was calling "environnementalisme" in the title.

The speciation in the subfamily Australopithecinae gives the impression to be a cladogenesis, a discontinuity, the specialisation in the

subfamily Homininae, gives the impression to be an anagenesis, a continuity. The evolution of culture and society (behaviour) gives also the impression to be continuous but the evolution of the Homininae and the evolution of their behaviour give the impression to progress at different speeds, biology faster for 2.9 m.y. and then, only 100.000 years ago, culture faster. This is what I was calling "comportementalisme" in the title, behaviourism being used for something else.

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