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Jean Chaline, Alain Durand, Didier Marchand, Anne Dambricourt Malassé,
M.J. Deshayes

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J. Chaline

A. Durand

D. Marchand

Paléontologie analytique et Géologie sédimentaire (UMR CNRS H5561) et Préhistoire et Paléoécologie du Quaternaire de l'EPHE, Université de Bourgogne, Centre des Sciences de la Terre, 6 bd. Gabriel, 21000 Dijon, France

A. Dambricourt Malassé

UMR CNRS 9948, Institut de Paléontologie humaine, 1 rue R. Panhard, 75013 Paris, France

M. J. Deshayes

*Rue Pasteur, 18
14000 Caen, France*

Chromosomes and the origins of Apes and Australopithecines

Comparison of molecular data suggests that the higher apes (*Gorilla*, *Pan*) and humankind (*Homo*) are closely related and that they diverged from the common ancestor through two speciation events situated very closely together in time. Examination of the chromosomal formulas of the living species reveals a paradox in the distribution of mutated chromosomes which can only be resolved by a model of trichotomic diversification. This new model of divergence from the common ancestor is characterized by the transition from (1) a monotypic phase to (2) a polytypic phase of three sub-species - pre-gorilla, pre-chimpanzee and pre-australopithecine. The quadruped ancestors of *Australopithecus* appear to have been one of the three components of the common ancestor. The question is whether *ramidus* is an australopithecine or a pre-australopithecine representative of the common ancestor. The new model of diversification of the common ancestor is resituated in the paleogeographic and paleoclimatic context which, through the north-south pattern of extension of aridity, provides a coherent scenario for the formation of extant species and sub-species of the *Gorilla* and *Pan* genera.

Key words: Evolution chromosomes, Apes, Australopithecines, Speciation model, Climatological model

1. Introduction

Research into hominoid evolution involves multiple disciplines. Although separate studies have been conducted in various areas --- molecular analysis (Miyamoto et al., 1988; Bailey et al., 1992; Goodman et al., 1994), blood serology (Wiener & Moor-Jankovsky, 1965; Socha & Moor-Jankovski, 1986), chromosomal design (Chiarelli, 1962; De Grouchy et al., 1972; Dutrillaux et al., 1986; Dutrillaux & Couturier, 1986; Stanyon and Chiarelli, 1981, 1982, 1983; Yunish and Prakash, 1982), developmental data (Dambricourt Malassé, 1987, 1988, 1992, 1993a & b, 1994; Shea, 1988) and the fossil record (Walker and Leakey, 1978; Coppens, 1986; Simons, 1989; Coppens and Geraads, 1992) --- there has never been a truly all-round approach to the subject. Current research into evolutionary concepts (Gould, 1985; Devillers & Chaline, 1993; Chaline, 1994) indicates that there is a hierarchized structure in the living world and that the relations among the various levels of integration are highly complex, ranging from close dependence to complete dissociation.

The aim of this paper is:

- (1) to critically review progress by analyzing two main levels of organization in Hominoids: molecular and chromosomal;
- (2) to put forward explanatory models of chromosomal and morphological evolution within a palaeoclimatic and paleoecological framework;
- (3) to test the model using paleontological data.

2- Evolution at the molecular level

Research at the molecular level (DNA and protein sequencing, DNA/DNA hybridization, mitochondrial DNA restriction mapping, protein electrophoresis and immunology, blood groupings, etc.) has confirmed the proximity between humans and the higher apes, but without conclusively settling the questions of kinship and the splitting of the different branches.

It is the general consensus that cladistically the chimpanzee groups with *Homo*, then with the gorilla and much further on with the orangutan. Molecular cladistic classification (Bailey et al., 1991, 1992; Goodman et al., 1994) places all great apes and humans in the same family (Hominidae)(Fig.1). Within this family, the subfamily Homininae is divided into one tribe for orangutans (Pongini) and another tribe for gorillas, chimpanzees and humans (Hominini). Gorillas are placed in the subtribe Gorillina, while chimpanzees and humans form the Hominina subtribe.

Estimated divergence between higher primates based on the $\psi\eta$ -globin gene region combined with available nucleotide data ranges from 1.61 % (humans versus common chimpanzees) to 3.52 % (orangutans versus humans and African great apes). *Pan* diverges from *Gorilla* by 1.84 % (Miyamoto et al., 1987, 1988), a figure similar to that obtained by DNA/DNA hybridization analysis (Sibley and Ahlquist, 1984, 1987; Caccone and Powel, 1989; Sibley et al., 1990). Broader investigation of the $\psi\eta$ -globin gene region (Bailey et al., 1991) and of the β -globin gene (Bailey et al., 1992; Perrin-Pecontal et al., 1992) confirms the previous relationships and classification.

The human-chimpanzee clade is corroborated by several other DNA sequence analyses involving the immunoglobulin epsilon and alpha pseudogene (Ueda et al., 1989), 12S ribosomal gene (Hixson and Brown, 1986), 28S ribosomal genes (Gonzalez et al., 1990), 0.9 kb region of the mt genome containing genes for tRNA^{His}, tRNA^{Ser}, tRNA^{Leu} and part of ND4 and ND5 (Hayasaka et al., 1988) and the cytochrome oxidase II locus of mitochondrial genes (Pruvolo et al., 1991; Horai et al., 1992). Only DNA analysis of the involucrin locus (Djian and Green, 1990) fails to confirm this clade, perhaps as a result of polymorphism.

It should be noted that the molecular analyses of chimpanzees were conducted on individuals labelled *Pan troglodytes* without specifying to which of the three living sub-species — *P. t. verus*, *P.t. troglodytes* or *P.t. schweinfurti* — they belonged (M. Goodman, personal communication). Similarly for gorillas. This imprecision explains in part why kinship is so difficult to specify, because divergence among the three sub-species is probably very different from that with humans.

We are in the paradoxical and unfortunately increasingly common situation where the most sophisticated analytical techniques requiring very thorough experimentation are applied to samples chosen haphazardly! The population variability of the study species is overlooked, even though its temporal and paleobiogeographical distribution is often highly complex.

Specialists generally accept that the separation of higher primates and humans results

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from a double split occurring very close together in time (M. Goodman personal communication), the first separating the lineage to *Gorilla* from the common ancestor of *Homo* and *Pan* and the second separating the lineages to *Homo* and *Pan*. These two ancestral speciation events looks like a trichotomy. But Smouse and Li (1987) suggested there was a true trichotomy, or a pair of ordered dichotomies with a very short time span between the first and the second split. They take the view that "the ancestors of all three taxa were still conspecific subsequent to the second split, perhaps no more different than the major races of extant *Homo sapiens*". This is an interesting suggestion to which we shall return.

3- Evolution at the chromosomal level

3.1 - Chromosomal data

A major advance in chromosome research was the development of R banding (Dutrillaux & Lejeune, 1971) and G banding techniques (Sumner et al., 1971; Dutrillaux et al., 1971).

Opinions differ about the role of heterochromatin. Dutrillaux and his team consider that the chromosome data from primates (Fig.2) provide no evidence either for positional effects or that alterations in heterochromatin influence gene expression. This idea is materialized at the phylogenic level by two equally feasible dichotomic diagrams (Fig. 3). These two diagrams entail acceptance of three convergences or reversions, but a third diagram, where each rearrangement is regarded as unique, implies complex populational evolution as described in the next section.

By contrast, Stanyon and Chiarelli (1982) argue that "genes can be (1) repressed by placing them in, or near, blocks of heterochromatin, or (2) activated by a shift in their position away from heterochromatin regions". They set great store by active regions detected by Ag-NOR (silver nitrate) type methods. This has repercussions for the phylogeny shown in figure 4, which differs from the hypotheses in figure 3. They conclude that common derived karyological features indicate that *Gorilla* and *Pan* share a common descent after the divergence of *Homo*.

3.2 - A new trichotomic chromosomal model

The common ancestral chromosome formula of all these species can be reconstructed by deduction. The reconstruction is based on the principle that if two, three or four species share a common chromosome, it is likely that some common ancestor transmitted it to all of them. This is the simplest relationship. We may also take the view that two identical chromosomal changes occur in the same way on the same chromosome in two related species derived from an ancestral form. This is statistically far less likely, though it is possible as convergence.

We can attempt to reconstruct the chronology of the formation of the various chromosomes and the successive events that marked the history of the family (Chaline et al., 1991).

Among anthropoid apes, the group with the most primitive chromosomal formula is logically the one that branched off earliest in the family history. This is the orangutan group which emigrated to Asia where it has been cut off from the African branch for more than 10 million years (Andrews & Cronin, 1982; Lipson & Pilbeam, 1982). It has been relatively stable from the chromosomal point of view, only two new chromosome mutations having occurred since that time.

After the separation of the orangutan lineage, the common ancestral lineage of the three extant genera — chimpanzees, gorillas and humans — remained in Africa. This phase corresponds to the "common ancestor" implied by genetic similarities. That there was a

common ancestor is irrefutably shown by the formation of seven specific mutant chromosomes (2q, 3, 7, 10, 11, 17 & 20) and by the retention of eleven non-mutated common chromosomes (1, 4, 5, 8, 9, 12, 13, 14, 15, 16 & 18) inherited by the three living species (Chaline et al., 1991) (Fig. 5).

The occurrence of seven characteristic mutant chromosomes found in the gorilla, chimpanzee and human descendants implies that the common ancestor was a single monotypic species, not divided into subspecies. Genetic pooling as a result of interbreeding produces a fairly even spread of chromosome variety, including chromosomal variations that appear in isolated individuals. This first part of the history of the common ancestor corresponds to what we shall term the "first homogenous common ancestor phase" (Fig. 5).

Thereafter, the common ancestor diversified and the lineages separated, leading on the one hand to the gorilla and chimpanzee and on the other to humans. This divergence raises a complex populational problem about the distribution of five new mutated chromosomes.

It is reported that chimpanzees and humans share three mutated chromosomes (2p, 7 & 9) that gorillas do not have. Conversely, chimpanzees and gorillas share two other specific mutated chromosomes (12 & 16) not found in humans. In other words, chimpanzees share three common mutated chromosomes with humans and two common mutated chromosomes with gorillas. But gorillas share no special rearrangements with humans!

This position is inexplicable by the standard hypothesis of a split into two branches (dichotomic model) leading to the gorilla/chimpanzee on one side and to humans on the other.

Though there is a possible solution to the puzzle: the "second heterogeneous common ancestor phase" (Fig. 5).

To explain this major paradox, it must be supposed that at a certain time in their history, after the first undifferentiated phase, the ancestors of chimpanzees and gorillas were able to interbreed and acquire two new chromosome mutations they alone possessed, and not humans. This accords with the suggestion of Smouse and Li (1987) "that the ancestors of all three taxa were still conspecific".

But it must also be accepted that for some time, perhaps different from the first period, the ancestors of chimpanzees and humans were able to interbreed and to incorporate three new chromosomal mutations into their genetic constitution, possessed by them alone and not gorillas.

However, the fact that the ancestors of gorillas and humans do not share exclusive mutations in their chromosomal formulas implies that they did not at that time have contacts allowing hybridization. They were geographically isolated.

Three hypotheses can be put forward, necessarily broken down into several phases and stages, summarized as follows:

3.3 - Hypothesis 1

In the first homogenous common ancestor phase, the ancestors of gorillas, chimpanzees and humans formed a common undifferentiated monotypic ancestral group in which all individuals could interbreed. There was a single common species, not yet identified in the fossil record, and so nameless.

In the second heterogeneous common ancestor phase, the ancestral group split into three subgroups. Probably into three subspecies as only subspecies could have retained the ability to interbreed in the areas where they came into contact and to pool their genetic heritage. We shall call them respectively pre-chimpanzees, pre-gorillas and pre-hominians or pre-australopithecines. By comparison with the geographical distribution of present-day species

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(Collet, 1988) (Fig. 6-7), which has probably not changed much over geological time, we can admit a plausible hypothesis about the distribution of these three subspecies as follows (Fig. 8):

— the pre-chimpanzee group must have been geographically centred around the present day Lake Victoria region. It stretched to north west Africa across the area north of the Zaire River in a forest-savanna mosaic or open woodland environment.

— the pre-gorilla group must have been located on the western edge of the former, still north of the Zaire River, in the very wet tropical rain forest zone.

— the pre-hominian group must have been located further east in the famous East African Rift Valley, the great crack in the Earth's crust running north-south through Africa.

This three-way division of the common ancestor into three geographical subspecies, forerunners of the three extant genera, accounts for the formation of the chromosomal formulas of the living species by the following scenario.

The pre-chimpanzees were in contact in the East with the pre-hominians and were able to interbreed with them. As a result, three chromosomal mutations occurred in this region, spread and are now found in the common chromosomal heritage of chimpanzees and humans.

Similarly, the pre-chimpanzees bordered on the west with the pre-gorillas and interbred. As a result, the two chromosomal mutations occurring in the common zone were included in the chromosomal heritage of living gorillas and chimpanzees.

However, pre-gorillas and pre-hominians had no contact at that time and were unable to acquire mutations common to both genera.

This suggests that the pre-chimpanzee group was distributed in a wide arc from north west Cameroon to the south of Lake Victoria, separating the pre-hominians in the east and the pre-gorillas in the west (Fig. 8).

This hypothesis is consistent with a true trichotomic model in compliance with the ideas advanced by Smouse and Li (1987).

3.4 - Hypothesis 2

This hypothesis suggests that after the first common phase, two subspecies, respectively, pre-gorillas and pre-australopithecines became geographically separated and chromosomally differentiated (Fig. 9). Only then, did two small populations of each subspecies meet and form the pre-chimpanzee stock! Chimpanzees could be hybrids of pre-gorillas and pre-australopithecines. A dichotomic model followed by genetic re-melding as has been reported in mice in Japan (*Mus musculus molossinus* results from the two remixed subspecies *Mus musculus castaneus* and *Mus musculus musculus*) (Bonhomme et al, 1984). A theory that cannot be ruled out *a priori*!

3.5 - Hypothesis 3

Another hypothesis may be envisaged, that of convergence. This would imply that two common mutations occurred at the same sites and on the same chromosomes in both pre-gorillas and pre-chimpanzees. Moreover, three further identical chromosomal mutations likewise occurred in pre-chimpanzee and pre-human chromosomes. Although possible, this solution seems statistically less probable than the previous one. It would be a double-dichotomic model consistent with the results of Bailey et al. (1992) and Goodman et al. (1994).

4- Evolution at the ecological level: a climatological model

The model of trichotomic divergence also implies that at some point between 5 and 4 millions years ago the three subspecies finally became three separate species. Either because new chromosomal mutations prevented them from interbreeding by abortion of hybrids or, more probably, because they had become geographically and ethologically isolated.

Since this separation, chimpanzees have acquired six chromosomal mutations (4c, 5, 9, 15, 17, 13) that they alone possess.

Similarly, gorillas have six different chromosomal mutations (1, 4b, 5, 17, 8, 10, 14) peculiar to their chromosomal make-up.

As for the pre-australopithecine and then human line, it acquired four specific chromosomal mutations (2 mutations on chromosome 1, 2, 18), including the famous fusion of the two chromosomes that formed the human chromosome 2.

To account for the separation into distinct species, a new decisive factor must be incorporated here, that of climatic change. This would have induced changes in the environment that must have been instrumental in the geographical isolation of the subspecies and species. Figure 8 explains the logic behind these changes.

The original common area in central Africa is currently a favoured climatic zone where the inter-tropical front (east-west) corresponding to the thermal and meteorological equator crosses the inter-oceanic confluence (north-south) (Leroux, 1983). Very schematically we find the permanent Atlantic monsoon domain and the tropical rain forest in the west; the forest is known in the Congo, Gabon and Cameroon basins from the onset of the Miocene (Boltenhagen et al., 1985). To the north lies the seasonal Atlantic monsoon domain and the savannah; in Nigeria a seasonal subtropical climate is reported since the Oligocene-Miocene boundary (Takashi & Jux, 1989). Further north still is the Sahara zone; evidence of a large arid zone in North Africa from Middle Miocene times is provided by rodents (Jaeger, 1975) and by flora (Boureau et al., 1983). In the south and east is the domain of the Indian Ocean monsoons and trade winds; tropical rain forest, open woodlands and montane forests are recorded to have co-existed since 19 Myrs and savannahs since 14-12 Myrs (Bonnefille, 1987; Retallack et al., 1990). Local reliefs are superimposed on this background pattern to form an environmental mosaic that is sensitive to climatic fluctuations (White, 1983; Pickford, 1990).

Our hypothesis is that differentiation occurred in connection with the environment as determined by climate (fig. 8). Starting from a monotypic common stock (acquisition of 7 chromosomal changes), the pre-gorillas split away in the permanent monsoon domain north of the Zaire River barrier. The pre-australopithecines developed on the eastern margin under the influence of the Indian Ocean monsoons and trade winds and spread north-south along the inter-oceanic confluence which roughly coincides with the eastern arm of the rift valley (fig.8) and may be westward around the permanent Atlantic monsoon range. The pre-chimpanzees spread widely east-west, on the northern boundary of the permanent Atlantic monsoon domain, ranging from Central to West Africa.

This geographical pattern of climates underwent many large changes. First because Africa has drifted relative to the equator which lay 5° further north about 10 Myr ago (Scotese et al., 1988). But also because of changes in atmospheric circulation. In the Upper Miocene tropical north Africa experienced at least four episodes of substantial climatic deterioration leading to aridity, the last at the top of the Miocene (ca. 6-5.3 Myrs) coinciding with a very distinct cooling of the Atlantic (Diester-Haass & Chamley, 1982; Sarnthein et al., 1982). Schematically, since Chudeau (1921) it has been accepted that extensions of the arid

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Sahara zone are related in part to a reduced summertime advance of the monsoon front (FIT-1; Fig. 8) which may even remain blocked in the southern hemisphere.

Such variations entailed changes in the seasonal and permanent monsoon ranges and thus in the three sub-species and could have separated them in a yet unknown history.

Allopatric break up of the ancestral form would have allowed gorillas, australopithecines and chimpanzees to become isolated, as evidenced by the autapomorphic features which have since appeared.

From the Upper Pliocene (*ca.* 3.2 Myrs) general atmospheric circulation changed radically for geodynamic reasons. Events such as the closure of the Panama isthmus, the opening of the Bering Straits and mountain building in North West America and Asia are thought to have been decisive factors in conjunction with variations in planetary orbit in triggering the northern hemisphere ice ages (Ruddiman & Raymo, 1988; Berger, 1992). Each glacial period is related to aridity in Africa north of the equator (Chudeau, 1921; Tongioli & Trevisan, 1942; Dubief, 1953; Tricart, 1956).

For more recent times where chronology is relatively precise, we now know that changes occur suddenly. After the last glacial maximum it is thought that the arid zone extended several hundred kilometres further South on three occasions between about 19,000 and 15,000 years ¹⁴C B.P. with each episode lasting only 500 to 1000 years (Durand, 1993). The dense humid forest became fragmented and mountain biotopes spread as a result of the fall in temperatures (Maley, 1987).

The repetition of these biogeographical mechanisms during the Pliocene-Pleistocene fluctuations is thought to be responsible for the current diversification of chimpanzees and gorillas, each characterized by three sub-species.

Starting from the initial pre-chimpanzee distribution, it is thought that common chimpanzees then diversified into three subspecies. One subspecies (*Pan troglodytes verus*) is isolated in Guinea (Collet, 1988; Fig. 6), probably as a result of a break in the forest caused perhaps by a southward shift of the Sahara desert zone in Quaternary times engendering aridity in what is now Nigeria.

This mechanism of separation of species into western and eastern populations may have been compounded because the pre-gorilla and pre-chimpanzee populations were unable to cross the great natural barrier of the marshland basin of the River Zaire. Only the pigmy chimpanzee (*Pan paniscus*) made the crossing or perhaps negotiated the river upstream. It is impossible at present to provide details and a chronology of what might have happened, but this mechanism is plausible. It can furthermore be tested, since if it is correct, fossils of pre-chimpanzees should be found in Tertiary deposits in areas where chimpanzees no longer occur from the Ivory Coast to Nigeria.

Finally, gorillas also split from the pre-gorilla stock into three subspecies, corresponding respectively to the lowland and the two mountain gorillas separated by the bend in the River Zaire (Collet, 1988) (Fig. 8).

Scarce Pre-hominians are known in the fossil record (Lothagam, Lukeino, Ngorora) and are more or less unrelated. They can be considered as pre-australopithecines, one of the components of the common ancestor.

This new model introduces australopithecines as a missing-link between the common ancestor and the human lineage proper. They are never considered by chromosome specialists for the obvious reason that, being extinct, their chromosomes are unknown. But as they formed a necessary intermediate stage, they must be included in the model. By deduction, the chromosomal formula of the extinct pre-human form *Australopithecus* can be evaluated fairly accurately, except for the four chromosomes that appeared after its genetic isolation.

The model of separation into three genera is therefore not simply one of divergence into two groups, as ordinarily occurs in the animal world. There is a true trichotomy.

5- Testing with paleontological data

This model can be tested from a paleontological point of view, as it is for palaeontologists to find the ancestors, to date their appearance in the fossil record and to reconstruct their history proper (Fig.10).

As said above, the ape group with the most primitive chromosomal formula is logically the orangutan group which emigrated to Asia where it has been cut off from the African branch for more than 10 million years. It is now accepted that *Ramapithecus* and *Sivapithecus* are the male and female of a single species related to orangutans (Andrews & Cronin, 1982; Lipson & Pilbeam, 1982). Our morphological analysis (Chaline, 1994), suggests the same is true of *Ouranopithecus macedoniensis* (Bonis and Melentis, 1977; Bonis et al., 1990) which has the same facial affinities with orangutans.

After the separation of the orangutan lineage, the common ancestral lineage of the three extant genera remained in Africa. But fossil remains dating from 10 to 5 Myrs are very sparse. Only four finds have been made to date. Two molars from Lukeino and Ngorora (Kenya) (Pickford, 1975) and a fragment of jaw with a molar Lothagam, again in Kenya, dated to 5,5 Myrs. The latest discovery is the most interesting, that of *Ardipithecus ramidus* found by White et al. (1994, 1995) in the Pliocene of the Middle Awash (Ethiopia) and dated to 4,4 Myrs. Most data about the teeth (metric, morphology, enamel thickness) and even features of the cranium "evincing a strikingly chimpanzee-like morphology" are very similar to chimpanzee form (Bonobo ?), but also have australopithecine characters. It may be that these fossils are of one of the components of the common ancestor - the pre-chimpanzee or pre-australopithecine!

The chromosomal model described here entails several anatomical implications that can be tested by paleontology. The first is that the cranial and dental morphologies of the three sub-species of the common ancestor should be highly simian. The discovery of *ramidus* is fully consistent with this hypothesis and is a first favorable test. The second implication concerns the shape of the pelvis. As gorillas and chimpanzees are quadrupeds and as bipedalism is the apomorphic feature characteristic of australopithecines and their human descendants, the three components of the common ancestor must therefore still have walked on all fours.

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Fig. 1 - The most p
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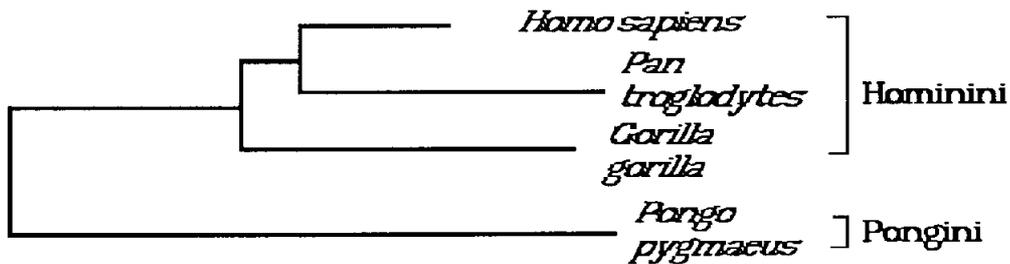


Fig. 1 - The most parsimonious arrangement of the sequence data of PPY: *Pongo pygmaeus*; GGO: *Gorilla gorilla*; PTR: *Pan troglodytes*; HSA: *Homo sapiens*. Branch lengths based only on unambiguous changes (after Miyamoto et al., 1987)

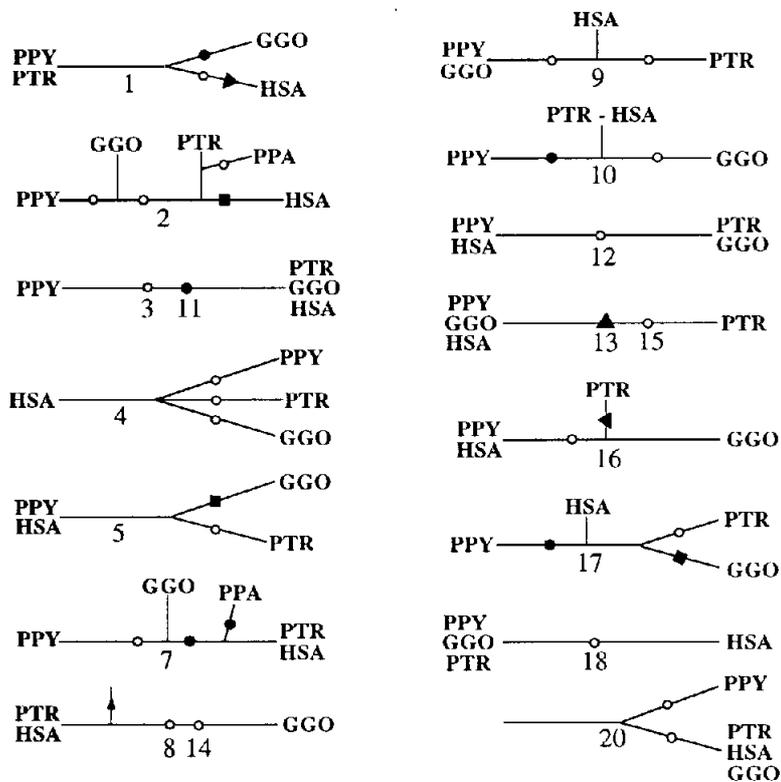


Fig. 2 - Comparison of chromosomal mutations in orangutan, gorilla, chimpanzee and man. PPY: *Pongo pygmaeus*; GGO: *Gorilla gorilla*; PTR: *Pan troglodytes*; HSA: *Homo sapiens*. White dots: pericentric inversion; black dots: paracentric inversion; triangles: gain in heterochromatine; black squares: reciprocal or terminal-terminal translocation (after Dutrillaux and Couturier, 1986).

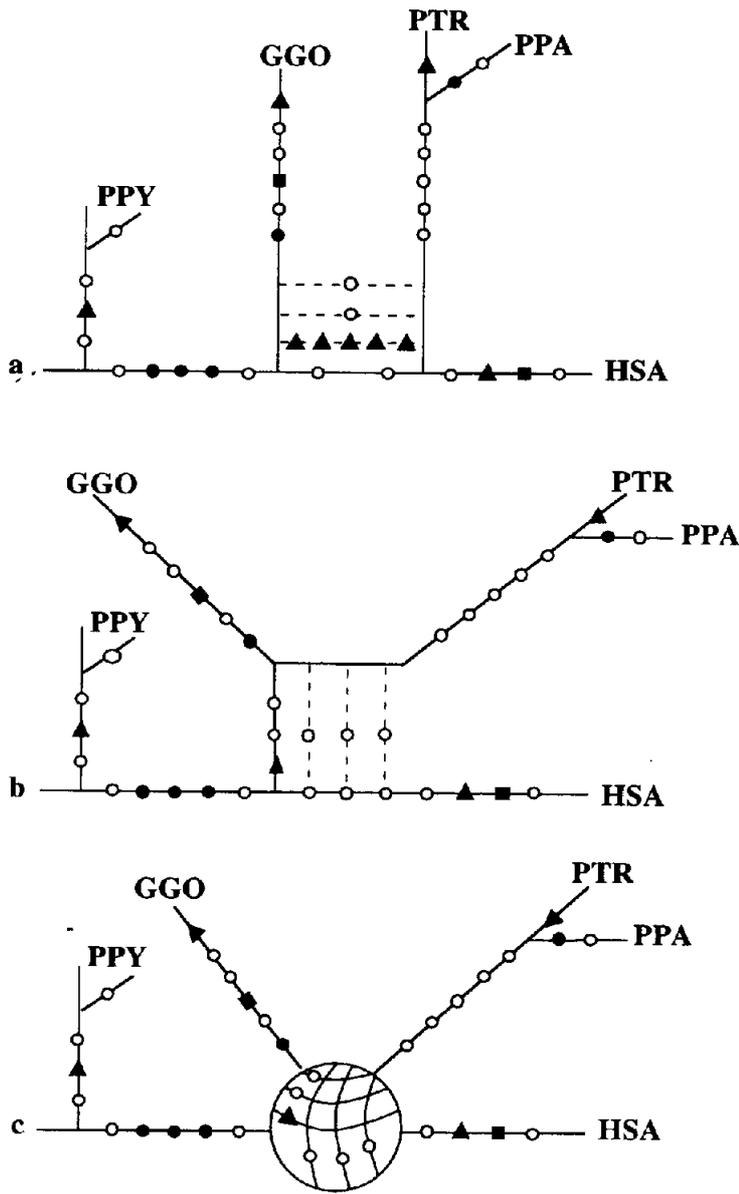


Fig. 3 - Three models explaining the distribution of mutated chromosomes in orangutans, gorillas, chimpanzees and humans. a - common mutations viewed as convergence in GGO and PTR; b - common mutations viewed as convergence in PTR and HSA; c - individual population evolution. PPY: *Pongo pygmaeus*; GGO: *Gorilla gorilla*; PTR: *Pan troglodytes*; PPA: *Pan paniscus*; HSA: *Homo sapiens*. White dots: pericentric inversion; black dots: paracentric inversion; triangles: gain in heterochromatine; black squares: reciprocal or terminal-terminal translocation (after Dutrillaux and Couturier, 1986).

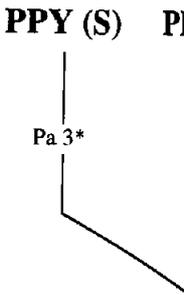


Fig.4 - Chromosomal phylogeny showing pericentric inversion in Pa 3* (5-M in gorilla; PTR: *Pan troglodytes*).

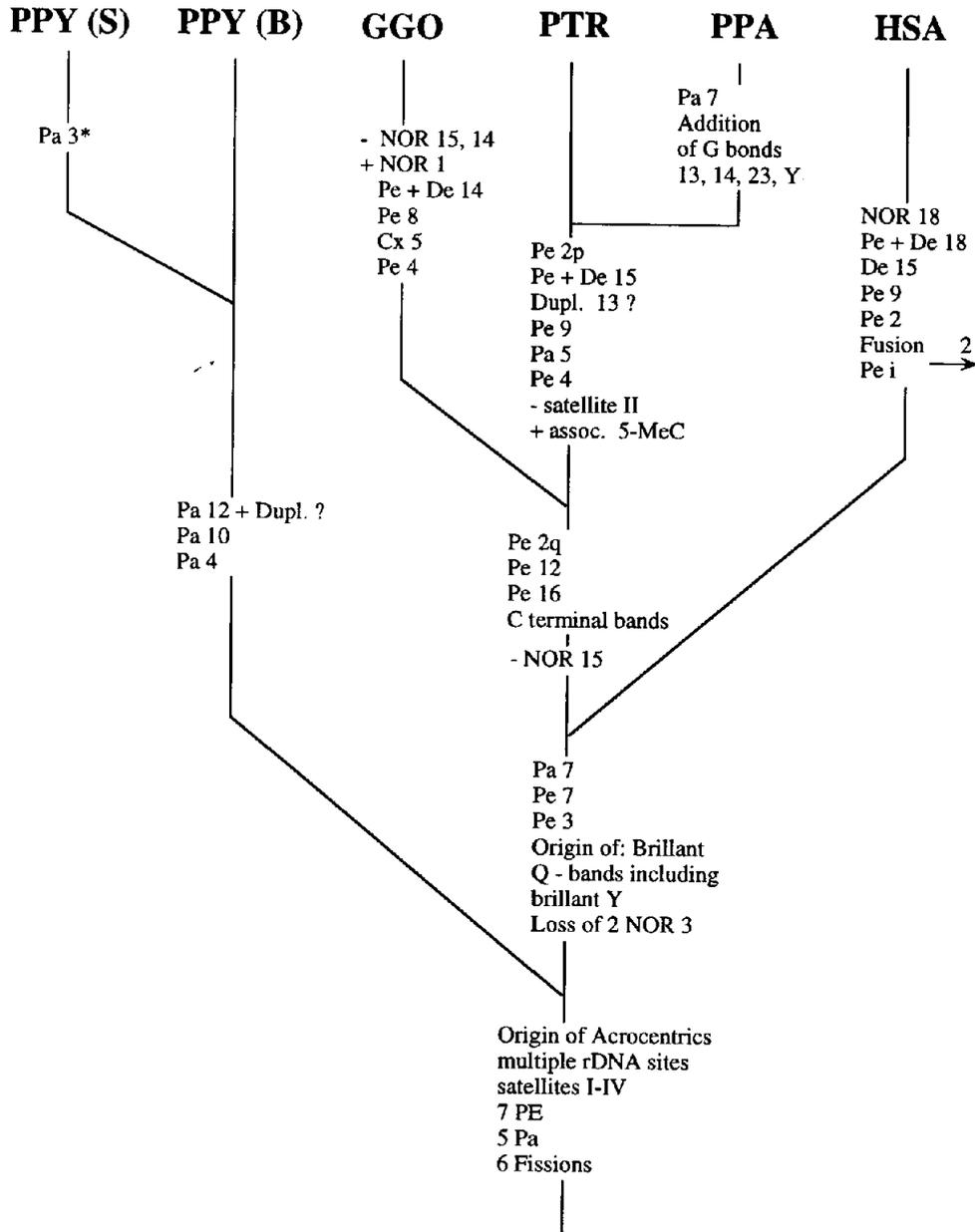


Fig.4 - Chromosomal phylogeny for the Hominoidea. Cx: complex change; De: deletion; Pa: paracentric inversion; Pe: pericentric inversion; 5-MeC: 5-methyl-cytosine. PPY: *Pongo pygmaeus* (S: Sumatra; B: Borneo); GGO: *Gorilla gorilla*; PTR: *Pan troglodytes*; PPA: *Pan paniscus*; HSA: *Homo sapiens*. (after Stanyon and Chiarelli, 1981).

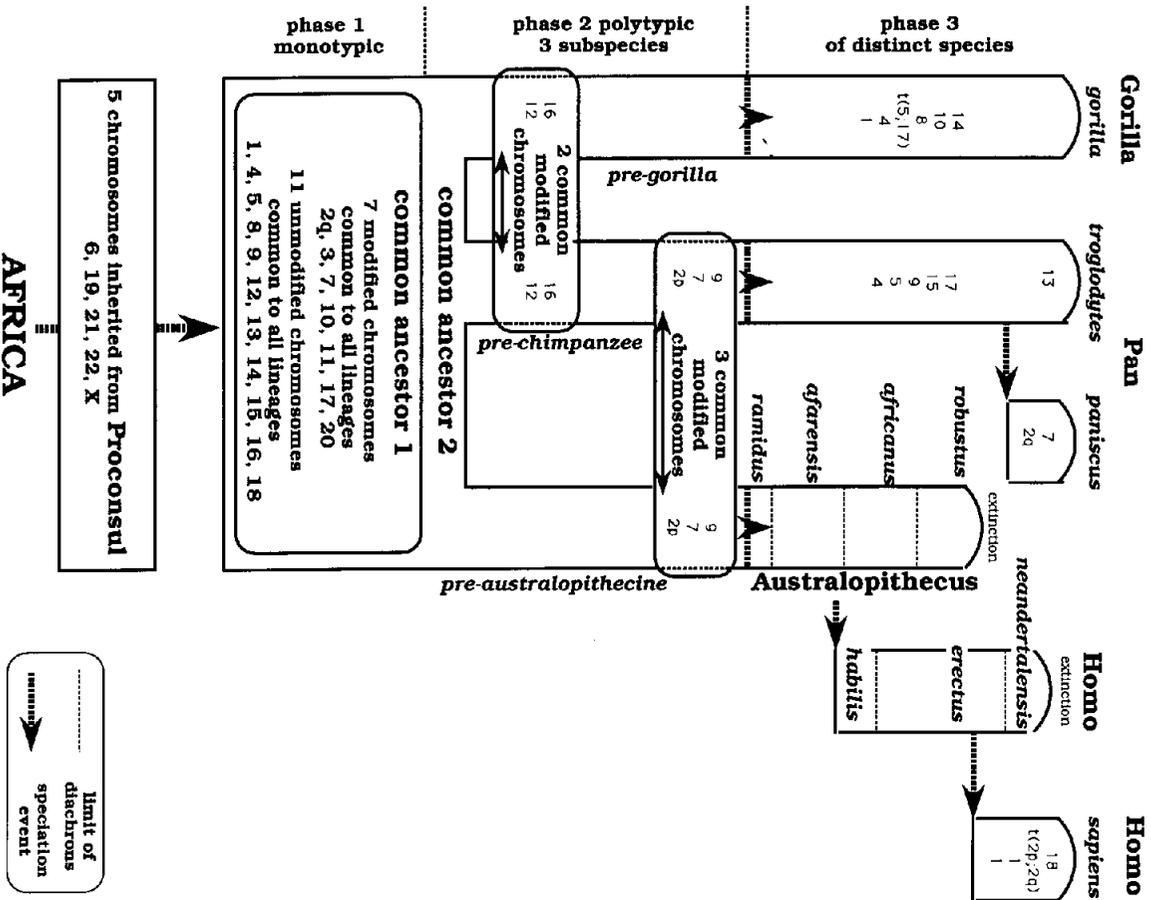


Fig. 6 - Distribution of panzee (*Pan troglodytes* panzee) typical common chim (Cameroon and Schweit 1988).

Fig. 5 - Trichotomic chromosome model incorporating paleontological and ontogenetic data. This model explains the distribution of chromosome formulas of living species and proposes a solution for shared *Pan/Homo*, *Gorilla/Pan* apomorphic mutated chromosomes and the absence of *Gorilla/Homo* apomorphic chromosomes. After a monotypic phase accounting for chromosomal apomorphs 2, 3, 7, 10, 11, 17 and 20, the common ancestor must have become polytypic and divided into three sub-species - pre-gorilla, pre-chimpanzee and pre-australopithecus. Some 5 Myrs back the three sub-species produced the three extant and fossil genera: *Gorilla*, *Pan* and *Australopithecus*. About 2 Myrs ago the *Homo* lineage derived from *Australopithecus* to give primitive man (*Homo erectus*) and around 0.18 Myrs ago modern humans (*Homo sapiens*). The figures refer to mutated chromosomes.

Fig. 7 - Distribution of *gorilla gorilla* in Congo *gorilla gorilla* (Bununu *gorilla beringei*) is in d

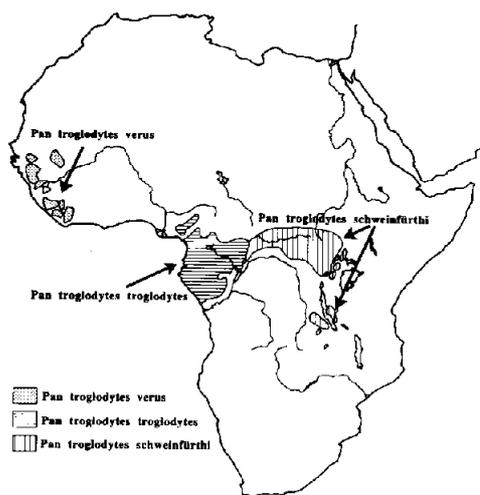


Fig.6 - Distribution of the three sub-species of common chimpanzees. The western-most sub-species, the black chimpanzee (*Pan troglodytes verus*), inhabits Guinea while the other are found north of the River Zaire (or Congo): the typical common chimpanzee (*Pan troglodytes troglodytes*) in the west in Congo, Gabon, Equatorial Guinea and Cameroon and Schweinfurt's chimpanzee (*Pan troglodytes schweinfurthi*) further east in northern Zaire (after Collet, 1988).

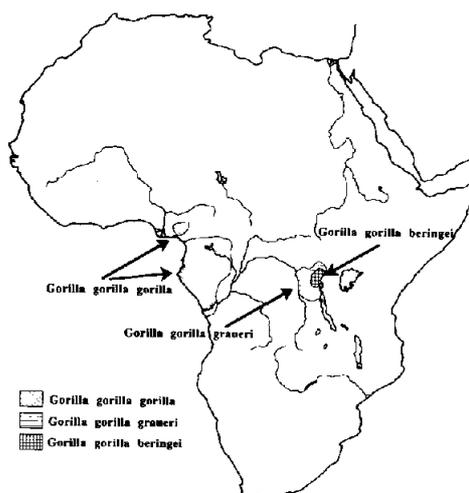


Fig.7 - Distribution of the three sub-species of gorillas. Gorillas are divided into western lowland gorillas (*Gorilla gorilla gorilla*) in Congo, Gabon, Equatorial Guinea and southern Cameroon and eastern mountain gorillas (*Gorilla gorilla graueri*) (Burundi and Rwanda). A third sub-species, the mountain gorilla of Rwanda and Uganda (*Gorilla gorilla beringei*) is in danger of imminent extinction (after Collet, 1988).

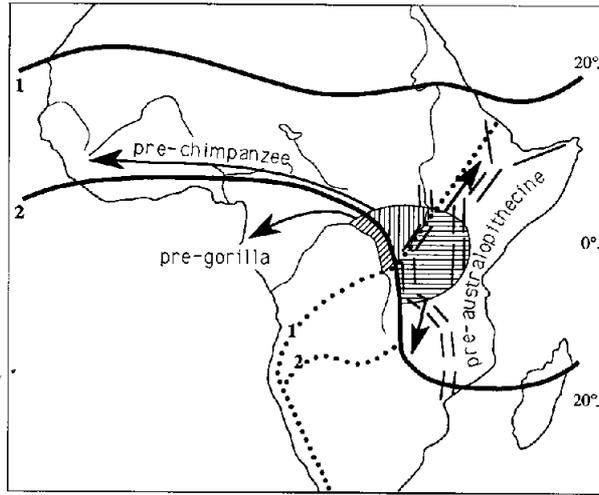


Fig.8 - Distribution of the common ancestor at the start of the polytypic phase. Pre-gorillas must have occupied the wet Atlantic monsoon zone (dense forest), pre-chimpanzees the less humid Atlantic monsoon zone (open forest) and pre-australopithecines the Indian Ocean monsoons zone (accacia savannah). 1: Summer; 2: Winter; thick solid line: Inter Tropical Front; pointed line: Inter Oceanic Confluence.

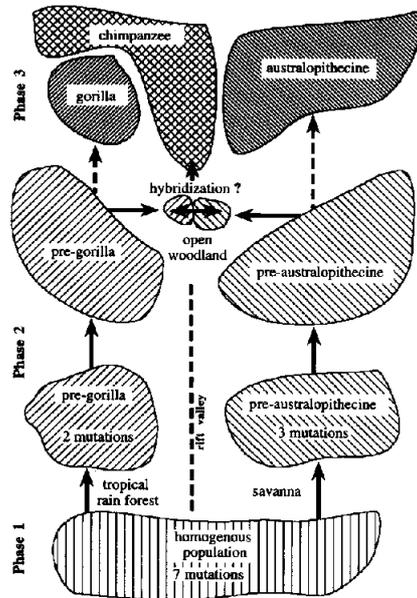


Fig.9 - Dichotomic model explaining the distribution of chromosomes in living species. This most parcimonious model suggests that after the monotypic phase, the common ancestor split into two sub-species - pre-gorilla and pre-australopithecine - and that the populations from the two sub-species interbred to produce the third, hybrid, sub-species - the pre-chimpanzees



Fig.10 - Phylogenetic diagram showing ages in Myrs and species names: Sivapithecus, Ramapithecus. Speciations occur by punctuated evolutionary change (chron...

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M. L. A. Ham
R. A. Foley

*Hominid Evolutionary
Research Group
Department of Biological
Anthropology
Downing Street, Cambridge
3DZ, U.K.*

Key words: Hominid e
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Introduction

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