

Skeletal growth allometry and the human-chimpanzee clade

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Abstract

Geneticists often regard the chimpanzee as the closest living relative of man while most morphologists link *Pan* with *Gorilla*. As phylogenetic lineages are conventionally interpreted as series of modified ontogenies, comparison of relative growth of great apes and humans may contribute to the solution of the African ape-human trichotomy. Allometric growth trajectories of cranial and postcranial dimensions relative to body weight are compared in chimpanzees, gorillas and humans. Modifications of skeletal growth patterns observed among African apes correspond with those observed among closely related vertebrate taxa, while differences in growth patterns are much more profound in the human-chimpanzee comparison. These results support an African ape clade rather than a *Pan-Homo* clade.

Résumé

Beaucoup des généticiens considèrent le chimpanzé comme le plus proche parent de l'homme moderne, tandis que des morphologistes rapprochent *Pan* de *Gorilla*. Les lignées phylogénétiques sont conventionnellement interprétées comme un série d'ontogènes modifiées : la comparaison des trajectoires de la croissance relative des hominoides pourrait contribuer à la division de l'ensemble *Homo/Pan/Gorilla*. Les modifications des trajectoires de croissance du squelette observées chez les chimpanzés et les gorilles correspondent à celles observées chez des espèces de vertébrés proches. Par contre, les différences des trajectoires chez les chimpanzés et les hommes sont très profondes. Ces résultats confortent l'idée de l'existence d'un clade des pongidés africains, plutôt qu'un clade *Pan/Homo*.

1. INTRODUCTION

While most workers agree that the African apes are the closest relatives of humans (Andrews, 1992; Bailey, 1993), a number of studies based on molecular and chromosomal data support a *Pan/Homo* clade to the exclusion of *Gorilla* (Bailey *et al.*, 1992; Goodman *et al.*, 1994; Horai *et al.*, 1992; Ruvolo *et al.*, 1991). Separating the morphologically and behaviourally so similar African apes in order to associate *Pan* with *Homo*, however, has encountered opposition. The obvious discrepancy between morphological and molecular investigations has not yet been reconciled (Corruccini, 1992; Marks, 1994) and the trichotomy proposed as a potential solution to this problem has not received general acceptance (Saitou, 1991).

Great hopes have been placed in the study of ontogeny as a vital link between genes and morphology and as a potential reflection of a common history of the species under investigation (Alberch *et al.*, 1979; Gould, 1977). As the evolution of form occurs through changes in developmental pattern, allometry growth trajectories are employed here to investigate differences in developmental pattern between species. Five models of comparative growth allometry (fig. 1) approximate all differences imaginable between two species (Hartwig-Scherer, 1993): ontogenetic

scaling (model 1), divergence (model 2), transposition (model 3), convergence (model 4) and intersection (model 5).

The concepts of heterochrony (changes in the timing of developmental events with respect to the ancestral condition) and allometry (changes in body size and subsequent morphological alterations) have gained increasing attention with respect to the evolution of form (Gould, 1977). The evolutionary significance of both concepts is that relatively small genetic modifications may result in considerable morphological alterations. The synthesis of both concepts—allometric heterochrony—is employed here in order to evaluate its phylogenetic potentials with respect to the African ape—human trichotomy. The growth variates size, shape and age are represented in Gould's clock model by three hands which can be moved independently across three scales (fig. 2). Moving one or more of these hands at a time may alter specifically the allometric growth trajectories (Gould, 1977). All possible differences between growth trajectories of the two species A and B are approximated by five models of ontogenetic modifications. From the genetic perspective, ontogenetic scaling certainly is the simplest "solution" for producing different adult shapes: Only one of the three parameter has to be changed: size change and subsequent shape change is the

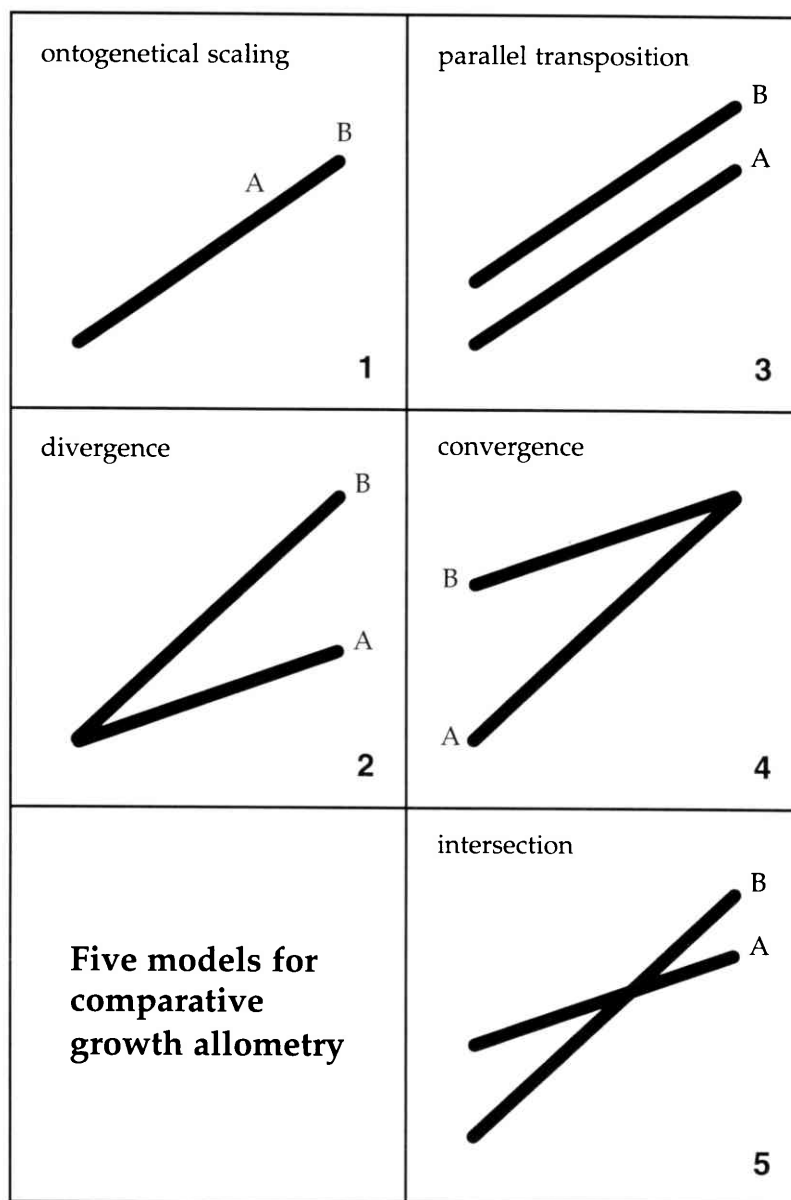


Fig. 1: Five models of comparative growth allometry. Relative growth trajectories of two species A and B may differ in five ways approximated by the five models presented.

consequence either of changing rate of growth or time of maturation. The decoupling of growth trajectories, *i.e.* dissociation of size and shape, leading to divergence and transposition (model 2, 3) is yielded through differential changes of growth rates and through differential changes in the timing, respectively. A more complex set of changes is required to obtain convergence (model 4) or intersection (model 5), as both initial shape and relative growth rate have been altered.

Previous studies have demonstrated similar growth patterns in African apes (Shea, 1981, 1983, 1985). Under the assumption that related species may share more aspects of relative growth programs than less related forms, allometric growth

patterns of 89 cranial and postcranial dimensions relative to body weight were determined in a previous study for five hominoid species (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*, *Homo sapiens*) (Hartwig-Scherer, 1993). Multivariate scaling of overall growth pattern revealed that African apes share most aspects of growth, while *Pongo* and especially *Homo* are set apart in opposite directions. In this study, allometric growth trajectories of cranial and postcranial dimensions relative to (predicted) body weight have been determined in *Pan troglodytes*, *Gorilla gorilla* and *Homo sapiens*. Between-species differences in growth trajectories are analysed with respect to the five models mentioned above

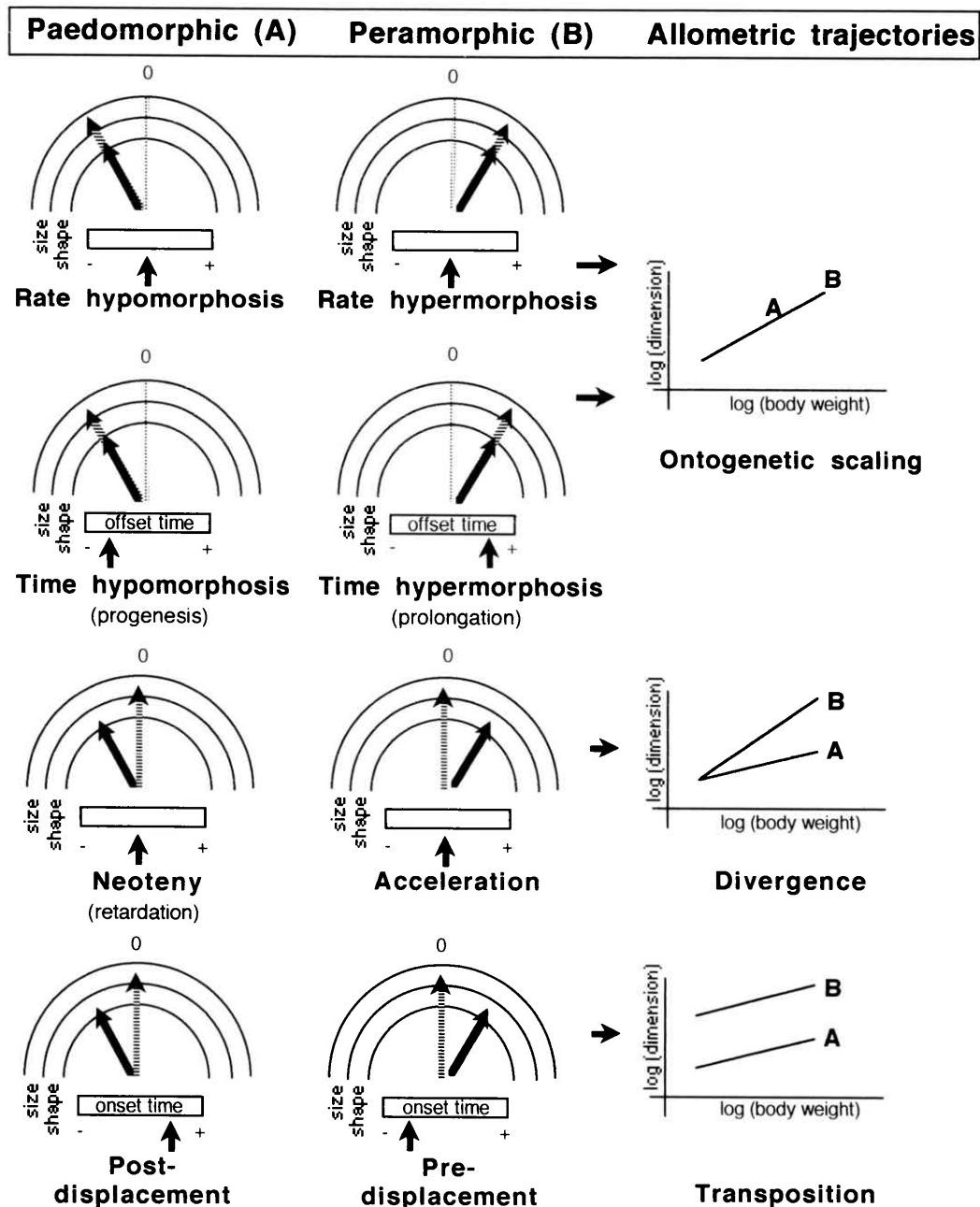


Fig. 2: Synthesis of the concepts of heterochrony and allometry (modified after Alberch *et al.*, 1979; Gould, 1977) relating developmental events (changes in size, shape or time), heterochronic processes (rate and time hypo- or hypermorphosis, neoteny or acceleration, post- or predisplacement) and allometric growth trajectories (ontogenetic scaling and size/shape dissociations; see also fig. 1). The two basic morphological categories are paedomorphosis ("juvenile" appearance in adulthood, represented by species A) and peramorphosis ("post-adult" appearance in adulthood, represented by species B). The clock with three scales size, shape and time assumes that some standardized form, presumably the ancestral condition, is located at 0, from which the two species A and B are derived through changes in one or more of the scales. Following allometric growth trajectories result from the indicated heterochronic processes, if one of the scales is changed at a time: (a) extension or truncation of a common ontogenetic pattern (ontogenetic scaling, model 1) is yielded through changes in the overall growth rate (rate hypo- or hypermorphosis) or (b) through changes in the overall developmental timing (time hypo- or hypermorphosis; offset time, *i.e.* time of maturation, earlier or later, respectively). (c) The decoupling of growth trajectories (dissociation of size and shape) resulting in divergence (model 2) may be generated through changes of relative growth rates (neoteny and acceleration). (d) The decoupling of growth trajectories (dissociation of size and shape) resulting in transposition (model 3) may be yielded through differential changes in the onset time (post- or predisplacement; onset time later or earlier) or through initial shape change at the beginning of development (not shown). (Modified after Gould, 1977 and Shea, 1989.)

and it is explored which potentials allometric heterochrony may hold for the analysis of hominoid phylogeny and the African ape-human trichotomy in specific.

2. MATERIAL AND METHODS

Allometric growth of 50 cranial and postcranial dimensions of *Pan troglodytes*, *Gorilla gorilla* and *Homo sapiens* are compared relative to body weight. As only a limited number of skeletons with recorded body weight was available, body weight has been predicted for a much larger sample of ontogenetic series (Hartwig-Scherer & Martin, 1992). Allometric growth is investigated relative to (predicted) body weight using only non-adult specimens. Reduced major axis analysis was used to fit a line to the log-transformed data. For definition of skeletal dimensions, for prediction equations, number and provenance of skeletons with and without recorded body weight and for growth exponents and coefficients see Hartwig-Scherer and Martin (1992) and Hartwig-Scherer (1993). Difference among the species pairs *Pan/Gorilla* and *Pan/Homo* are approximated by five models of comparative allometric growth as depicted in figure 1.

3. RESULTS AND DISCUSSION

Postnatal relative growth patterns of common chimpanzees are specifically compared (a) with gorillas and (b) with humans. A small selection of the dimensions investigated in this study is given in figure 3. The corresponding ontogenetic modifications (models 1 to 5) have been visually determined for the two species pairs, *Pan troglodytes*–*Gorilla gorilla* and *Pan troglodytes*–*Homo sapiens* analysing 50 dimensions which correlate well with body weight (table 1). While ontogenetic scaling, transposition and divergence characterize the chimp-gorilla comparison, the human-chimp comparison displays a variety of converging and intersecting growth trajectories in addition to strong divergence and transposition. Models 1 to 3 which theoretically require less genetic changes than models 4 and 5 occurred in 98 % of cases in the *Pan/Gorilla* comparison, while in the *Pan/Homo* comparison models 4 and 5 were found in almost half the cases. Assuming that the concept of allometric heterochrony indeed is an appropriate approach to infer phylogenetic relationships, this would suggest an African ape, rather than a human-chimp clade. It should be emphasized

Models ¹	(a) <i>Pan-Gorilla</i>	(b) <i>Pan-Homo</i> ²
1 (ontogen. scaling)	15	4
2 (divergence)	10	6
3 (transposition)	24	12
4 (convergence)	1	20
5 (intersection)	0	6

Table 1: Occurrences of model 1 to 5 in the comparison of *Pan* with *Gorilla* (a) and with *Homo* (b)

¹ Models of comparative growth allometry (fig. 1) observed in the two pairs of species comparisons, *Pan troglodytes*/*Gorilla gorilla* and *Pan troglodytes*/*Homo sapiens*. Occurrences are given for 50 dimensions which display considerable correlation with body weight.

² Two cases in the *Pan-Homo* comparison are ambiguous.

that this study focusses on the comparison of allometric trajectories and not on heterochronic processes itself: although allometric trajectories may be predicted from underlying heterochronic processes, the reverse is not unequivocal: for instance, if ontogenetic scaling is observed in two species, it may result from four different heterochronic processes (*rate* hypo/hypermorphosis or *time* hypo/hypermorphosis which have quite different genetic bases) or from a combination of them.

The concept of allometric heterochrony has previously been applied successfully to taxa with known relationships and employed to clarify uncertain genealogies. The assumption that growth trajectories may be employed for phylogenetic reconstruction is also supported by additional evidence: A review of the literature reveals that a consistent set of ontogenetic modifications can be derived from the comparison of taxa whose genealogical ties are known to be close. This consistent pattern should allow phylogenetic inferences for taxa of unknown relationship. Only those published cases which fit the criterion of genealogical proximity were evaluated in this study (for references see Hartwig-Scherer, 1993). These are (i) species that produce viable hybrids, (ii) forms that belong to a single breed, (iii) forms that are genetically transformed and (iv) the two sexes of a single species. Relative growth studies among closely related primate species (Cole, 1992; Falsetti and Cole, 1992; Gomez, 1992; Jungers and Cole, 1992; Shea, 1992) as well as among breeds which have been selected for different sizes (Cock, 1966; Walton and Hammond, 1938; Wayne, 1986), genetically transformed giant mice (Shea *et al.*, 1990) and the two sexes of a given species (Leigh, 1992; Martin *et al.*, 1994; Masterson and

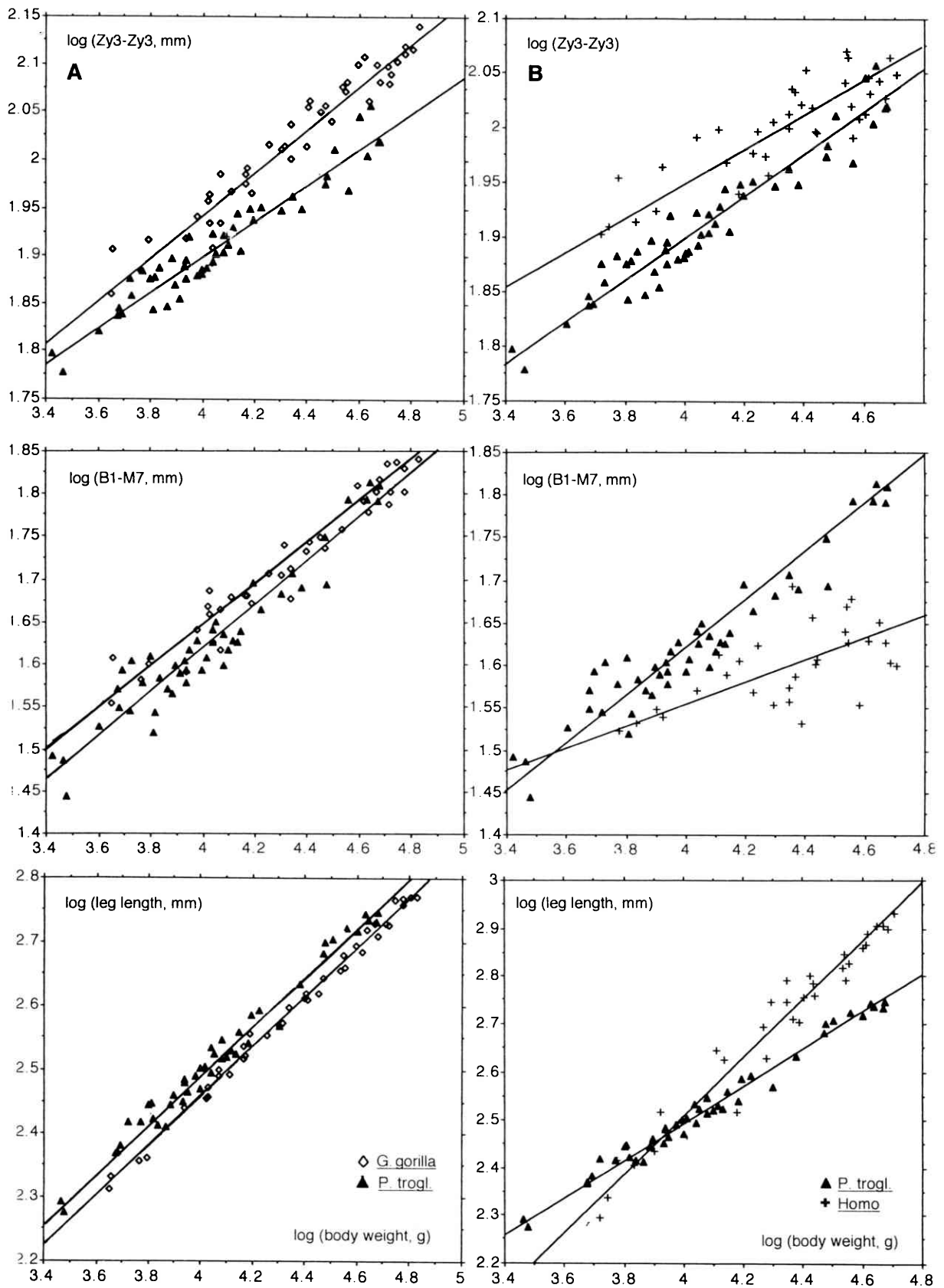


Fig. 3: Growth trajectories of selected skeletal dimensions relative to body weight. Different sets of ontogenetic modifications (models 1 to 5; see fig. 1) are observed when growth patterns of chimpanzees are compared with gorillas (A) and with humans (B). Cranial and postcranial dimensions: Zy3-Zy3: bizygomatic breadth; B1-M7: distance between basion and staphylion; leg length: maximum lengths of femur plus tibia.

Leutenegger, 1992) display ontogenetic scaling (model 1), divergences (model 2) and transpositions (model 3), but no convergencies or intersections (models 4, 5). Since this pattern is observed consistently in a number of closely related forms, it may be extrapolated to groups of uncertain or ambiguous relationship: models 1 through 3 suggest close relationship, while models 4 and 5 are indicative of a more distant relationship (a similar observation can be found in Gomez, 1992). These results also corroborate assumptions about genetic changes required to generate ontogenetic modifications: models 1–3 assumably require less genetic changes than model 4 and 5 (fig. 1 and 2).

The following conclusions can be drawn: (i) Overall similarity of postnatal growth patterns is far greater between chimpanzees and gorillas (African apes) than between chimpanzees and humans. This has been also shown by multivariate analyses using oranges as outgroup (Hartwig-Scherer, 1993). (ii) Ontogenetic modifications among African apes parallel those observed for closely related forms. This is not the case for the ontogenetic comparison of chimpanzees and humans. (iii) If evolutionary lineages are series of modified ontogenies, chimpanzees share a closer phylogenetic relationship with gorillas than with humans. (iv) The developmental process of neoteny which played a central role in the discussion on human evolution, is not at all sufficient as an all-embracing explanation to derive human from a *Pan*-like ontogeny (see also Shea, 1989). In fact, a much more complex combination of several heterochronic processes must be postulated for a hypothetical chimpanzee-human transformation.

These results may corroborate doubts of several authors concerning the human-chimp clade (Marks, 1994). Various chromosomal (Marks, 1993), molecular (Brown *et al.*, 1982; Templeton, 1983), morphometric (Oxnard, 1981), and morphological data (de Bonis, 1983; Gantt, 1983; Martin, 1986; Martin, 1990) also support an African ape clade rather than a human-chimp clade.

The overall striking discrepancies between morphological, behavioural and ontogenetic distinctiveness and the close genetic similarity (as far as nucleotide sequences are concerned) between humans and chimpanzees still await an explanation. Before one or the other data set is discarded as inappropriate for phylogenetic reconstruction, much remains to be discovered with respect to what links genes with morphology. Perhaps molecular data sets are not as much superior over other data sets as assumed to date. In order to reconcile the obvious gap between "molecules and

morphology", it has been suggested that only a relatively small number of changes in the regulatory genes controlling ontogenetic processes may be necessary to bring about substantial morphological differences. Clearly, the determination of such unknown genetic singularities (Washio *et al.*, 1992) is of paramount importance as they may constitute the genetic basis for the morphological, physiological, and developmental uniqueness of a given species. Other non-genetic factors still to be discovered may be involved in the developmental process as well. The discrepancy remains a challenge for future research for both developmental and molecular biologists.

Acknowledgements

I am grateful to the organizers of the symposium "Ontogenèse et hominisation" for their invitation. Thanks are expressed to the curators of various museum collections—Drs B. Latimer, J. Jacobs, D. Hunt, D. Howlett, W. van Neer—for access to the specimens and for assistance. I am grateful to R. D. Martin, Zürich, and B. A. Wood, Liverpool, for discussions.

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