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16 June 1983; accepted 22 September 1983

Paedomorphosis and Neoteny in the Pygmy Chimpanzee

Abstract. *The strongly paedomorphic skull form in the pygmy chimpanzee results from the heterochronic process of neoteny. This cranial paedomorphosis and neoteny in* Pan paniscus *may be related to reduced sexual dimorphism in morphology and behavior. The interspecific differences in form result from shifts in the rate and timing of similar patterns of development.*

The nature of the morphological differences between the "pygmy" and "common" chimpanzees and the meaning of these differences for our understanding of ape and human evolution have long been of interest to primatologists. Early investigators (*1, 2*) suggested that the pygmy chimpanzee (*Pan paniscus*) represented a "dwarfed, paedomorphic" form of chimpanzee (*1, 2*); later others (*3, 4*) also invoked paedomorphosis and neoteny to account for the differences between the chimpanzee species, but detailed studies to support these hypotheses have not been made.

I have integrated studies of allometry [size and shape relations (*5*)] and heterochrony [shifts in the timing of developmental patterns (*6–9*)] in an analysis of chimpanzee (and gorilla) morphology (*9–16*). My results indicate that most of the shape differences between adult pygmy and common chimpanzees are allometric because of "ontogenetic scaling." That is, the primary differences in shape result from a simple extension of common growth allometries to different terminal sizes (Fig. 1a) (*17*). This has been found to generally hold within the skull (*13–15*), within the trunk (*14*), and within each limb (*10*), but not in a comparison of hind limb length relative to trunk or forelimb length (*10, 14*). I now discuss new findings concerning these issues, resulting from more detailed comparisons among various body regions in the two species of chimpanzees.

Although ontogenetic scaling of proportions holds for almost all comparisons within the major body regions of the head, trunk and forelimbs, and hind limbs, the pygmy and common chimpanzees clearly do not fall along a common ontogenetic trajectory when comparisons are made between these major body regions. In fact, the data show a "gradient" of differential size (and correlated shape) change among the major body regions in a comparison of *P. paniscus* with *P. troglodytes* chimpanzees (*18*) (Table 1). Adult pygmy chimpanzees do not have overall proportions that match any single ontogenetic stage in *P. troglodytes*. Rather, given a large-to-small vector of size change, the skull is most strongly reduced in size, the forelimbs and body trunk are somewhat reduced, and the hind limbs are not reduced at all (*19*). The opposite changes characterize a small-to-large vector of size increase (that is, *P. paniscus* to *P. troglodytes*) (Fig. 1B) (*20*). A comparison of the ontogenetic allometries of maximum skull length against head-and-trunk length in the chimpanzee reveals a strong divergence of the growth trajectories; at a given body size, *P. paniscus* has a smaller overall skull size than *P. troglodytes* (Fig. 1C) (*21, 22*). Because of the strong ontogenetic scaling of cranial growth patterns, the smaller skull size in the

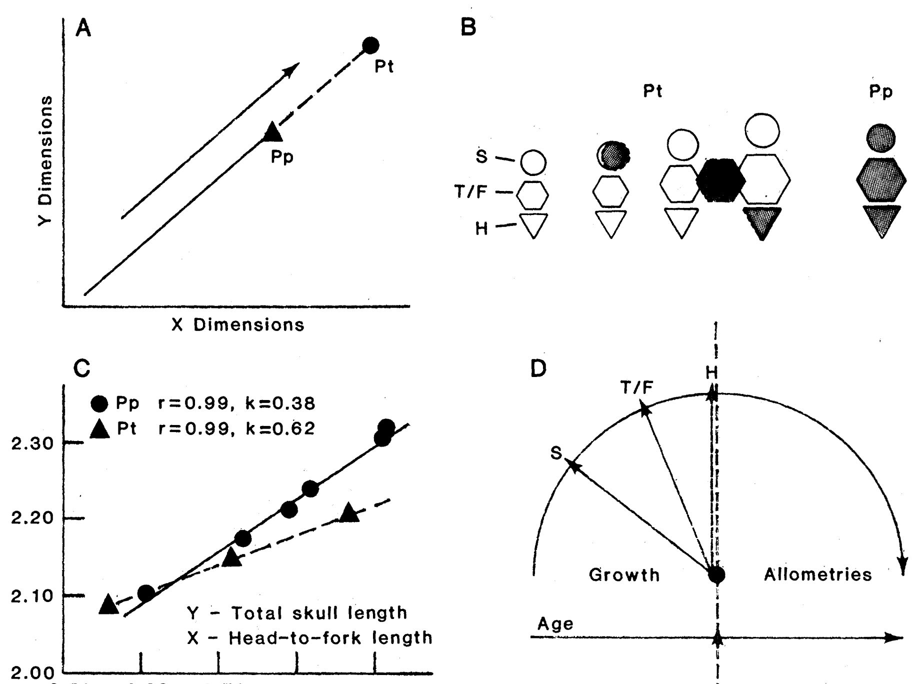

Fig. 1. (A) Paedomorphosis in *Pan paniscus* adults and the extension of common growth allometries to larger sizes in *Pan troglodytes* adults. (B) Relative size of the skull (*S*), trunk and forelimbs (*T/F*), and hind limbs (*H*) in adult *Pan paniscus* (shaded symbols) when placed on an ontogenetic sequence of infant, juvenile, subadult, and adult *Pan troglodytes* (open symbols). (C) Skull length (in millimeters) is plotted against a measure of trunk length (in millimeters) in ontogenetic sequences of the chimpanzees. The lower slope in the pygmy chimpanzees (k = 0.38; standard deviation, 0.01) compared to the the common chimpanzee (k = 0.62; standard deviation, 0.03) reflects slowed growth of the skull relative to overall body size, yielding paedomorphosis via neoteny. (D) Gould's (*7*) "clock model" of heterochrony, where the curved trajectory represents differential travel along common growth allometries. If the dashed vertical line is taken as the condition in adult *Pan troglodytes*, the position of the clock's "hands" for the skull, trunk and forelimbs, and hind limbs indicates the relative position of adult *Pan paniscus* (*17–22*); compare to (B).

Table 1. A comparison of body dimensions between adult *Pan paniscus* and an ontogenetic sequence of *P. troglodytes*. Values are age-group means. The dimensions of head, trunk and forelimbs, and hind limbs for adult *P. paniscus* fall at different points along the growth trends of *P. troglodytes*.

Item	Body dimensions (mm)				
	Pan troglodytes				Adult *Pan paniscus*
	Infant	Juvenile	Subadult	Adult	
Total skull length	148	163	175	195	163
Arm length	373	417	504	574	555
Arm span	1225	1405	1526	1795	1588
Trunk height	451	526	570	733	665
Hind limb length	347	397	478	543	542

pygmy chimpanzee is correlated with a paedomorphic or juvenilized shape relative to *P. troglodytes* of equal size or age.

The shifts in patterns of size and shape relative to age among the major body regions in a transformation of *P. troglodytes* to *P. paniscus* (Fig. 1D) demonstrate that the adult pygmy chimpanzee exhibits paedomorphosis of skull form via neoteny; it is characterized by an overall skull size and shape closely resembling younger subadult stages of *P. troglodytes* (*23*). Neoteny is the appropriate heterochronic process in this case because the paedomorphic skull form in *P. paniscus* is produced by a dissociation of the ancestral relation of skull to body growth, and a slowing or retardation in the overall rate of shape change in skull form relative to overall body growth (see Fig. 1, C and D). Conversely, if size increase from *P. paniscus* to *P. troglodytes* is considered, the timing shifts in Fig. 1D would yield a mirror image, and acceleration of skull growth relative to overall body size growth would produce the peramorphic (*8*) cranial shape in common chimpanzees.

The cranial paedomorphosis and neoteny in *P. paniscus* may be related to reduced sexual dimorphism in morphology and behavior since reduction or truncation of a structure's growth yields reduced sexual dimorphism (*24*), and *P. paniscus* exhibits less sexual differentiation of behavior and grouping patterns than *P. troglodytes* (*25*).

Gould (*7*) and others (*26*) have suggested that analyses of heterochrony may provide a vital link between studies of morphological evolution and regulatory genetics. The seeming disparity between the morphological and genetic distance separating humans and chimpanzees has led many to conclude that small changes in the genetic material controlling regulatory systems might account for significant organismal change in evolution (*7*, *26–28*). Although the morphological differences between pygmy and common chimpanzees do not approach those characterizing a human-to-chimpanzee contrast, the above results show how substantial morphological differentiation may result from shifts in developmental timing and rates of growth among various major body regions, with little or no change in the ontogenetic patterns within each region. The data are consistent with the idea that "features of an organism are bound . . . in covariant sets, and these sets are often dissociable as blocks" (*28*). This "shuffling" of the developmental trajectories of various body regions may provide new adaptive morphological configurations with minimal genetic changes.

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17. Figure 1A illustrates, in schematic form, ontogenetic scaling of proportions in the two chimpanzee species. Shape differences result from the extension or truncation of a common growth allometry, and thus may be correlated with overall size change of a region or the body as a whole.
18. Data are mean values from (*11*). Sexes are pooled for all dimensions. Ages: infant, deciduous dentition plus M^1; juvenile, M^2 erupted; subadult, C or M^3 erupted; adult, all permanent teeth fully erupted. Dimensions: total skull length, opisthocranion-prosthion; arm length, humerus plus radius length; arm span, length of outstretched arms between the fingertips of cadavers shot in the wild; trunk height, head-to-fork length of wild-shot cadavers minus cranial vault height; hind limb length, femur plus tibia length.
19. The small size of the skull (and teeth) in *P. paniscus* relative to *P. troglodytes*, compared to other body regions, has also been stressed by McHenry and Corruccini (*4*) and A. L. Zihlman [*The Human Evolution Coloring Book* (Barnes & Noble, New York, 1982), p. 89].
20. The circle, hexagon, and triangle represent head, trunk and forelimbs, and hind limbs, respectively. They are not drawn precisely to scale, although an attempt has been made to reflect known ontogenetic trends in *P. troglodytes*—for example, the relative decrease in head size throughout growth. Compare with the quantitative data in Table 1.
21. It would appear from this plot of skull length against trunk ("head-to-fork") length that the shape difference between adult pygmy and common chimpanzees results primarily from a decrease in the coefficient of ontogenetic allometry, rather than a downward shift or transposition in the growth trend early in ontogeny. Points for the two subadult *P. paniscus* are taken from information given in P. Rode [*Mammalia V* **2**, 50 (1941)] for the subadult and in Coolidge (*2*) and Weidenreich (*22*) for the infant. In addition, A. H. Schultz's [*Am. J. Phys. Anthropol.* **18**, 61 (1933)] comparative study of *P. paniscus* and *P. troglodytes* fetuses indicates no clear difference in skull and trunk proportions at this early stage. The proportion differences observed most clearly in the adult stages become progressively more marked throughout growth due to the differences in the respective coefficients of ontogenetic allometry.
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7 February 1983; revised 22 June 1983