

Heterochrony and geometric morphometrics: a comparison of cranial growth in *Pan paniscus* versus *Pan troglodytes*

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SUMMARY Heterochrony, the classic framework in which to study ontogeny and phylogeny, in essence relies on a univariate concept of shape. Though principal component (PC) plots of multivariate shape data seem to resemble classical bivariate allometric plots, the language of heterochrony cannot be translated directly into general multivariate methodology. We simulate idealized multivariate ontogenetic trajectories and explore their appearance in PC plots of shape space and size–shape space. Only if the trajectories of two related species lie along exactly the same path in shape space can the classic terminology of heterochrony apply and pure dissociation of

size change against shape change be detected. Regional heterochrony—the variation of apparent heterochrony by region—implies a dissociation of local growth fields and cannot be identified in an overall PC analysis. We exemplify a geometric morphometric approach to these issues using adult and subadult crania of 48 *Pan paniscus* and 47 *Pan troglodytes* specimens. On each specimen, we digitized 47 landmarks and 144 semilandmarks on facial curves and the external neurocranial surface. We reject the hypothesis of global heterochrony in the cranium of *Pan* as well as regional heterochrony for the lower face, the upper face, and the neurocranium.

INTRODUCTION

The study of heterochrony has a long history incorporating extended debates, many of them lacking a consensus even today (see e.g., Gould 1977; Alberch 1985; McKinney and McNamara 1991; Godfrey and Sutherland 1995, 1996; Raff 1996; Zelditch and Fink 1996; Klingenberg 1998). The term “heterochrony” has also been applied—very controversially—to explain human evolution (Bolk 1926; de Beer 1951; Pilbeam and Gould 1974; Gould 1977; Montagu 1989; Shea 1989; Penin et al. 2002). One prime example of heterochrony among primates is *Pan paniscus*, the pygmy chimpanzee, which is often regarded as pedomorphic relative to *Pan troglodytes* (Coolidge 1933; Giles 1956; McHenry and Corruccini 1981; Shea 1983a, b, 1989). These and many other older studies rely on bivariate allometric plots of some selected distance measurements. The advancement of landmark-based geometric morphometrics (Bookstein 1991; Marcus et al. 1996; Dryden and Mardia 1998; O’Higgins 2000a, b; Slice 2005) makes possible far broader analyses of ontogeny and phylogeny based on an extended list of shape variables and a multivariate statistical toolkit (see e.g., O’Higgins et al. 2001; Ponce de Léon and Zollikofer 2001; Penin et al. 2002; Bookstein et al. 2003; Mitteroecker et al. 2004a).

In this article, we attempt an appropriate fusion of these two lines of argument. We argue that the classic univariate notion of shape does not provide a scientifically effective concept of heterochrony in any canonical way to translate the most commonly applied morphometric definitions of heterochrony from Gould (1977) and Alberch et al. (1979) into a multivariate framework. Using simulated data we demonstrate how to interpret principal component (PC) scores along the lines of heterochrony and exemplify this approach in an analysis of the cranial development of *P. paniscus* and *P. troglodytes*.

The classical concept

Natural selection is based on biological variability, which in turn emerges through differences in ontogenetic pathways. Developmental biology has thus become a central discipline for evolutionary studies (see e.g., Raff 1996; Hall 1999; Wagner 2000; Arthur 2002). Heterochrony has played a crucial role in the study of ontogeny and phylogeny since its introduction by Ernst Haeckel (1866), who invented it as a class of exceptions to his theory of recapitulation. It was Gavin de Beer (1930, 1951) who redefined and broadened the concept into a more active and significant evolutionary mechanism. He understood heterochrony as relative retardation or

acceleration in the rate of development of the body as compared with the reproductive organs. He also acknowledged that these temporal alterations may be mosaic—developmental retardation or acceleration can be different from organ to organ. Gould (1977, 1992) provides a detailed historical discussion of this topic.

Today's experimental developmental biologists know many examples of how temporal shifts of actual biological processes like gene expressions or tissue inductions alter adult morphology (see e.g., McKinney and McNamara 1991; Raff 1996; Hall 1999). Heterochrony is also applied as an explanatory framework for purely descriptive morphometric data. This is especially the case in paleontology, primatology, and anthropology, where experiments are rarely possible. The most influential work on the morphometrics of heterochrony comes from Stephen J. Gould and colleagues. His book *Ontogeny and Phylogeny* (Gould 1977) provided a terminology, called the clock model, based on three variables: age, size, and shape (as a proxy for development). The adult morphology of a species can differ from that of an ancestor in any or all of these three aspects, and the word “heterochrony” refers to the evolutionary dissociation of size, shape, and age during ontogeny (Fig. 1). As biological age is often not available, most studies focus on the dissociation of size and shape alone.

Alberch et al. (1979) extended this approach to compare growth trajectories in age-versus-shape or size-versus-shape plots. In this scheme, a linear (or linearized) ontogenetic trajectory can be sufficiently specified by five control parameters: α for the onset age of growth, β for the age of cessation of growth, k_S for change in size, k_σ for change in shape, and S_0 for the initial size at the commencement of the growth period. When differences between ontogenetic trajectories are described as perturbations of these five parameters, there results a terminology of different heterochronic processes. Figure 2A

shows two trajectories in age–shape space. Both species reach maturity at the same age, but the descendant's shape (development) is retarded relative to its ancestor. This, again, is the case of neoteny.

Central to both approaches is the use of a single shape variable, usually construed as a ratio of two length measurements. These univariate approaches provide a heterochronic term for every possible version of size–shape dissociation. Figures 1B and 2B illustrate the terminologies of Gould (1977) and Alberch et al. (1979), respectively, that interpret every possible pattern of parameters in terms of heterochrony. But this renders the general description of heterochrony untestable, as it cannot be falsified in any way (Zelditch and Fink 1996; Roopnarine 2001). The classic scheme is descriptive rather than explanatory.

Multivariate morphometrics

Methodological improvements in the study of heterochrony are closely bound to improvements in the multivariate characterization of shape. Classic multivariate morphometrics usually is based on a set of log-transformed distance measurements (Blackith and Reyment 1971; Jungers et al. 1995). Modern morphometric techniques are landmark-based instead, so as to include more information than classical methods do. Geometric morphometrics is the statistical analysis of landmark coordinates after the forms are superimposed by Procrustes registration (Bookstein 1991; Marcus et al. 1996; Dryden and Mardia 1998; O'Higgins 2000a). This superimposition includes three steps: translation to a common origin, scaling to a common size, and a rotation to minimize summed squared interlandmark distances among the forms (Rohlf and Slice 1990). The resulting Procrustes coordinates capture shape information only, whereas overall size is explicitly

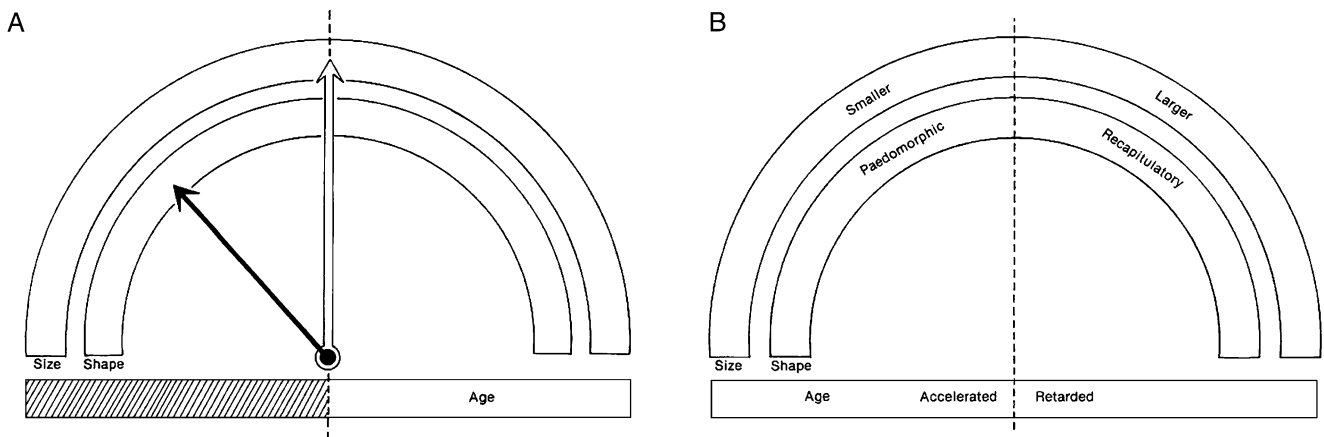


Fig. 1. Clock model of Gould (1977): The hands for size and shape describe the morphology of a species relative to its ancestor. The dashed line in the middle marks the position when ancestral and descendent values are identical. (A) Neoteny: Size is the same for both species being compared but shape is retarded (paedomorph) in the descendent. (B) The possibilities for altering size, shape, and age separately during evolution.

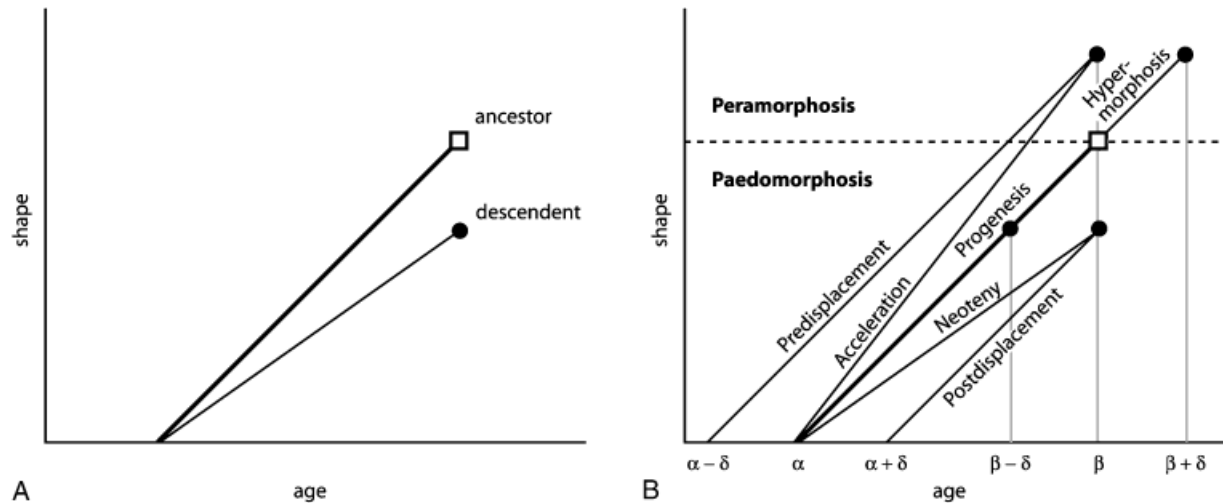


Fig. 2. Two ontogenetic trajectories in age–shape space: (A) Neoteny: Age (size) is identical for ancestor and descendent but shape became retarded during evolution. (B) Terminology of heterochrony for typical trajectories following Alberch et al. (1979). Redrawn after Klingenberg (1998).

expressed in the variable called Centroid Size. As the Procrustes approach to geometric morphometrics distinguishes between size and shape from first principles, it is highly appropriate for studying heterochrony (Penin et al. 2002). The arguments in this article, however, apply to other multivariate morphometric approaches like Euclidian distance matrix analysis (EDMA) (Lele and Richtsmeier 1991; Richtsmeier and Lele 1993) as well, as long as they are cast into a space of explicit shape variables permitting the necessary least-squares operations that underlie the regression on size.

Heterochrony in a multivariate framework

With the advance of modern morphometrics, there have been several attempts to translate heterochrony into a multivariate setting (e.g., McKinney and McNamara 1991; Richtsmeier and Lele 1993; Godfrey and Sutherland 1996; Zelditch and Fink 1996; Bruner and Manzi 2001; Ponce de Léon and Zollikofer 2001; Roopnarine 2001; Eble 2002; Penin et al. 2002; Vinicius and Lahr 2003; Mitteroecker et al. 2004a). These studies vary in the way the univariate concept of heterochrony is adapted to a multivariate framework. In both original approaches, Gould (1977) and Alberch et al. (1979), shape is measured by a single variable. Relative to its ancestor the descendent development (i.e., shape change) can be truncated, extended or differently associated with size and/or age. It is implicitly assumed that both ontogenies undergo the same sequence of shape changes—just differently timed. Otherwise no single shape variable would be sufficient to describe the differences in ontogeny. For this to apply to multivariate data, the species must share the same ontogenetic trajectory in multivariate shape space, differing only in length or associated size when plotted in size–shape space (see Fig. 3 and Godfrey

and Sutherland 1996; Roopnarine 2001; Vinicius and Lahr 2003; Mitteroecker et al. 2004a). The shape variable in Gould (1977), which is β in Alberch et al. (1979), would correspond to the position along this common shape trajectory. In other words, both species must maintain the same allometric development but differ in their duration or timing of development—they are “ontogenetically scaled.” To distinguish between the specific heterochronic modes (like neoteny, progenesis, etc.) additional information on the age of the investigated specimens as well as their phylogenetic relationship is often necessary, so that not all cases can be diagnosed by size and shape information alone (Fink 1982; Godfrey and Sutherland 1995; Klingenberg 1998). However, the general hypothesis of heterochrony can be rejected without information on time or phylogeny if the ontogenetic trajectories do not overlap in shape space.

Allometry is the linear or linearized characterization of the dependence of shape on size. It is frequently used to describe average trends of shape change during ontogeny. Multivariate allometry for interlandmark distance data is often estimated by the first eigenvector of the variance–covariance matrix of log-transformed distances (Jolicœur 1963) as long as all loadings of this eigenvector are positive. For landmark data, it is the multivariate regression of the shape coordinates on log Centroid Size (see Bookstein 1991 and Klingenberg 1996, for general reviews of that topic). Generally, the first PC for interlandmark distance data as well as that for landmark coordinate data often correlates with overall size, but usually the first PC is not precisely the optimal description of allometry in the presence of any other factors or grouping variables. The regression of shape on size, in contrast, is the optimal least-squares prediction of shape change during growth. In grouped studies, for instance, the resulting (linear or

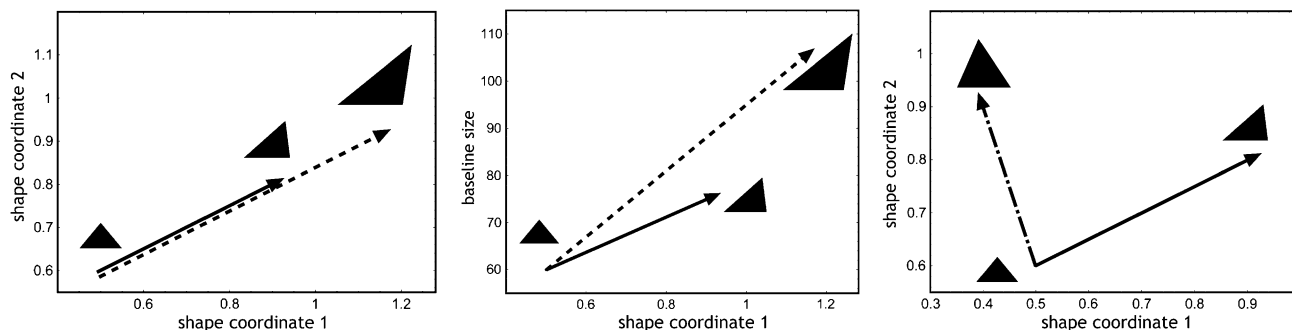


Fig. 3. Ontogenetic trajectories of two related species with three landmarks each: These triangular forms can be completely described by two Bookstein shape coordinates along with baseline length. The trajectories overlap in shape space (A) but diverge in size–shape space (B); heterochrony is a valid description. If two trajectories diverge in shape space instead (C), a global description in terms of ontogenetic scaling is not possible.

nonlinear) regressions, one for each group, can be tested for equality and the positions of adults along these trajectories can be compared.

In geometric morphometrics, principal component analysis (PCA), which is called relative warp analysis when applied to Procrustes coordinates (Bookstein 1991; Rohlf 1993), has become the standard tool for the analysis of ontogeny and phylogeny (see e.g., O’Higgins and Jones 1998; Dean et al. 2000; O’Higgins 2000a, b; O’Higgins et al. 2001; Ponce de León and Zollikofer 2001; Ackermann and Krovitz 2002). However, identity of position or direction between different growth trajectories in a PCA has to be examined with care. A scatterplot of the first two PC scores for more than two species often reveals similar trajectories for at least two of the investigated species. But this can be an artifact of the plot: in displays of more than two PCs these trajectories usually will differ (see Fig. 4 and also Oxnard 1983; Cobb and O’Higgins 2004).

PCA is a projection of a high-dimensional dataset onto a few components that summarize most of the variance present in the data. Two PCs, however, are not enough to depict all differences of even two ontogenetic trajectories. Three dimensions are necessary for a complete representation of two different (linear) trajectories. Figure 5 illustrates that different projections of such a three-dimensional space onto paper yield strikingly different apparent relations between the two trajectories. This is a general phenomenon, not restricted to PCA or to linear trajectories. Consider any four different forms described by at least three shape variables that define two non-parallel ontogenetic trajectories (two young and two adult forms). In all but exceptional cases the resulting three-dimensional shape space can be projected onto two dimensions so that the trajectories either intersect, are parallel, are skew, or diverge from one single point (compare also Bookstein 2001).

This theorem can even be extrapolated to the choice of measurements itself. Imagine any four different biological forms—again constituting two ontogenetic sequences—that differ in several morphological characteristics. There is in-

duced a high-dimensional (theoretical) space of description (that is actually still unmeasured). Measuring two distances on each form can be seen as a projection of this high-dimensional space onto these two variables. Dependent on the choice of the two variables, the ontogenetic trajectories in a scatterplot of the two variables can again possess any of the geometries described above.

The identity of trajectories in shape space is a geometric matter that cannot be read from any single projection or bivariate plot of measurements. It has to be shown in all principal projections or in the full space by testing that all the regressions of shape on size lie on the same curve. Only then can heterochrony (differences in regressions along this curve) be tested.

Regionally dissociated heterochrony

It is unlikely that any global heterochronic process, such as early cessation of overall growth or over-expression of some global growth hormones, would result in an ideal allometric scaling uniform for all variables. Experiments of Corner and Shea (1995) and Shea et al. (1987, 1990) indicate that many but not all variables scale identically even between normal mice and a transgenic mouse population with a very high global level of growth hormone. Circulating hormones that have overall effects on growth can also have specific local effects and can stimulate the localized production of other growth factors in particular tissues. These tissue-specific effects are mediated by the expression of hormone receptors and the organization of the corresponding second messenger systems in the target tissue. Additionally, there is autonomously controlled growth in individual structures expressed by a number of locally acting growth factors (Raff 1996). Thus, there may exist many more localized effects of allometric scaling in morphometric data (“mosaic heterochrony,” David (1990) or “dissociated heterochrony,” McKinney and McNamara (1991)). Independent evolutionary change of local

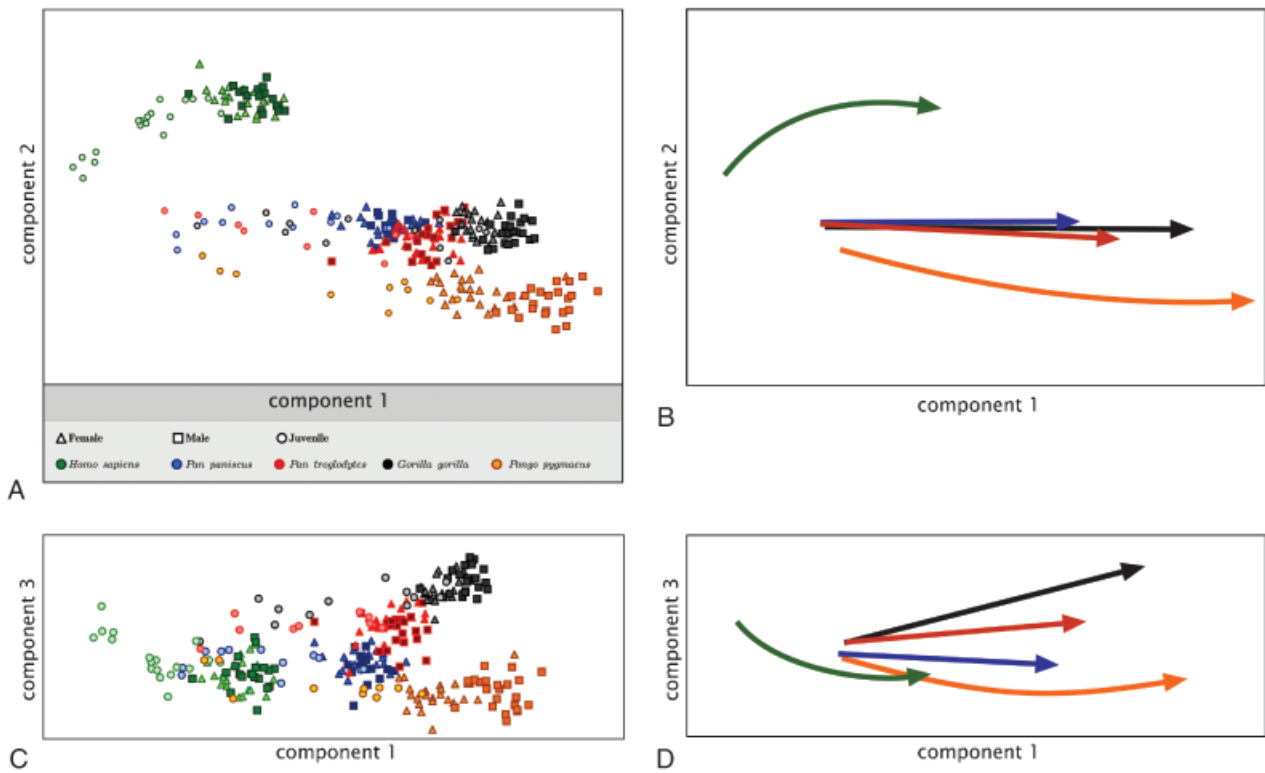


Fig. 4. Principal component (PC) analysis of cranial landmarks from adult and subadult *Homo sapiens*, *Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus* (from Mitteroecker et al. 2004a). The forms are superimposed by a Procrustes registration so that the analysis is of shape only. The PCs are rotated so that the common direction of allometry is aligned with component 1. (A) Scores of component 1 versus 2 and a schematization of the five growth trajectories in this space (B). Note that *P. paniscus*, *P. troglodytes*, and *Gorilla* overlap in this plot. (C) Components 1 versus 3. (D) Schematization of the respective growth trajectories. The three previously overlapping trajectories now diverge.

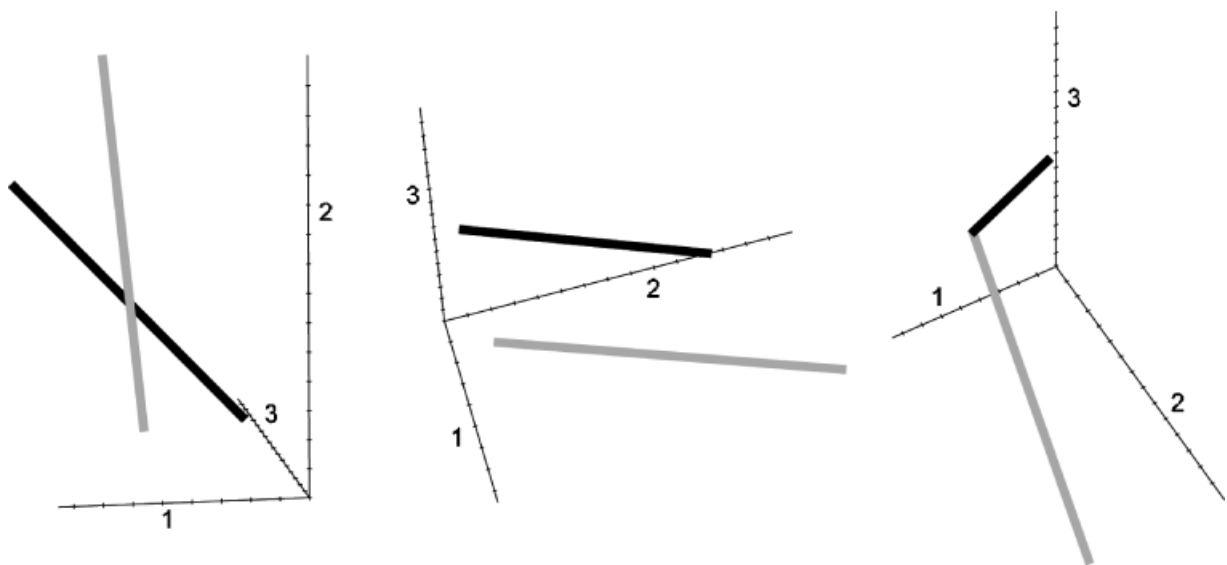


Fig. 5. Two hypothetical trajectories in a three-dimensional space that is rotated into three different orientations. The relation of the trajectories is fundamentally different across these two-dimensional projections onto the paper.

growth processes does not result in an overall dissociation of size and shape (i.e., pure heterochrony) but in the dissociation of local growth fields (Gould 1977; Raff and Wray 1989; Godfrey and Sutherland 1996). The effects of dissociated heterochronic processes need not necessarily be restricted to isolated and adjacent regions; they may be overlapping or of a hierarchical nature. In Mitteroecker et al. (2004b), we showed that two ontogenetic trajectories in shape space diverge even if they differ only in regionalized ontogenetic scaling. When the regions of dissociated heterochrony are analyzed separately instead, the local trajectories overlap and differ only in length (Fig. 6). But even when regional allometric scaling can be found, the descriptive data alone cannot clarify whether a change in a single global hormone with tissue-specific response or instead a series of alterations in local growth control systems is responsible for the different adult phenotypes. Whereas the first possibility would require evolutionary change of a single factor only, the latter one involves several independent evolutionary adaptations.

When studying regional ontogenetic scaling, it turns out to be difficult to find the actual regions that possess a common evolution of ontogeny for all their morphometric variables. The focus moves from a classic study of allometry and heterochrony to the study of modularity (Raff 1996; Bolker 2000; Callebaut and Rasskin-Gutman 2005). Expectations about modularity are often based on “good biological intuitions about the nature of developmental and evolutionary processes” (von Dassow and Munro, 1999, p. 308), but they can also come from the data themselves. Allometric growth within a species can be visualized by principal strains (Bookstein et al. 1985), as a thin-plate spline deformation grid (Bookstein 1991), or as displacement vectors for each landmark. All these visualizations are local descriptions that can be used to find similar ontogenetic trends for different regions separately. Another approach is the iterative search of modules to find an optimal description of the data by regional heterochrony (Williams 2001). Of course, if the description is reduced to a series of single variables, each of them

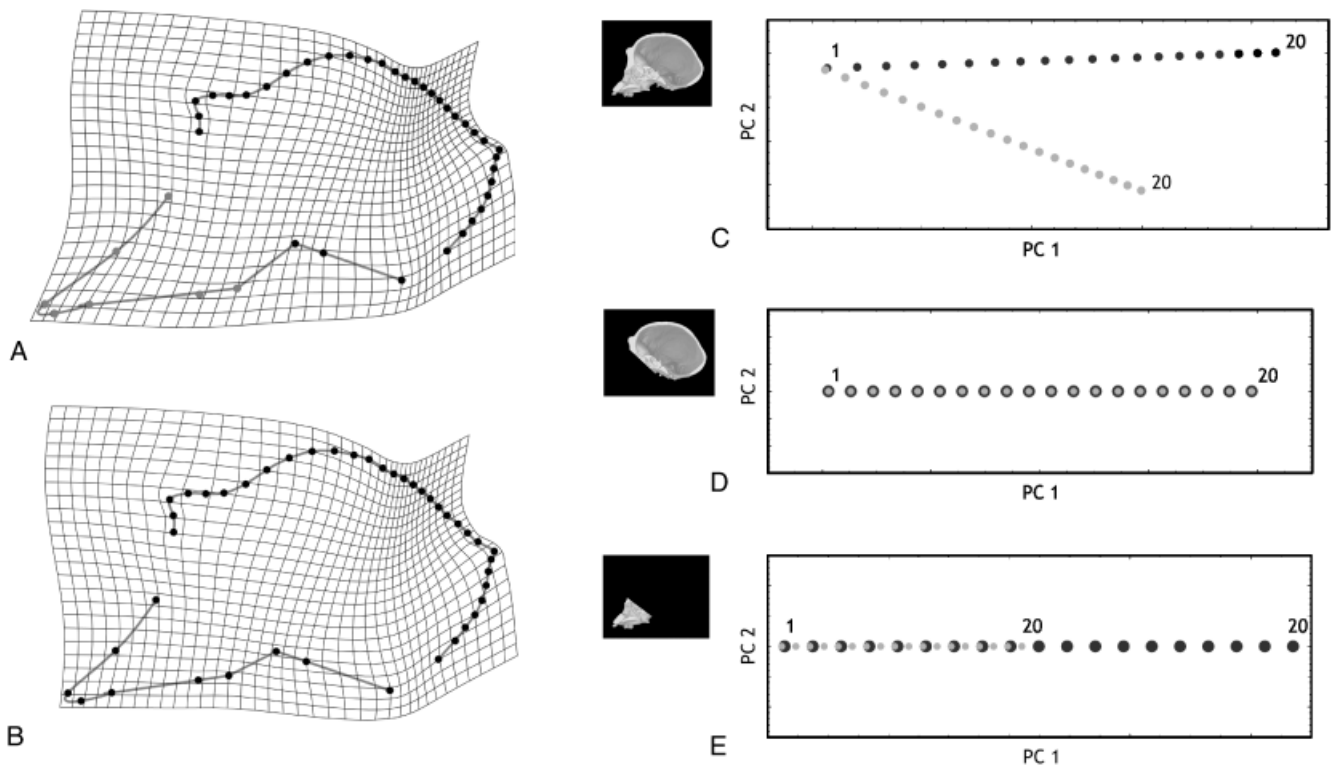


Fig. 6. In a dataset of midsagittal cranial landmarks of adult and subadult *Pan paniscus* we calculated allometric growth and visualized it by a thin-plate spline deformation grid (A). This allometric vector was modified to construct a regionally pedomorphic artificial species: landmark displacement of the lower facial landmarks was divided by two (B). As such, this results in two different shape deformations (A and B), one for each species, that are identical in the neurocranium and differ in the face by allometric scaling—the second species' face is pedomorphic. We then sampled 20 artificial specimens along each of the two growth vectors and performed a principal component analysis (PCA) of Procrustes coordinates (C). The two trajectories diverge in this shape space. When analyzing the neurocranium and the face separately the trajectories overlap (D and E). In the PCA of the face, the modified species' trajectory is shorter than the original one, revealing the constructed allometric scaling among the two species (E). After Mitteroecker et al. (2004b).

can be interpreted separately as heterochrony, but then this description would lose its power again. The more variables one single description of (regional) allometric scaling can explain (i.e., the larger the modules), the more powerful is that description.

The identification of spatial modules can also be based on the covariance structure among morphometric variables (Olsen and Miller 1958; Cheverud et al. 1989; Cheverud 1996) or on the covariation of asymmetry (Klingenberg et al. 2001). However, modularity seems to be a question of degree instead of discrete and clearly distinct modules (Klingenberg et al. 2003). It is thus not to be expected that a decomposition of the total structure in several parts would often result in a pattern of regionalized allometric scaling as clear as that simulated in Fig. 6.

Misinterpretation of PC scores

Some authors (e.g., McKinney and McNamara 1991; Eble 2002) suggest interpreting PC plots of interlandmark distance data in very much the same way as allometric plots. They diagnose different heterochronic types when the trajectories differ in a plot of the first two PCs. But this is not consistent with any of the classic concepts and does not make sense in a multivariate morphometric context. For instance, when the first PC is something like General Size, the second PC is always a contrast of two ways of attaining that size, and so necessarily refers to two different combinations of distances, such as arise from two different regions. If one region is hypermorphic, the other is necessarily neotenus at the same time. There is another methodological mistake in the literature when interpreting PC scores along the lines of heterochrony that is most explicitly formulated in Eble (2002). He declares for each PC separately that a species is neotenus for this particular PC, or progenetic, and so forth. But PCs are statistical constructions that, especially in data spanning several anatomical regions over several species, almost never correspond to actual biological factors. (For instance, PCs are forced to be mutually uncorrelated, but real biological factors will rarely be completely independent.) Additional information about genetic and epigenetic control of development is always needed to interpret linear combinations of the original variables as responsive to different biological processes. It is of little interest whether some artificial linear combinations of the data are neotenus or not and it presumably answers no reasonable biological or paleontological question. This kind of misinterpretation seems to originate in the superficial resemblance of PC plots to the plots of size (or age) versus shape in Alberch et al. (1979). But the appropriate extension of this formalism should be the one we presented above. Also, when breaking down the interpretation to the different PCs separately, there is again the problem that any single component can be described separately as heterochronic without

any possibility of falsification. PCs should not be read component by component; rather, the first few PCs should be interpreted jointly (Oxnard 1983).

Some authors (e.g., Ponce de Léon and Zollikofer 2001; Penin et al. 2002; Berge and Penin 2004) interpret different but parallel trajectories as heterochronic if one of them is longer or shows different associations with age. But if the compared species do not share the same trajectory they cannot be regarded as heterochronic variants. In the late developmental period that is investigated, both species seem to possess the same direction of shape change, which might be as a result of the same developmental processes; yet they do not result in heterochronic morphologies. A longer trajectory for a given time period reflects more and thus accelerated shape change, but this should not be called heterochrony so as to keep the terminology straight. Zollikofer and Ponce De Léon (2004) suggest the term “generalized heterochrony” to describe two ontogenetic trajectories that are parallel for some segments. Adding yet another label, however, does little to disentangle the contradicting terminology of heterochrony. Also, the problems with PCA hold true for notions about parallel ontogenetic trajectories as well. Figure 5 shows that two trajectories with different origin and direction in full shape space can appear parallel in a two-dimensional projection. Ponce de Léon and Zollikofer (2001), Ackermann and Krovitz (2002), and Penin et al. (2002) report parallel trajectories for different hominoid species, but display just two components of their data. As the data of Ackermann and Krovitz (2002) included five species, the relation of the trajectories would be expected to change when more PCs are considered (Cobb and O’Higgins 2004). Whenever two trajectories are known not to be parallel in full space, but appear parallel in some PCA or similar projection, biological interpretations should not be based on the assumption of identical directions of allometric shape change (as in Berge and Penin 2004).

Allometric heterochrony

Many authors (e.g., Shea 1983a, 1985, 1989; Leigh et al. 2003) focus their attention on the simplest case of allometric scaling, the extension or truncation of ontogenetic trajectories in a logarithmic plot of two size variables. The bivariate concept of allometric scaling is a hypothesis that has an alternative, namely a modification of the ancestral allometry (i.e., the trajectories differ). This alternative can also easily be tested statistically by a test of equal slopes and intercepts for regressions within different taxa. When this approach is frequently applied to several measured variables simultaneously, different pairs of variables are judged visually or statistically for allometric scaling and conclusions about “overall” allometric scaling are drawn from the presence of “some” pairs of variables that scale allometrically. But this kind of conclusion

is problematic. Overall allometry is maintained in a descendent species only if *all* bivariate allometries keep the same for the two species. If only one bivariate allometric coefficient differs, then overall allometry has changed (compare Fig. 7 and Vinicius and Lahr 2003). The hypothesis of global allometric scaling needs to be tested with appropriate multivariate methods (see Klingenberg 1996, for a review). Especially when using interlandmark distance data, it is of unclear biological importance to know that some variables scale allometrically if we are not told how the others scale at the same time.

A multivariate analysis from first principles can deal with some of the formal problems mentioned above. Instead of applying heterochrony as a post hoc typology for single shape variables, the multivariate formulation allows one to state a hypothesis of global ontogenetic scaling. The hypothesis is verified just when the studied ontogenetic trajectories overlap in multivariate shape space and differ only in initial or final position (Fig. 3). In all other cases, the trajectories differ in shape space and so the hypothesis is falsified. Different positions along the common trajectory can be quantified by calculating “allometry scores.” If \mathbf{a} is the normalized p -dimensional vector of common allometry (e.g., regression coefficients of Procrustes coordinates on log centroid size) and \mathbf{F} the $n \times p$ matrix of specimens then $\mathbf{F}\mathbf{a}$ is the n -dimensional vector of scores along the direction of allometry. These scores can be averaged among age cohorts and used as a shape variable in the formalism of Alberch et al. (1979). Thus, in this special case the classic terminology can still be applied. In fact, in the majority of cases in primates that we have checked, this model does not fit the data at all well; and whenever the

ontogenetic trajectories differ in shape space no global explanation in terms of heterochrony can be applied.

Ontogenetic trajectories can also be studied in size–shape space, which is best constructed as a PCA of the Procrustes shape variables augmented by the natural logarithm of Centroid Size (Mitteroecker et al. 2004a). If the trajectories overlap in this space, then the descendent retains the ancestral relationship of size *and* shape—they are ontogenetically scaled in full size–shape space. The same conclusion can be drawn from overlapping but extended or truncated trajectories in a PCA of length measurements, as overall size is not partialled out from that kind of data. This comes closest to the multivariate version of Shea’s “allometric scaling” wherein size and shape remain associated during evolution.

Statistical tests for heterochrony

When ontogenetic trajectories overlap in shape space but differ in length or in size–shape space, heterochrony is a valid and useful description. If the trajectories clearly differ without overlap of the groups in a PCA plot then heterochrony can be rejected. But we have shown above that overlapping trajectories in the first PCs are no guarantee for overlapping trajectories in full shape space; a test based on all variables should be preferred. Some authors (e.g., Zelditch et al. 2000 and several studies in Zelditch 2001) suggest a resampling approach to test the angle between two linear trajectories and accepts heterochrony when an angle of zero cannot be rejected significantly. This test criterion is insufficient as parallel trajectories (differing by an angle of zero degrees) might still be not identical and the adult morphologies would not be

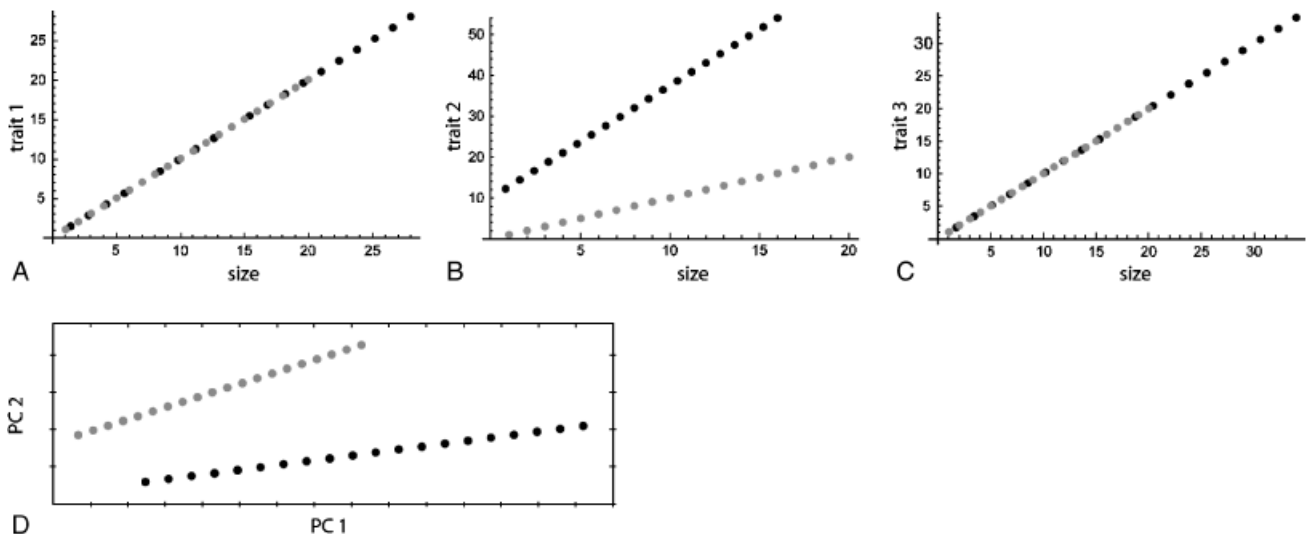


Fig. 7. Three variables are compared with a size variable (A–C): The two trajectories scale allometrically for traits 1 and 3 but do not share the same allometry with respect to trait 2. A principal component analysis (D) shows that the multivariate (i.e., overall) ontogenetic pattern differs between the two groups.

heterochronic variants of each other. Roopnarine (2001) compares the initial and final points of Procrustes landmark displacement vectors among different species. The hypothesis of heterochrony, however, does not require same initial and final points for such vectors—they are, after all, permitted to differ in their position along the common trajectory.

We suggest a permutation test based on within-species multivariate regressions of the shape variables on size (the logarithm of centroid size for landmark data). The regressions can be linear, quadratic or even of higher order. If these regressions were *identical* among some species, their trajectories would be identical in full size–shape space (for a given size, the average forms of all species would be identical). This is a test criterion for an elongation or truncation of growth when size and shape remain associated. A different heterochronic process involves decoupling of size and shape—for a given size, the species shapes need not be identical but would have to lie on the same growth trajectory in shape space. Although the regressions thus would not necessarily be identical, still their curves would need to overlap.

A test statistic for the first case (identical regressions) might be the summed squared residuals of the within-species regressions. Compute for each species separately a multivariate regression of the shape variables on size, then sum the squared residuals for each shape from its prediction. Randomly reassign the species affiliation for each specimen and recompute the new “species”-specific regressions and the summed squared residuals on the permuted data. Repeat this last step a large number of times. Under the assumption of identical trajectories, the original test statistic should not be an outlier in the permutation distribution of summed squared residuals. For N permutations, the hypothesis of identical trajectories in size–shape space is rejected when $(C+1)/(N+1) \leq \alpha$, where C is the number of cases that result in a smaller test statistic than that for the original data.

For the second case (overlapping trajectories—i.e., regression curves—in shape space) the test statistic cannot be the total sum of squared residuals of the regression. When a decoupling of size and shape occurs the shapes would vary in position along one single trajectory. For this second test, the regression residuals should be taken only as the component normal to the regression curve in shape space, ignoring deviation along the trajectory. The test for overlapping trajectories is then similar to the test explained above except that the test statistic is not the summed squared residual but rather the summed squared distance from each shape to its nearest point on the regression curve. Note that these residuals do not take into account the size–shape relationship—the residuals are normal to the regression curve in “shape space.”

It is possible that a PCA of an ontogenetic dataset might show overlapping trajectories in the first few dimensions even though the permutation test rejects overlapping trajectories. We find that a projection of the shape space that is more

specific than PCA usually gives a clearer picture to assess heterochrony. For this purpose, we suggest a PCA of predicted shapes along the trajectories (that is ignoring the variation perpendicular to the trajectories, which is of course not ignored in standard PCA). Calculate the within-species multivariate regressions of the shape variables on size and choose reasonable size values (say, for each species, 10 equally distributed values in their total within-species size range or the size values of the specimens themselves). For each regression, then, calculate the predicted shapes for the sizes and perform a PCA of these shapes. The shapes of the original specimens can then be projected into this new space (compare Figs. 10 and 13).

To yield a two-dimensional projection of their shape space, Penin et al. (2002) and Berge and Penin (2004) used the vector of common allometry and a discriminant function as the two components to produce their scatterplots. In both studies, they found these two components to be approximately orthogonal and the ontogenetic trajectories appeared parallel in this projection. Both results, however, are more or less a formal necessity. A discriminant function is the vector of group differences multiplied by the inverse of the within-group covariance matrix (see e.g., Johnson and Wichern 1998). In most cases, the major factor in an ontogenetic sample is allometry; multiplying by the inverse of the covariance matrix then mainly means reducing the contribution of allometry to the group difference vector. If the groups did not differ by allometric scaling alone, the vector of common allometry and the discriminant vector tend to be orthogonal. For two ontogenetic trajectories that are different in direction and origin, the best vector of discrimination is the one perpendicular to both trajectories. When taking common allometry as the first component and the discrimination function as the second, this corresponds to a projection of the shape space so that the trajectories appear to be parallel. We have shown above that such a rotation is possible for any kind of two trajectories with at least three shape variables (Fig. 5). Therefore, both findings in the two studies are nearly independent of the actual data.

EXAMPLE: CRANIAL GROWTH IN *P. PANISCUS* AND *P. TROGLODYTES*

Hypotheses about chimpanzee development

We analyze craniofacial growth of *P. paniscus* and *P. troglodytes* with a geometric morphometric approach applying the principles introduced above. Diverse theoretical and empirical work supports the assumption that ontogenetic trajectories of related species will diverge during ontogeny after a conserved stage in midembryonic development (von Baer 1828; Schultz 1924; Sander 1983; Richtsmeier et al. 1993; Slack et al. 1993; Richardson 1995, 1999; Raff 1996; Wimsatt 1996; O’Higgins

2000a; Galis and Metz 2001; O'Higgins et al. 2001; Mitteroecker et al. 2004a; Cobb and O'Higgins 2004). Several morphometric studies on primate cranial development indicate that this divergence may be early in development, so that species differences are already established around birth (Bruner and Manzi 2001; O'Higgins et al. 2001; Ponce de Léon and Zollikofer 2001; Ackermann and Krovitz 2002; Penin et al. 2002; Vidarsdottir et al. 2002; Berge and Penin 2004; Mitteroecker et al. 2004a). One classic assumption is that the ontogenetic divergence of common chimpanzee and pygmy chimpanzee is between size and shape only—that is, global heterochrony of the skull (Coolidge 1933; Giles 1956; McHenry and Corruccini 1981; Shea 1983a, b, 1989). *P. paniscus*, the pygmy chimpanzee, is then regarded as a pedomorphic variant of its sister taxon *P. troglodytes*. Other, more recent, multivariate approaches do not confirm this notion, but find that allometric scaling can explain the morphological differences between the two species at least in part (Williams et al. 2002, 2003; Mitteroecker et al. 2004a).

We can formulate several alternative hypotheses concerning the pair of ontogenetic trajectories in shape space:

- H₁: *Ontogenetic scaling*. The trajectories in shape space are ontogenetically scaled and may differ in length and association with size and/or age (i.e., divergence in size–shape space)—global heterochrony in the cranium.
- H₂: *Parallel ontogenetic trajectories*. The complete divergence in shape occurs before the investigated time range (prenatally). Thereafter both species of *Pan* share the same postnatal morphogenetic processes in the cranium. These parallel trajectories in late development might have the same or different lengths.
- H₃: *Different ontogenetic directions in shape space*. As discussed above, this can arise for different reasons. The

differences of morphology might not be explained by heterochrony at all, or perhaps a single global heterochronic cause might result in a mosaic pattern of morphological effects as different modules respond to a global signal like a growth hormone. There could also be several more localized and dissociated heterochronic processes that sum to a pattern of mosaic heterochrony. These two possibilities of dissociated heterochrony (one cause with several distinct responses vs. several causes) cannot be distinguished on the basis of morphometric data alone. We can examine, however, whether the globally different trajectories can be decomposed into regional trajectories that are each allometrically scaled.

We do not study form differences below the species level such as sexual dimorphism or subspecific differences. But see Schaefer et al. (2004) for a more detailed analysis.

MATERIALS AND METHODS

Three-dimensional coordinates of 191 anatomical landmarks and semilandmarks on ridge curves and the neurocranial surface (Fig. 8) were measured on a cross-sectional sample of dried skulls of 48 *P. paniscus* and 497 *P. troglodytes* including both sexes. The age of the specimens ranged from newborns to adults in both species. The measurements were taken by a single person in two separate sessions per skull because not all landmarks could be reached in one orientation. The two sets of landmarks were matched by superimposing five fiducial points that were measured in both sessions. For detailed information on the sample and the measurement protocol, see Bernhard (2003) and Mitteroecker et al. (2004a).

Semilandmarks are points sampled along outlines that are allowed to slide along these curves or surfaces so as to minimize

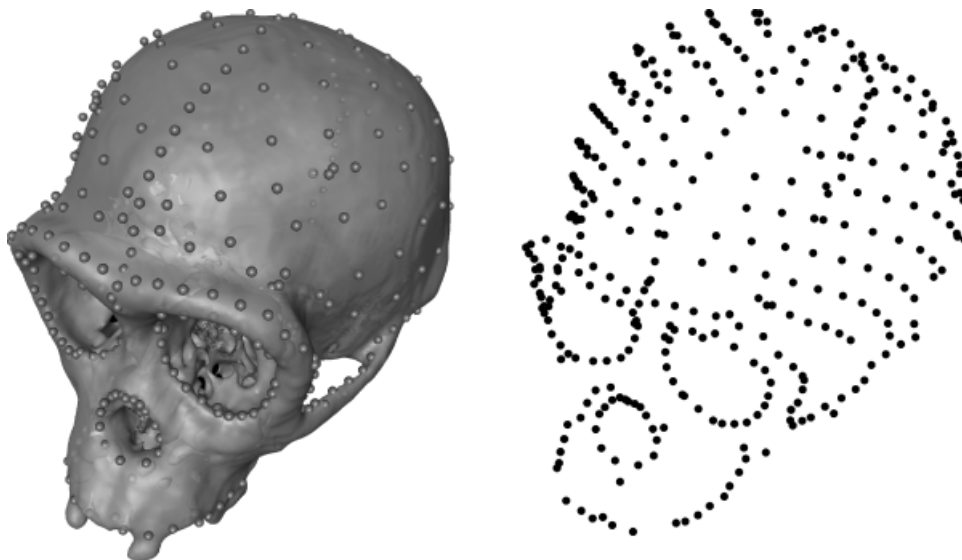


Fig. 8. Juvenile skull of a chimpanzee with the 191 landmarks and semilandmarks.

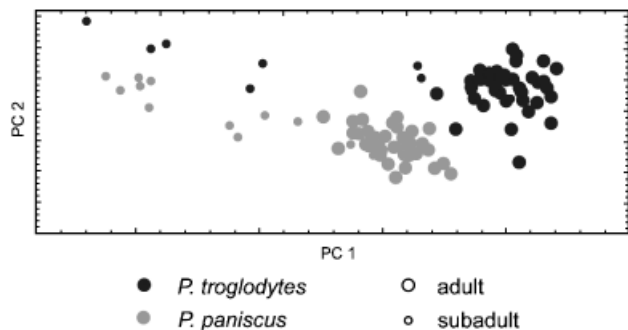


Fig. 9. Principal components of Procrustes coordinates (relative warps) of *Pan troglodytes* (dark points) and *Pan paniscus* (light points). The small points are subadult and the large ones adult individuals. The youngest specimens are a few days old in both groups.

“bending energy” (Bookstein 1997; Bookstein et al. 1999; Gunz et al. 2005). Under reasonable assumptions, the sliding warrants the use of semilandmarks in the subsequent analytic toolkit of geometric morphometrics as if they had been homologous point locations. Coordinates were superimposed using generalized least-squares Procrustes superimposition (Rohlf and Slice 1990) and analyzed using PCA, which is called relative warp analysis when applied to Procrustes coordinates (Bookstein 1991; Rohlf 1993). As discussed above, biological interpretations based on two-dimensional scatterplots of PC scores can be influenced by the choice of projection of a higher-dimensional phenomenon onto two dimensions. We try to minimize this effect by showing reasonable rotations of the first three components of the data decomposition. This gives us a much better chance to understand the complex pattern of trajectories in their high-dimensional space. The 3D graphs are isometric—their axes are scaled equally—but due to the rotation they can appear foreshortened when printed.

Ontogenetic allometry is estimated by multivariate regression of the Procrustes shape coordinates on the natural logarithm of Centroid Size. For testing the identity of regressions among the two species we use a permutation test as described above. All the morphometric and statistical routines were programmed by P. G. and P. M. in *MATHEMATICA*[®].

RESULTS

A plot of PC1 versus PC2 of the Procrustes coordinates reveals different ontogenetic trajectories for the two species of *Pan* (Fig. 9). They clearly already differ at the earliest stage and seem to diverge until adulthood. The linear within-species shape regressions differ by an angle of about 14° in full shape space. A permutation test, however, does not indicate significant differences in the direction of the two trajectories ($P \approx 0.14$). *P. troglodytes* possesses a clearly longer trajectory than *P. paniscus*. Figure 10 also shows that the differences between shapes with the same size in both species (gray deformation grids) do not coincide with shape changes as a

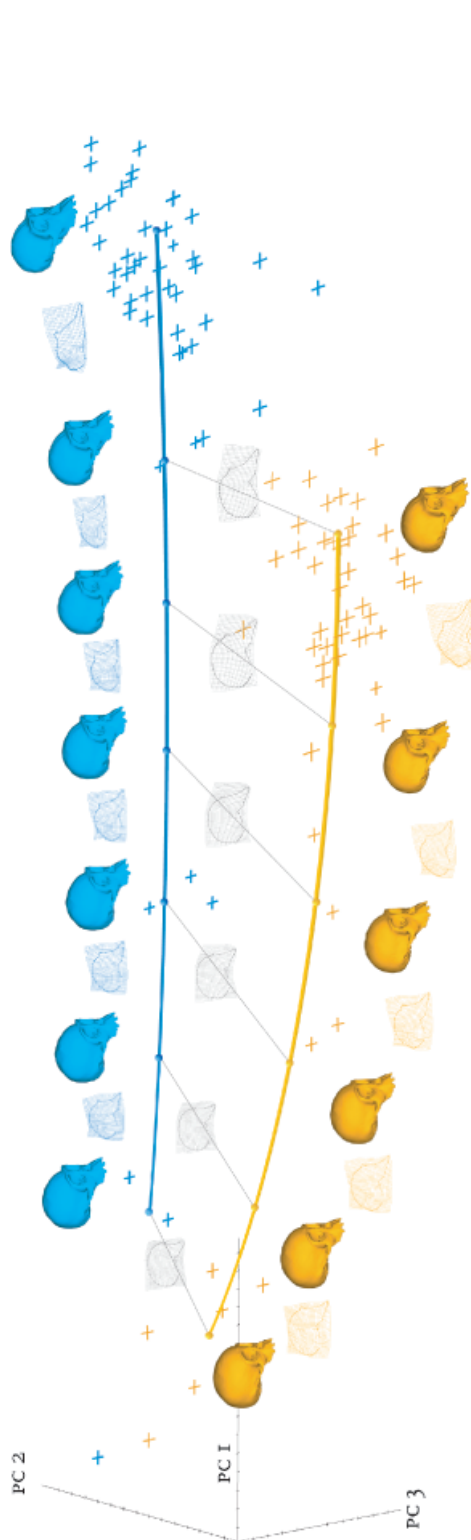


Fig. 10. Three-dimensional plot of the principal component scores of *Pan troglodytes* (blue crosses) and *Pan paniscus* (yellow crosses). The two colored lines are quadratic regressions of the shape coordinates on log centroid size and thus estimate allometry within the species. The gray lines connect interpolated shapes that have the same overall size, and the gray deformation grids visualize these shape differences for the midsagittal plane. Between the surface morphs there are colored deformation grids showing the midsagittal shape change related to allometric effects. If the two chimpanzee species differed only by heterochrony the differences between the shapes of identical size should be allometric ones (i.e., the colored and gray grids for one stage should just differ in amount of bending but be otherwise very similar as deformations).

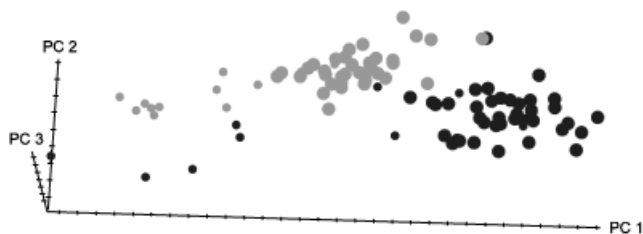


Fig. 11. Relative warp analysis of the neurocranial landmarks. The trajectories are different from birth on. The legend here and in all subsequent figures is as in Fig. 9.

result of growth (colored grids) as would be expected for heterochrony.

For further regional analysis we have chosen three distinct parts: the neurocranium, the upper face, and the lower face. The neurocranial analysis includes 95 landmarks, mainly surface semilandmarks, from the cranial vault and the cranial base. The PCA in Fig. 11 clearly shows different trajectories. In the PCA of the upper face, 62 landmarks and semilandmarks on the nasal aperture, the orbit, the brow ridge, and the zygomatic arch are included. Figure 12 indicates different trajectories again. The analysis of the lower face comprises semilandmarks along the alveolar ridge, landmarks on the palate, hornion, prosthion, and nasospinale (a total of 20 landmarks). The analysis of the first three relative warps suggests overlapping trajectories in shape space with *P. troglodytes* slightly extending this common trajectory (Fig. 13A). A permutation test as described above, however, rejects overlapping trajectories with $P < 0.01$. To visualize these differences between the trajectories we project all specimens onto a low-dimensional space that results from a PCA of predicted shapes along the two trajectories. Figure 13B shows that within this projection the two trajectories differ from the earliest stage on.

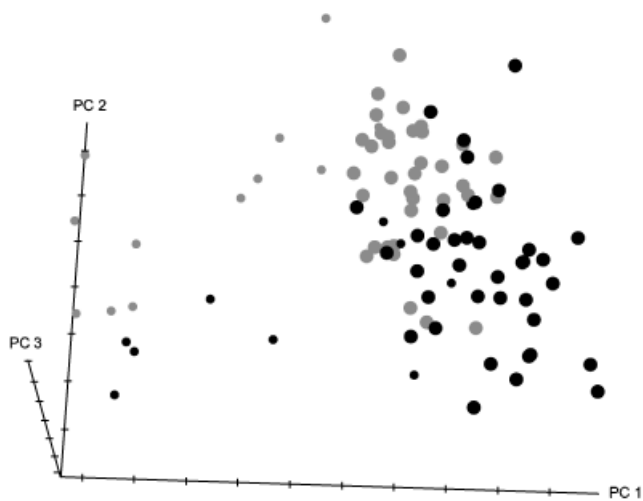


Fig. 12. Relative warp analysis of the landmarks from the upper face. The trajectories are different from birth onward.

SUMMARY AND DISCUSSION

Analysis of heterochrony

In their 1991 discussion of heterochrony, McKinney and McNamara note that “As long as we can say that the descendent species has more of something than the ancestor, produced by faster, sooner, or later acting processes, we can make meaningful inferences (pp. 25–26).” We would argue instead that as this view of heterochrony can describe nearly everything it rarely allows any useful inference. Likewise, any single measurement or a single PC can always be interpreted in terms of heterochrony—there is no alternative description. The general univariate hypothesis of heterochrony cannot be falsified. We think that a single morphological characterization, descriptions in terms of bigger/smaller or more/less of something, should generally not be subjected to heterochronic interpretation, nor should single ratios. Multivariate analysis circumvents this theoretical problem when heterochrony is defined as multivariate ontogenetic scaling along a common ontogenetic trajectory.

Heterochrony, global or local, is a sufficient description only if “the same morphogenetic processes,” inducing several variables, are at work but are differently timed. It is falsified whenever the ontogenetic trajectories differ in their central tendency within shape space. Such a test does not yet require a choice for the metric of developmental time, which is a controversial issue (Godfrey and Sutherland 1995; Klingenberg 1998; Roopnarine 2001), nor does it require information on the phylogenetic context. Whereas heterochrony is always true for the bivariate case, it becomes theoretically less probable when the number of variables that are included in a multivariate analysis increases. This closely resembles the idea of Popper that the probability of a hypothesis to be true inversely relates to its predictive power and thus its empirical value. We therefore argue that heterochrony is intrinsically a multivariate concept that should be described and tested only via the appropriate multivariate methods.

In fact, the shape axis in Alberch et al. (1979) needs to be a multidimensional shape space, and the arc-like scale for shape (Fig. 1) in Gould (1977) should be a hemisphere or hyper-hemisphere instead. When heterochrony is found, the single shape variable of either classic approach may be taken as the position along the common ontogenetic trajectory in shape space. However, the actual biological processes behind this class of morphologies (like different amounts of global or local growth factors, timing of tissue inductions, etc.) can only rarely be inferred from morphometrics alone.

Heterochrony in the chimpanzee skull

Cranial development of the common chimpanzee and the pygmy chimpanzee is often cited as a classical example of allometric scaling crucial for the understanding of hominoid evolution. Our analysis of the complete data has falsified H_1 ,

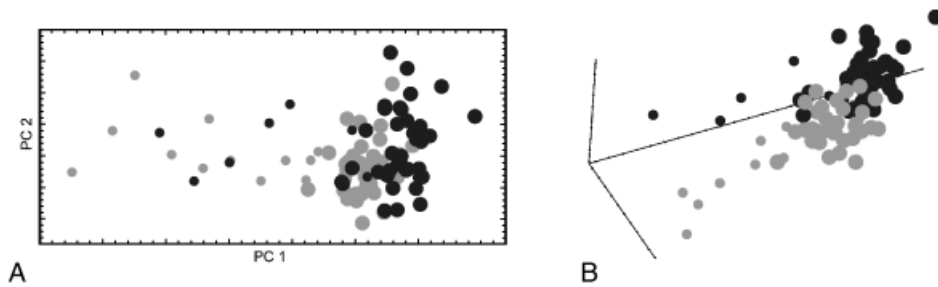


Fig. 13. (A) Relative warp analysis of the lower face. The trajectories overlap. (B) Optimized projection of the full shape-space based on a principal component analysis (PCA) of predicted shapes along the species-specific quadratic regression curves. The trajectories differ for the complete age period.

the hypothesis of global heterochrony. The trajectories are clearly different in the PCA plot of Fig. 9. The hypothesis of parallel trajectories, H_2 , could not be rejected by a permutation test. But the sample is highly unbalanced concerning age—there are far fewer subadults than adults; the test for H_2 thus lacks power. Three regional analyses show different trajectories for the three different parts. The hypothesis of regional allometric scaling is thus falsified as well, confirming the analyses by Williams et al. (2002, 2003) who found that neither global nor regional heterochrony could suffice to explain *P. paniscus* and *P. troglodytes* shape differences.

Outlook

Several multivariate studies reevaluating traditional assumptions about heterochrony do not find overlapping trajectories and thus contradict the classic explanations (e.g., Zelditch et al. 2000; Ponce de Léon and Zollikofer 2001; Roopnarine 2001; Webster et al. 2001; Williams et al. 2001, 2003; Ackermann and Krovitz 2002; Penin et al. 2002; Berge and Penin 2004; Mitteroecker et al. 2004a). It seems that global ontogenetic scaling is rarely found in higher animals, nor can clearly separated regional allometric scaling be identified easily. So, ironically, the concept of heterochrony that was and still is so popular in morphometrics, partly because of its simplicity, is hard to apply when defined strictly.

A promising approach to study the evolutionary significance and morphological effects of heterochrony, however, might be experiments manipulating specific regulatory systems of growth and development. Corner and Shea (1995) and Shea et al. (1987, 1990) compared growth patterns between normal and giant transgenic mice and found many although not all variables to scale allometrically. It does not seem likely that evolution results in such isolated changes of single developmental processes like the expression of specific hormones, yet a description of the real evolutionary changes in terms of these isolated effects is often desirable. Knowing the morphological effects of increased or decreased levels of specific growth factors allows inferences from data on morphological evolution onto their physiological and developmental background. It might be possible to study heterochrony not merely of single measurements or of particular regions but instead of shape changes that are known to be

responsive to specific factors. Experiments could provide directions of shape changes (linear combinations of morphometric variables) that are then used to describe actual evolutionary alterations.

Summarizing, we think that future research should leave behind the search for vague similarities among bivariate allometric patterns in order to focus on how multivariate ontogenetic trajectories “differ” among regions and age periods. Within the scope of such an analysis, multivariate heterochrony found for particular regions, time frames, or a priori known developmental factors would be of much higher theoretical and biological importance than studies based on classic bivariate analyses.

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