The Ontogeny-Phylogeny Nexus in a Nutshell: Implications for Primatology and Paleoanthropology

Peter R. Menke

Contents

Abstract

This chapter aims to review the relevance of ontogenic data in an evolutionary perspective. Phylogenetic investigation through developmental information is one of the most promising avenues to the elucidation of our natural history. First, the problematic integration of biological subdisciplines into the evo-devo synthesis is considered: the homeobox as Pandora's box is discussed and the important role of a comparative morphology program is emphasized. Second, the study of development reveals essential aspects of primate supraordinal relationships and does not support an archontan reality. A special note defines the traditional superorder Archonta as (1) an artifact of the *Scala naturae* concept, since archontans were supreme public servants of the Greek ancient world. On the other hand, it is (2) a vehicle to explain the existence of flying mammals (Chiroptera) via a gliding intermediate stage (Dermoptera). Third, the

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P.R. Menke (✉)
Institut für Anthropologie (1050), Johannes Gutenberg-Universität Mainz, Mainz, Germany
e-mail: pmenke@gmx.de

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impact of neotenic ideas on paleoanthropology is retraced, and current contributions describing the evolution of the human cranial base and bipedalism are presented. Man's domination by neoteny seems to be a *burlesque*, accurately related as pithecocentrism.

> *Partout où quelque chose vit, il y a, ouvert quelque part, un registre où le temps s'inscrit.*
> *Henri Bergson*
>
> *Bestimmt sich nicht auch unsere Erwartung und unsere Bereitschaft, das Neue zu hören, notwendig von dem Alten her, das uns schon eingenommen hat?*
> *Hans-Georg Gadamer*

Introduction

The polymath Johann Wolfgang von Goethe was fascinated by the anatomical diversity of the animal kingdom and its variability of form. In 1817 (11 years before Karl Ernst von Baer published his embryological manifesto), he wrote:

> Man findet daher in dem Gange der Kunst, des Wissens und der Wissenschaft mehrere Versuche, eine Lehre zu gründen und auszubilden, welche wir die *Morphologie* nennen möchten [. . .] Er abstrahiert bei diesem Ausdruck von dem Beweglichen, er nimmt an, daß ein Zusammengehöriges festgestellt, abgeschlossen und in seinem Character fixiert sei. Betrachten wir aber alles Gestalten, besonders die organischen, so finden wir, daß nirgend ein Bestehendes, nirgend ein Ruhendes, ein Abgeschlossenes vorkommt, sondern daß alles vielmehr in einer steten Bewegung schwanke. . ..[1]

Life is obviously not a static arrangement but the particular result of a dynamic, ongoing process. This phenomenon is nowhere more relevant than for ontogenetic studies.

This review approaches some important aspects of ontogeny and phylogeny by presenting a selection of studies that exemplify this scientific field. Embryology, comparative anatomy, and especially molecular biology demonstrate an amazing unity among organisms, and sometimes, bizarre variations among them stem from a series of basic themes, some of which are common to all living beings (Nielsen 1995). I concentrate here on broader matters, such as (1) comparative embryology, especially with regard to K.E. von Baer and its modern derivative: evolutionary developmental biology. The ancient realm of morphology plays a major role in this context.

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[1] "It can be observed that in the course of art, knowledge, and science, several efforts are made to create and cultivate a doctrine that we may call *morphology*. . .One abstracts the reality of fluctuation by supposing that a belonging together and a fixation of its character can be fulfilled. Considering all shaping, especially in organic forms, we can state that there is no stability, no resting or completing-but rather a fluctuation of all phenomena" (pp 55, my translation and emphasis).

By the 1980s, molecular biology and paleoanthropology had developed their own concerns and controversies. Yet the significance of studies going beyond the analysis of adult phenotypes was already necessary and self-evident (Howell 2002).

Since hominin fossils, such as those from Dikika, Taung, Mojokerto, Nariokotome, Tešik-Taš, Kiik-Koba, or Le Moustier, represent infantile or juvenile stages, studying our phylogeny via ontogeny should be of particular importance, although, as Krovitz et al. (2003) pointed out, juvenile fossils are lacking for most species in the genus *Homo*. Here, therefore, studies are reviewed that are based on (2) embryological data sets. Generally, the methodological approaches taken to the analysis of the ontogeny of modern individuals and the fossil record differ strongly and accordingly have different meanings for the study of evolution (MacPhee 1981).

Focusing mainly on current primatological and paleoanthropological aspects, the far-reaching influence of (3) Bolk's fetalization hypothesis is retraced. Gould's (1977) interpretation is reconsidered (4), based not only on modern studies but also on traditional work that nowadays maintains only a shadowy existence, although its explanatory power is astonishing. As one may well imagine, any review of the ontogeny-phylogeny question must at present be incomplete. However, *gutta cavat lapidem, non vi sed saepe cadendo* (constant dripping wears away the stone).

Comparative Embryology and Evolutionary Developmental Biology

Karl Ernst von Baer and *Gallus domesticus*: The Beginnings of Comparative Embryology

Nineteenth-century comparative embryology lies at the origin of evolutionary developmental biology or, more briefly, *evo-devo*. Von Baer's and Haeckel's works are the most popular examples of that period, and these authors' "laws" describing the general development of organismic form are of great interest.

Karl Ernst von Baer, a pupil of Ignatius Döllinger, a professor at Würzburg, is known as the founder of embryology as a scientific endeavor. Although representatives of German transcendentalism had provided some insights into the field of embryology, it was only in 1828 that von Baer's *Über die Entwickelungsgeschichte der Thiere: Beobachtung und Reflexion* appeared in print and made even contemporaries recognize him as the founder of embryology. In the first volume of his masterpiece, von Baer concentrated on the development of the chicken (*Gallus domesticus*), but he also bore general laws of development in mind. He worked with dissecting needles and a simple microscope: the "Scholia" describe the deductions he made. The accuracy and minuteness of his fundamental observations is absolutely astonishing. Russell (1982, p. 114) was unable to hide his admiration: "His account of the development of the chicken is a model of what a scientific memoir ought to be. . .."

Von Baer's ideas incorporate the truly important distinction between the *type* (Wiesemüller et al. 2002) of organization (the structural plan) and the *grade* of differentiation (modifications of this plan). The aim of comparative anatomy to reveal group-specific *Baupläne* now had a prominent new tool by integrating embryological data.

As Charles Darwin was not a professional morphologist, it was others who introduced evolutionary thinking into the realm of comparative embryology. Ernst Haeckel's formulation of the biogenetic law (ontogeny as the short and rapid recapitulation of phylogeny) presents a radicalized phylogenetic approach. Recapitulatory ideas were not new since Müller (Russell 1982) had already supported a similar hypothesis in 1864. Yet Haeckel's verve and passion – very striking in a commemorative speech in 1909 (*Das Weltbild von Darwin und Lamarck*), on the occasion of the 100th birthday of Charles Darwin, favoring Goethe's monistic world view as being the *ultima ratio* – made it famous. The interpretations of *heterochrony* and its implication for paleoanthropology are discussed later on. However, how does today's evolutionary developmental biology reflect the ideas of von Baer and Haeckel?

The Newcomer: Evolutionary Developmental Biology

Von Baer and Haeckel: Outmoded?

The fancy term *evo-devo biology* represents an emerging field (Gould 2002; Carroll 2005) that has been specially featured in semipopular journals such as *PNAS* (2000) or *Nature* (2003). It refers to the quest by evolutionary biologists to understand how organisms change shape and form. Hall (2002, p. 8) explained that "… evolutionary developmental biology is more than a name for an emerging subfield of biology. It is a reflection of a level of analysis, synthesis, and understanding not possible through the study of evolution or development alone."

So how are the laws of von Baer and Haeckel interpreted nowadays? Gould (1977) supported von Baer's explanation and regarded it as being essentially correct while Haeckel's law is incorrect. Arthur (2002, p. 757) disagreed and argued that when comparisons are made between different levels of complexity, a pattern emerges that is broadly (although only in a very imprecise way) recapitulatory. The *déjà vu* occurs by recapitulating levels of complexity rather than precise morphological details. Haeckel and von Baer are both right in assuming that "evolution leads both to embryonic divergence and, in some lineages, to a lengthening of the ontogenetic trajectory leading to more complex adult phenotypes with greater numbers of cells, their embryos passing through simpler, quasi-ancestral forms."

Sander (1983) defined a "phylotypic" stage by describing a point of maximum similarity and a succeeding period of divergence. In this scheme, von Baer's principle of divergence only applies after this stage. Richardson et al. (1997) revealed a phylotypic period, rather than a stage, by screening more vertebrate species: this supports a broader comparative view. The hourglass model of development (Duboule 1994) might prima facie have reduced the explanatory power of von Baer. We should, however, be aware that this is a different kind of hourglass, the point of constriction being close to the beginning (Richardson 1999).

Homeobox: Pandora's Box for the Integration of Biological Subdisciplines?

Lewis (1978), Nüsslein-Volhard and Wieschaus (1980), and others (see also Lemons and McGinnis 2006) have revealed the meaning of *homeobox* genes and their importance for investigating the *Baupläne*. One application of this discovery which causes headaches for many scientists (Kuratani 2003) is the vertebrate cranium: is it a novelty that lies anterior to the head of a prevertebrate organism, or is it homologous to a special region of the amphioxus nerve cord? Holland et al. (1992) recognized a homology based on a comparison of expression patterns of *AmphiHox 3* (an amphioxus *Hox* gene) and *Hox-2.7* (the supposed mammalian homolog) and consequently denied the vertebrate brain as representing a novelty of the animal kingdom.

Hillis and Moritz (1990, p. 502) emphasized that the power and the rapid development of these techniques "has produced an euphoria in evolutionary biology, because so many new problems can be addressed, it is a commonly held misconception that all evolutionary problems are solvable with molecular data...." Nielsen (1995) worried that without morphological characters, the molecular data can produce only "naked" trees. Müller's (2005) review explained inter alia the importance of a comparative morphology program as a prerequisite for an evo-devo synthesis.

Furthermore, Conway Morris (2000, p. 4429) warned about "the risk of losing the overall evolutionary context. [...] Not only that, but there are intriguing mismatches between genomic architecture and bodyplan complexity." He pointed out that in all likelihood, a substantial proportion of the metazoan genome was available well before the Cambrian explosion and that a corresponding genetic architecture of genes and bodyplans is required, although he admits that we are still far from understanding either their interconnections or evolution. Arthur (2002) also met the challenge by demonstrating the change of tendency from general laws to specific pathways. He thus called attention to emerging concepts that integrate the overwhelmingly complex data.

As there is no one-to-one correspondence between genotype and phenotype, another important aspect of the problem lies in the interaction of genetic and nongenetic factors that act in different ways upon gene expression and create phenotypic diversity during development and evolution (Hall 1990, 1998b, 2002). Thus begins an appreciation of epigenetics. Goodwin et al. (1983), Raff (1996), and Hall (1998a, b, c) have called attention to the fact that change in development and evolution must be considered as an interaction of several "biological levels" so that consequently a hierarchical structural analysis is needed.

The timeless stimulus of Carl Gegenbaur – once called the most important morphologist in the world – and his legacy for the twenty-first-century evolutionary developmental biology lies in his methodological reflections about the relationship between embryology and comparative anatomy. Gegenbaur's emphasis of careful and detailed observation over tempting and far-reaching speculation should be the aurea mediocritas (the golden mean) in our fast-moving world. The modern scientific endeavor faces therefore similar challenges to those of the nineteenth-century evolutionary morphologists, "namely to distinguish between several possible phylogenetic scenarios" (Laubichler 2003, p. 29).

As to the formal integration of evo-devo with neo-Darwinian theory, not much progress has yet been made. The way toward a unified theory, however, seems to be open, and the stimulation of the biosciences through evo-devo biology is quite evident (von Dassow and Munro 1999; Müller 2005).

Primates and Supreme Public Servants of the Greek Ancient World

Primates and Their Supraordinal Relationships

Although primate origins and supraordinal relationships are discussed twice in Vol. 2 (chapters "▶ Primate Origins and Supraordinal Relationships: Morphological Evidence" on morphological and "▶ Molecular Evidence on Primate Origins and Evolution" on molecular data), I would like to mention some studies that have used ontogenetic data in this context. According to Hofer, one of the ultimate goals of primatology (Spatz 1964) is the elucidation of the phylogenetic position of primates compared to other mammals. Gregory (1910) formulated the concept of the Archonta, which unites Chiroptera (bats), Dermoptera (colugos), Menotyphla (Macroscelidea, elephant shrews; Scandentia, tree shrews), and Primates into one single superorder. Later on, modified versions of this hypothesis excluded the Macroscelidea (Novacek and Wyss 1986), while Adkins and Honeycutt (1993) surprisingly favored a revival of this grouping based on molecular data (*COII* gene). Even after the Hennigian revolution (1950), many morphologists confirmed the traditional version of primate supraordinal relationships by defining synapomorphies (Hooker 2001). Noncladists, such as Szalay (Szalay and Drawhorn 1980; Szalay and Lucas 1993), supported the evolution and diversification of archontans in an arboreal milieu. The approach is based on the aim of "Darwinian evolutionary classification" to include both adaptive similarity and monophyly sensu Bock and von Wahlert (1965). Critical comments can be found in Grande and Rieppel (1994).

Murphy et al. (2001), however, proposed the new superorder "Euarchontoglires," based on nuclear and mitochondrial gene sequences of 42 placental specimens. This new grouping (Asher et al. 2005; Nishihara et al. 2006) consists of the Euarchonta (= Dermoptera + Primates +Scandentia) and the Glires (= Lagomorpha + Rodentia). Surprisingly, bats are excluded and do not seem to be closely related to primates. MacPhee (1993, p. 372) already noted (based on Adkins and Honeycutt 1993) that ". . . something is pulling the rodents toward the primates in this data set. . .."

These radical changes in primate supraordinal relationships consequently deny the Volitantia hypothesis (Illiger 1811), which favors a sister group relationship of bats and colugos (Leche 1886; Thewissen and Babcock 1991; but see Beard 1993).

Wible and Martin (1993) documented that the ontogeny of the tympanic floor and roof does not provide any characters distinguishing all extant archontans from other eutherians. Actually, Archonta (archontans were supreme public servants of the Greek ancient world) has *Scala naturae* written all over it and represents a vehicle to explain the existence of flying mammals (Chiroptera) via a gliding intermediate stage (Dermoptera) in the absence of appropriate fossils (see also Sears et al. 2006). It should be emphasized that the concept of *Scala naturae* was long developed *before* the theory of natural selection (Martin 1973). Darwin (1859) promoted the view that nature does not make leaps – natura non facit saltum – in order (1) to fill the gaps in the fossil record and (2) to strengthen his intellectual position (Schwartz 2000). Although Darwin's motives are plausible, accepting the Volitantia concept might be an immediate consequence of the emerging battle against supporters of divine creation. Rasmussen (2002, p. 7) specified in a more diplomatic manner: "However, it is fair to say that at this juncture we do really not know if primates are more closely related to Scandentia, Plesiadapiformes, Chiroptera or Dermoptera. These four orders are conveniently lumped together as 'archontan' in what may be a true clade but which for lack of unambiguous evidence is often used as an informal grouping." *Faute de mieux:* chimeric archontans? (see also Hardt et al. 2006; Menke and Henke 2008). In the context of primate evolution, some important examples of cranial and postcranial anatomy are presented here.

The Myth of Primate Entotympanics: Consulting Embryological Data and Its Phylogenetic Implications

It is now more than a century since embryological studies [the Reichert-Gaupp theory, refuted by Otto (1984)] demonstrated the homology of the mammalian malleus and incus with the articular and quadrate bones which formed the ancestral jaw joint of gnathostomes. This tremendous transition can be traced in fossils by comparing basal synapsids through therapsids to early mammals. A fetal mammal shows that the angular (tympanic), articular (malleus), and quadrate (incus) develop in the same positions they occupy in the cynodont skull (Allin 1975; Maier 1987). The importance of new fossils (Rich et al. 2005), however, is demonstrated by Martin and Luo (2005): the separation of the middle ear bones must have evolved independently among the therians and the monotreme mammals. The middle ear and surrounding basicranium have played a decisive part in mammalian systematics over the past years (e.g., Sánchez-Villagra et al. 2002).

In 1979 – 2 years before the *Auditory Regions of Primates and Eutherian Insectivores* was published – R.D.E. MacPhee presented a new interpretation of the disputable issue of "primate entotympanics." Not all mammals show these mysterious skeletal elements. As otic characters are essential for primate taxonomy, this was a potential criterion for distinguishing primates from their relatives [e.g., colugos (Fig. 1) and tree shrews]. Mivart (1881) defined this specific element as "entotympanic," while Wincza (1896) introduced the term "metatympanic" (van Kampen 1905). A few influential morphologists (van Kampen 1905; van der Klaauw 1931) already championed the existence of primate entotympanics.

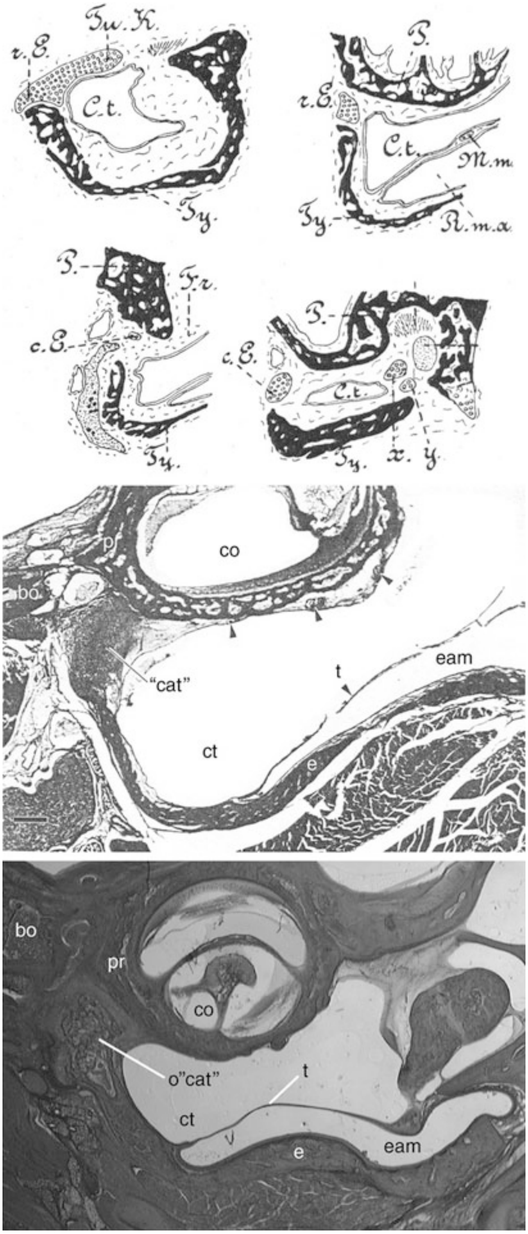

Fig. 1 *Top*: fetal *Cynocephalus volans* (Dermoptera). Cranial length 41 mm, frontal section. Note the entotympanics. *c.E* caudal entotympanic, *C.t.* cavum tympani, *F.r.* fenestra rotunda, *M.m.* manubrium mallei, *P*Petrosal, *R.m.a.* recessus meatus acustici externi, *Tu.K.* tuba auditiva cartilage, *Ty* tympanic, *x,y* cartilage. Sections have a thickness of 25 µm. Not to scale. (Modified from van der Klaauw 1922). *Center*: late-fetal *Cynocephalus variegatus* (DUCEC 806). Crown-rump length 136 mm. It shows a frontal section through the promontorium in front of the tegmen

Van der Klaauw (1922) published an ingenious work (*Über die Entwicklung des Entotympanicums*) in which he made a strong case for two different types of entotympanic, rostral and caudal. Developing in the anteromedial corner of the membranous tympanic floor, the rostral entotympanic grows posteriorly. Unlike the tympanic processes, entotympanics grow and develop within the fibrous membrane of the tympanic cavity (MacPhee 1979).

Starck (1975, p. 143) reported for *Tarsius* that the existence of an entotympanic is not yet proven. In the younger stage, the tympanic region does not show any peculiarities and an entotympanic cannot be detected. However, an older specimen showed a floor of the middle ear cavity that is formed by endochondral bone. It was closely connected with the otic capsule, but it showed a rostral extension near the auditory tube: “The ossified bone still contains some cartilaginous tissue, and this *would indicate the presence of a true entotympanic*, since the petrosal components of the floor are usually formed by periosteal bone. These results are in accordance with the findings of van Kampen (1905)” (my emphasis). According to MacPhee (1979), primate tympanic floor elements do not develop like any known entotympanic but, rather, like other tympanic processes. Prenatal *Microcebus* demonstrates secondary cartilage in the rostral tympanic process of the petrosal, which is interpreted as an embryonic adaptation – the explanation of the primordial fusion of once separate entities is no longer required. The hypothesis of a suppressed entotympanic is made more unlikely by the endochondral development of the caudal tympanic process of the petrosal (contra Starck 1975). To quote MacPhee (1979, p. 43): “Therefore, with regard to the constitution of the primate ventral wall, and with some necessary violence to Newton’s quip, *non fingo ossa* – I posit no bones.” *Eureka*, a new primate characteristic was identified via the careful interpretation of ontogenetic data.

Postcranial Ontogenetic Data and the Origin of Primates

Stafford and Thorington (1998) and Hamrick (2001) presented important data on the hand proportions in developing and adult mammals. Using a ternary plot (Hamrick 2001), relative metacarpal, proximal, and intermediate phalanx lengths among fossil and extant taxa deliver an elegant possibility of distinguishing primates from other “archontan” mammals. Primates differ from flying and gliding

Fig. 1 (continued) tympani. *Arrowheads point* to branches of the internal carotid nerve running in a transpromontorial position. Scale bar = 0.33 mm. *“Cat”* fused cartilage of the auditory tube and rostral and caudal entotympanics, *bo* basioccipital, *co* cochlea, *ct* cavum tympani, *e* ectotympanic, *eam* external acoustic meatus, *pe*Petrosal, *pr*Promontorium of petrosal, *t* tympanic membrane. (Modified from Wible and Martin 1993, © Plenum Press.) *Bottom*: the next step. Frontal section of a juvenile *Cynocephalus volans* specimen, of 145 mm crown-rump length, from the collection of the Institute of Systematic Zoology in Tübingen. It illustrates the ossification of the fused cartilage of the auditory tube and the rostral and caudal entotympanic (*o“cat”*). Hunt and Korth (1980) reported but they did not illustrate the fate of this important anatomical detail. Sections have a thickness of 40 μm. Not to scale mammals in having much longer proximal phalanges relative to their metacarpals and are unique among the sampled mammals in having elongated proximal phalanges relative to their metacarpals. A comparative analysis of hand development in the mouse lemur *Microcebus murinus* and other meta- and eutherian mammals reveals that "interspecific variation in relative digit and metapodial proportions has high-developmental penetrance; that is, adult differences are observed at early ontogenetic stages" (Richardson 1999, p. 348). Hamrick's (2001) results suggest an evolutionary scenario that describes an "invasion" of the fine branch niche based on a hand with a short palm and long fingers yielded by a change in digital ray patterning and segmentation.

Recent advances in developmental genetics elucidate patterns of postcranial growth in primates. Another study is based on a comparison of developmental data of CD1 mice fetuses and Rhesus macaques: Hallgrímsson et al. (2002) demonstrated the evidence for morphological integration of the limbs as serially homologous structures by reporting the covariation structure of forelimb and hindlimb skeletal elements. This proves that link structures between the limbs are caused by developmental modules, producing the covariation that would be needed to be overcome by selection for divergence in fore- and hindlimb morphology.

Since primates have more distally concentrated limb mass than most other mammals, Raichlen (2005) studied the unique kinematics of primates by testing a longitudinal ontogenetic sample of baboons (*Papio cynocephalus*). He concluded that the evolution of primate quadrupedal kinematics was tied to the evolution of grasping hands and feet.

The Impact on Paleoanthropology

Bolk's Fetalization Hypothesis: Its Successors and Critics

Forever Young?

Many contributions have emphasized the relevance of phylogenetic conclusions from ontogenetic information (Minugh-Purvis and McNamara 2002). One of the most influential books on developmental change and (human) evolution is Stephen Jay Gould's *Ontogeny and Phylogeny* (1977). Tuttle's (1978, p. 287) review of this book was not rhapsodic: "Perhaps the author attempted too much in this chubby volume [. . .] Time will tell whether it is in fact a hemicentennial classic as implied on the dust jacket." Well, in the meantime it has become probably one of the most frequently cited compendiums. Howell (2002, p. xi) commented that "its effect was immediate, substantive and far-reaching." Looking briefly at the bibliographies of modern studies often gives the impression that the consideration of developmental change in human evolution began in 1977 (Coqueuniot et al. 2004). Here, I focus partly on some of the "ancient" morphological studies that negate "essentially neotenous" ideas, to show how profound their explanatory power really is.

Why assume an *impact* on paleoanthropology? The ideas of Louis Bolk, a Dutch anatomist, have in fact had an enormous influence on scientists working in many different fields. The paleontologists Beurlen and Schindewolf (1936, 1950) supported a phenomenon called “proterogenesis” by pointing out that some evolutionary lineages that are present in successive strata may be interpreted as a process of maturing of former embryonic or postembryonic form levels. I mention these thoughts – although they do not deal with anthropological questions – because they show that Bolk’s thoughts are part of a greater, speculative construct of evolutionary ideas. Portmann (1960) already assessed the situation by claiming that criticism of Bolk’s considerations has to be criticism of the entire construct and argued that it is still in progress and may not be considered completed.

As Starck (1962) argued, Hilzheimer (1926, 1927) and others have pointed to morphological and physiological data to explain the principle of fetalization. Starck (1962) traced the hypothesis of neoteny back to Strickland and Melville (1848), but Bolk was the one who applied it to human evolution. A sequence of papers (the version of 1926 being the most frequently cited) takes us away to a non-Darwinian construct. So which are the essential elements?

Bolk (1926, p. 5) split human characters into (1) primary and (2) consecutive features. Primary characters are those products of developmental factors that caused the origin of human morphology. Consecutive characters, on the other hand, are phenomena of bipedal adaptation. Hence, the primum mobile of human evolution is not bipedalism, the “secondary” characters of which strictly follow functional aspects. Bolk (1926) considered the primary human characters to be the (1) reduction of body hair, (2) form of the external ear, (3) epicanthic eye fold (Mongolian eye fold), (4) loss of pigmentation in skin, (5) orthognathy, (6) foramen magnum in a central position, (7) a long persistence of cranial sutures, (8) subcerebral position of orbits, (9) high relative brain weight, (10) position of the spinal column relative to the cranial cavity, (11) women’s labia majora, (12) structure of hand and foot, (13) form of the pelvis, (14) women’s sexual canal in a ventral position, (15) multipapillary kidneys, and (16) the branching pattern of the arch of the aorta [the last two characters are not mentioned by Gould (1977)]. What is the common denominator of these characters?

The characters listed by Bolk are phenomena which temporarily appear during primate ontogeny. Although Bolk (1926, p. 44) differentiated the problem by separating (1) the relatives of *Homo sapiens* and (2) the development of human shape, as Slijper (1936, p. 504) explained, he advocated the idea that our ancestor must have been an *extant*Primate species. Characters of human fetalization consequently represent persisting ontogenetic primate characters. Human ontogeny therefore demonstrates conservative traits, while humans’ primate ancestors showed “propulsive” (advanced) characters. Bolk’s (1926, p. 26) bottom line is *H. sapiens* represents a sexually mature primate fetus. However, how did he explain the inhibitive force that fixes man’s physical appearance at a certain point in time?

“The obvious answer is: The slow progress of his life’s course” (Bolk 1926, p. 470) and the fact that “human life progresses like a retarded film” (Gould 1977, p. 360). Bolk (1926, p. 38) asserted that the development of dentition, consciousness, and the late closure of cranial sutures act as indicators of a dominant retardation phenomenon. The chain of causes starts with the modification of the endocrine gland function (for a modern hypothesis, see Crockford 2002) by *internal* alteration, not by external factors of the environment (Bolk 1926, p. 22).

Slijper (1936), another Dutch scientist, published an outstanding analysis that considered cetacean relationships, the fetalization hypothesis, and the clarification of fundamental terms. Ironically, Gould (1977, p. 365) called Slijper's criticism "famous," which is quite euphemistic since even the German-speaking Starck (1962) complained about it as not being easy accessible and often ignored. One major problem of Bolk's idea is the *subjective* splitting of primary and consecutive features. Slijper (1936, p. 509) recapitulated Bolk's scientific career and stated: "... we get the impression that Bolk did not present primary characters (mostly human) at first and discovered their fetal character afterwards, but rather observed a contrarian procedure: he discovered fetal characters and defined them subsequently as primary. This explains the remarkable correlation of primary features with fetal phenomena and diminishes its objective value" (my translation). Slijper also denied any general neotenous influence on human ontogeny.

Two prominent morphologists concerned with primordial cranial studies were Benno Kummer and Dietrich Starck. In 1962, they published the first modern study on fetal *Pan troglodytes* (Fig. 2). Starck and Kummer followed Hofer (1958, 1960) in distinguishing basal and prebasal kyphoses. Gould (1977, p. 378) excellently summarized their findings thus: (1) All fetal mammals have a prebasal kyphosis at the junction of the presphenoid and ethmoid bones (a bending with the concave side toward the body, as opposed to a lordosis). (2) This kyphosis decreases during ontogeny, the sphenoethmoidal angle opens out, and the face comes to lie in front of the cranium. (3) While the prebasal kyphosis develops within the basicranial axis during human ontogeny, a different kyphosis develops between the basisphenoid and presphenoid bones at the level of the dorsum sellae. This second kyphosis produces a secondary decrease in the sphenoethmoidal angle following the earlier increase conditioned by straightening of the prebasal kyphosis. (4) The "fetal" value of the sphenoethmoidal angle in human adults does not reflect the retention of a fetal condition but arises from development of the new, sellar kyphosis. It is a new feature – not a paedomorphic retention.

Amazingly, Gould (1977, p. 379) concluded: "These authors have used this single contention as the basis for a campaign against the hypothesis of fetalization..." A single contention? *A campaign*? To be blunt, Gould himself started a campaign. In relation to Bolk's explanation of skull development, Portmann (1960, p. 586) already commented that "... skull development is a complex issue which makes Bolk's solution suspicious" (my translation). Reflecting the development and evolution of the human chin, Vogel (1964) warned against too "localized" a view and called for the consideration of the complexity and interaction of *all* developing skull components. Schwartz and Tattersall (2000) revisited the presence of a chin in hominins and examined the importance of developmental epiphenomena.

Furthermore, Gould (1977, p. 379) claimed that the "... tradition of excellence in descriptive morphology is combined with a general avoidance of quantification,

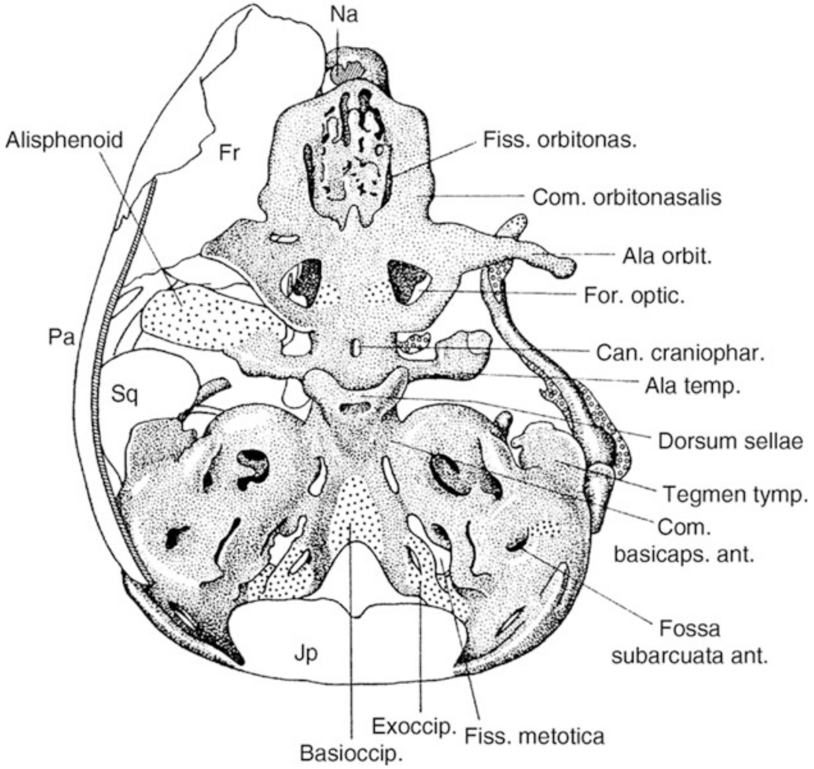

Fig. 2 Dorsal aspect of a fetal cranial model of *Pan troglodytes*. Crown-rump length: 71 mm. Not to scale (Modified from Starck and Kummer 1962)

and this may have hindered a full assessment." He might have overlooked an essential part of Starck and Kummer's (1962, p. 213) paper because "these findings can be characterized as quantitative. . .": (1) different relative sizes of the neurocranium and auditory capsule, (2) tegmen tympani, (3) frontal nasal region, (4) canaliculus chordae tympanic posterior, (5) commissura orbitonasalis, and others. Gould (1977, p. 384), however, did not fall into the Bolkian trap of an all-or-nothing law. Instead, he argued that "most of the classic 'exceptions' to human paedomorphosis are really consequences of retarded development," which Gould described as being the central phenomenon of our heterochronic evolution. Yet his ideas represent an analytic continuation of the Bolkian hypothesis.

Starck and Kummer (1962) did not exclude retardation (as in the commissura orbitonasalis) as an important factor of human development, but they emphasized that accelerations (e.g., the earlier closing of the intermaxillary suture in *Homo*) as well as deviations (e.g., the basicranium) should influence specific developmental processes. Starck's (1962, p. 23) summary revealed that the principles of human evolution cannot be understood through Bolk's hypothesis: important structures of the skull, very often taken as a result of fetalization, are indeed progressive compared with the pongid skull. It is emphasized that the bending of the skull base in man and apes is absolutely different, caused by different morphological structures. Identity of causal factors is not established, if we find external similarities, such as the same size of angles, of relative measurements or indices. This may happen by addition of completely different components.

This statement seems not to be a *furor teutonicus* but rather a well-balanced point of view. Hence, morphometrics might work, but the comparison of morphological details must occur in a correct manner. How do contemporary anthropologists interpret morphological changes of this important cranial region?

Developmental Aspects Concerning the Evolution of the Human Cranial Base

The cranial base represents the oldest component of the vertebrate skull (De Beer 1985). Thus this "conservative" structure is profoundly important in reflecting man's phylogenetic history and comparing primates to reveal essential aspects of human evolution. The keystone of the primate skull is definitely the basicranium. Several regions, such as the upper airway, the brain, and other parts, impinge upon one another here and consequently interact during ontogeny (Moss et al. 1982; Dean and Wood 1984; Lieberman et al. 2000). Biomechanically, the cranial base supplies a platform on which the brain develops and around which the face grows. The cranial base also forms a bridge connecting the cranium with the rest of the corpus: providing conduits for all circulatory and vital neural connections, articulating with the mandible and the vertebral column, forming the roof of the nasopharynx, and connecting the sense organs in the skull. Lieberman et al. (2000, p. 120) stated that "the shape of the cranial base is therefore a multifactorial product of numerous phylogenetic, developmental, and functional interactions."

Scientists are confronted with the problem of complicated circumstances in studying this truly important region. It is not only complexity that matters but also problematic ways of measuring. Furthermore, the fragmentary nature of fossil remains causes major difficulties. Novel analytical techniques, however, have helped to engross our thoughts over the past years. Different hypotheses exist that deal with ontogenetic spatial processes and their phylogenetic implications. I mainly follow Jeffery (2003) in reviewing some of the most popular versions. The *general spatial-packing hypothesis* states that the modern human basicranium is caused by a short cranial base and an enlarged brain. Ross and Ravosa (1993) and Ross and Henneberg (1995) revealed significant positive correlations between increases of relative brain size and cranial base flexion across adult primate taxa: correlation of increasing relative brain size with (1) a coronal reorientation of the petrous bones across extant primates (Spoor 1997), (2) a cranial base flexion using different measurements and landmarks (Spoor 1997; McCarthy 2001), and (3) a cranial base flexion after controlling for the influence of phylogenetic correlations (Lieberman et al. 2000). Enlow and colleagues (Enlow and Hunter 1968; Enlow 1976, 1990) also attempted to demonstrate a determination of cranial base flexion through increases in relative brain size during primate development. Jeffery and Spoor (2002) could not verify these authors' arguments. They analyzed specimens from 10 to 29 weeks of gestation and documented that petrous orientation remains independent of significant increases in relative brain size. Furthermore, a retroflexion of the midline cranial base with relative endocranial size increases has been suggested. This observation contradicts the predicted flexion pattern.

The *infratentorial spatial-packing hypothesis* has been revitalized by Dean (1988), who argued that having coronally oriented petrous bones and a highly flexed basicranium poses the spatial problem of fitting an enlarged cerebellum on a short posterior cranial base. Jeffery and Spoor (2002) showed that ontogenetic data, collected during the second and early third trimesters of human prenatal development, do not support Dean's (1988) claim. They indicate that the petrous orientation and cranial base angulation do not correlate with increases in infratentorial volume relative to posterior cranial base length.

The influence on skull form of patterns of brain growth is addressed by two interesting models. Hofer (1969) and Lieberman et al. (2000) favored the *brain shape hypothesis*, while Ross and Henneberg (1995), Chklovskii et al. (2002), and Sporns et al. (2002) supported a *neural-wiring hypothesis*. These ideas have in common a suggested necessary change in brain topography to maximize cognitive efficiency by reducing neural-wiring lengths. The resulting spatial changes produce a petrous reorientation and cranial base flexion. Distinct volumetric scaling trajectories can be detected across adult extant primates for different regions of the brain (Stephan et al. 1981, 1984; Frahm et al. 1982, 1998; Baron et al. 1987, 1990). Dean and Wood (1984) and Strait (1999) further demonstrated an association of those trends with interspecific variations in basicranial angulation. Lieberman et al. (2000) also confirmed a significant correlation of cranial base flexion with increases of cerebral volume over brainstem volume.

Moss et al. (1956) suggested that brain topography is shaped by differential encephalization patterns which lead to developmental changes in posterior cranial fossa morphology.

A few studies (Guihard-Costa and Larroche 1990, 1992; Jeffery 2002) on the human fetal brain showed greater increases in expansion of the supratentorial portion (containing the cerebrum) compared to the infratentorial portion (consisting of cerebellum and brainstem). However, the independence of human cranial base angulation and petrous orientation of changes from the volumetric proportions of the brain between the ages of 10 and 29 weeks gestation are corroborated by Jeffery and Spoor (2002).

Jeffery (2003) tested the key hypotheses by imaging fetal samples of *Alouatta caraya* and *Macaca nemestrina* using high-resolution MRI. He noted marked increases in brain size, especially "disproportionate increases in the size of the cerebrum" (p. 281), disproportionate growth of the anterior midline basicranium compared with the posterior midline basicranium, coronal reorientation of the petrous bones, and cranial base retroflexion. Contrary to the spatial-packing hypotheses, increase in relative brain size is not accompanied by flexion of the midline basicranium. Retroflexion is documented for the cranial base in both taxa. There is also little evidence supporting the spatial-packing hypothesis for the fetal period of the howler monkey and macaque due to significant and "seemingly" consistent associations with petrous orientation arise based on background covariations with somatic growth. Jeffery (2003) therefore suggested that laryngeal size might be the reason for basicranial retroflexion. He finally compared it to human fetuses and concluded that the establishment of notable interspecific differences in the basicranium occurs much earlier than in the phase he studied.

Craniofacial growth patterns have been studied by several scientists (Giles 1956; Shea 1983, 1985a, b; Jungers and Hartman 1988; Ravosa 1991, 1992; Zumpano and Richtsmeier 2003; Cobb and O'Higgins 2004; Mitteroecker et al. 2004). Lieberman et al. (2000) provided a comprehensive review of primate cranial base studies. As Zumpano and Richtsmeier (2003) pointed out, many previous studies documented postnatal growth processes, usually beginning with growth during the juvenile period. The infant growth period has been incorporated by Ravosa (1992), Richtsmeier et al. (1993), or Shea (1983), while Zumpano and Sirianni (1994) compared fetal to postnatal craniofacial growth patterns. Collections of fetal primates very often do not contain representative specimens (Zumpano and Richtsmeier 2003, p. 340). Yet it is desirable to attempt an integration of these stages since only a completely documented ontogeny delivers deeper insight to reveal whether heterochronic processes are responsible for the modifications that have occurred between human and nonhuman primates.

Zumpano and Richtsmeier (2003) investigated, for the first time, growth-related shape changes in the fetal craniofacial region of humans and pigtailed macaques (*M. nemestrina*), using three-dimensional comparative analysis via cross-sectional samples of CT image data. As they emphasized, a long tradition of studies concentrated on examining the sites of growth of the cranial base, the sites of cranial base flexure, and the determination of the cranial base angle (Bjork 1955; Ford 1956; Dubrul and Laskin 1961; Houpt 1970; Lavelle 1974; Bosma 1976; Lestrel and Moore 1978; Moore 1978; Sirianni and Van Ness 1978; Sirianni and Newell-Morris 1980; Ross and Ravosa 1993; Ross and Henneberg 1995; Zumpano and Richtsmeier 2003). Zumpano and Richtsmeier (2003) showed that decreases in human cranial base length are achieved through the differential growth of posterior and anterior elements. The length of the posterior cranial base decreases, while increases occur in the length of the anterior cranial base. They further argue that a cranial base angle decrease may lead to a total reduction in cranial base length in human fetuses. At a comparable stage, the fetal macaque cranial base does not show a corresponding reduction (increased basicranial flexion). The associated distinctiveness of the differences in midfacial growth and the progression of prenatal cranial base flexion are said to be factors separating these two species. Zumpano and Richtsmeier (2003) also contradicted Bjork (1955) and Ford (1956) in noting a basicranial flexion – not a constant angle – during the fetal period. They further support Lestrel and Moore (1978), and Sirianni and Newell-Morris (1980) are also supported in assuming a constant macaque cranial base angle during fetal growth, although they report a lesser angle (153°). The human anterior cranial base undergoes more relative growth than the macaque anterior cranial base. For the posterior cranial base, no significant growth differences between these two species are observed. Zumpano and Richtsmeier (2003) speculated that the increases in relative length of the anterior cranial base in humans may reflect the faster rate of growth of the frontal lobes of the cerebral cortex in humans relative to macaques (Enlow and Hunter 1968; Moss and Salentijn 1969; Moss 1973; Sirianni and Newell-Morris 1980) and conclude, based on their own observations and the studies of Anemone and Watts (1992) and Swindler (1985), that midface differences between humans and macaques reflect a delayed rate of maturation of the human deciduous dentition *or* an accelerated rate of development. In a tabula rasa manner, Zumpano and Richtsmeier (2003) supported earlier investigations in suggesting the occurrence of shape changes within the fetal craniofacial complex during the last trimester of fetal growth (Grausz 1991; Plavcan and German 1995) rather than assuming an isometric growth process that is, e.g., characterized by size increase without corresponding shape change (Mestre 1959; Houpt 1970; Kvinnsland 1971a, b; Lavelle 1974; Moore and Phillips 1980; Sirianni and Newell-Morris 1980; quoted from Zumpano and Richtsmeier 2003). Zumpano and Richtsmeier (2003, p. 349) finally concluded that “fetal macaques and humans do not share a common pattern of relative growth of the craniofacial complex, both species undergo increases in mediolateral dimensions (widening) of the skull and increases in palatal and anterior cranial base length.”

One of the ultimate goals in paleoanthropology is to reveal the precise relationship of humans to the great apes, our closest living relatives. Morphological data favor the monophyly of the African great apes, while molecular biology unites humans and chimpanzees (Mann and Weiss 1996; Ruvolo 1997; Enard et al. 2002; Kaessmann and Pääbo 2002). Wildman et al. (2003) even placed chimpanzees within *Homo* based on molecular data. Pääbo (1999) emphasized the importance of investigating a few genes that are responsible for specific effects during ontogeny (or in adulthood) instead of concentrating on chromosomal rearrangements or the accumulation of point mutations. Hence, Mitteroecker et al. (2004, p. 680) stated that “as it is difficult to study gene expression on a molecular level for the whole organism, we confine ourselves to the study of the morphological effects of gene expression during ontogeny.” They therefore created a shape space where each specimen (i.e., its landmark configuration) is represented by a single point. In this context, an ontogenetic trajectory corresponds to the ontogenetic sequence which belongs to one species within this space. As Klingenberg (1998) or O’Higgins (2000a, b) showed, geometric contrasts among ontogenetic shape trajectories distinguish the development of different species. Geometric morphometrics is a promising and complex method of collecting and interpreting data based on morphological patterns (Bookstein 1991; Marcus 1996; Dryden and Mardia 1998; Slice 2005).

Some hominid craniofacial growth studies, applying geometric morphometrics, found more or less parallel trajectories from dental stage I (which corresponds to the first permanent molar) to adulthood (Ponce de León and Zollikofer 2001; Penin et al. 2002). The development of hominid cranial morphology consequently diverges from that of the other apes in an early postnatal or prenatal stage. However, O’Higgins (2000a; O’Higgins et al. 2001) confirmed Richtsmeier et al.’s (1993) assumption of related species subsequently diverging after a similar period of early development. In a comprehensive study, Mitteroecker et al. (2004) measured landmarks and semi-landmarks in relevant specimens following a few days after birth to reveal essential insights into hominid ontogeny. Several principal patterns can be deduced from the set of ontogenetic trajectories. The authors tested three specific hypotheses: (1) “pure heterochrony” of human cranial growth relative to *Pan* is a valid interpretation if the ontogenetic trajectories are identical in shape space, (2) the divergence of human ontogeny corresponds to a similar developmental stage at which the great apes diverge among themselves, and (3) an early divergence of trajectories from common ontogeny could elucidate the considerable morphological differences between humans and great apes because early modifications in development explain drastic transformations of the adult form (Richardson 1999). Studying 206 adult and 62 subadult crania of *Homo sapiens*, *Pan paniscus*, *P. troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*, Mitteroecker et al. (2004) collected three-dimensional coordinates of 41 homologous ectocranial anatomical landmarks on the face and cranial base. They demonstrated the expected pattern whereby the youngest specimens are much more similar than the adults (von Baer’s omnipresent discovery). Already at birth, human craniofacial morphology differs markedly from apes (p. 692) “in accord with previous studies based on more traditional methods” (Starck and Kummer 1962; Dean and Wood 1984). The first hypothesis, in contrast, can be rejected because there is no sharing of a common ontogenetic trajectory. Penin et al. (2002) tried to revitalize the “neotenic theory” sensu Gould (1977, p. 365). They do not, however, support a “general, temporal retardation of development” but rather stress that “all the bipedal traits studied, whether in the skull (basicranium) or postcranium (pelvis and femur, see above), do not result from neotenic processes but rather from structural traits” (p. 61).

Additionally, the second hypothesis is falsified, and the third hypothesis is supported, by an earlier divergence of the human growth trajectory from the common hominid allometry (Mitteroecker et al. 2004, p. 692). The African apes also do not seem to be pure allometric variants of one single type. Mitteroecker et al. thus concluded (p. 694) that “pure heterochrony does not sufficiently explain human craniofacial morphology nor the differences among the great apes.” McBratney-Owen and Lieberman (2003) also provide insight into the postnatal ontogeny of facial position in *H. sapiens* and *P. troglodytes* by emphasizing that the ontogenetic integration of complex phenotypes, such as the face, occurs on multiple levels of development, and they further speculate about the effectiveness of ontogenetic analyses for testing hypotheses about natural selection.

Ackermann (2005) investigated similarities in cranial covariation patterns by obtaining measurements from 677 crania of adult and nonadult African apes and sub-Saharan humans to locate underlying developmental and functional causes for the patterning. Defining the points of divergence of the covariation patterns can offer insights into the action of selection on development. Ackermann’s work shows that patterns of integration are similar (not identical) among adult African apes and sub-Saharan humans. Ontogeny documents a sharing of patterns, with each species showing contributions to total integration from the oral region as well as from the zygomatic and to a lesser extent the nasal regions. However, she documented important differences between apes and humans, stating:

"In particular, the lower overall integration within and lack of covariance structure similarity among adjacent ontogenetic stages in early human ontogeny differs from what we see in the other apes. It is not entirely clear why this might be so, although it indicates that selection was working in this lineage – either on humans or the apes – to distinguish them not only in morphology, but in variation patterning" (p. 195).

Quo Vadis? Developmental Aspects Concerning the Evolution of Bipedalism

I have already mentioned Bolk's (1926, p. 6) interesting ideas concerning human bipedalism "… since form became human the posture became upright" (my translation). Summarizing his growth studies on primates, Schultz (1924, p. 163) asserted that "man in some respects is less specialized and has hence remained phylogenetically as well as ontogenetically more original and 'primitive' than various other primates."

Structural and mechanical aspects of the locomotion of primates play a considerable role in many discussions of human evolution (Preuschoft 1971; Schaffler et al. 1985; Demes and Jungers 1993; Connour et al. 2000; Ruff 2002; see also Senut, Volume III). Schultz (1953) analyzed over 350 limb bone circumferences and related the results to locomotion. The evolution of bipedal walking has, naturally enough, inspired scientists to associate locomotor mode with the relative lengths of the forelimb and hindlimb bones (Schultz 1937; Napier and Napier 1967; Jungers 1982). Changes within the hominin lineage in the relative size of the upper and lower limb bones are indications of our transition to bipedality (McHenry 1978; Johanson et al. 1982; Wolpoff 1983; Hartwig-Scherer and Martin 1991; McHenry and Berger 1998; Asfaw et al. 1999; Richmond et al. 2002; Ward 2002).

A few French scientists (Berge 1998) have tried to integrate heterochronic processes into analyses of morphological changes during hominid evolution. These works have concentrated on such classic anthropological topics as the anatomy of the pelvis. Berge (1998, p. 443) emphasized separating the debate on neoteny by negating the idea "that identical heterochronic processes occur in skulls and postcranial skeletons, although we know that the growth of cranial and long bones differs in time, rhythm and velocity." She studied the morphology of two adult pelves and a juvenile hip bone of australopiths, 60 juvenile and adult pelves of modern humans, and 150 juvenile and adult pelves of African apes. The results confirmed a marked difference of the pelvic growth pattern in African apes and humans as reflected in multivariate results, ontogenetic allometries, and growth curves. Two conclusions emerged: (1) a comparison of modern humans to juvenile and adult australopithecines reveals that a unique feature of *Homo* seems to be a prolonged growth in length of hindlimb and pelvis after sexual maturity, while pelvic growth of *Australopithecus* was probably closer to that of apes than to that of humans and that some pelvis traits of adult *Australopithecus* resemble those of neonate *Homo*. Furthermore, (2) at the time of human birth, the appearance of the acetabulo-cristal buttress and the cristal tubercle allows the addition of features, such as the attainment of a proportionally narrower pelvis, with more sagittally positioned iliac blades. In early childhood (as bipedalism is practiced), pelvic orientation and proportions change progressively, while other changes in proportions occur later with the adolescent growth spurt. Neonate *Homo* and adult *Australopithecus* show similar patterns concerning the position of the acetabulo-cristal buttress. This could suggest a later displacement during human evolution. Berge (1998) further documented a progressive displacement of the acetabulo-cristal buttress on the ilium occurring during human growth (from neonate to adult) and hominid evolution (from *Australopithecus* to *H. sapiens*). She finally suggested that the evolution of pelvic morphology in hominids is based on a threefold process – predisplacement, acceleration, and time hypermorphosis – and she rejected pure fetalization (p. 457) by stating that "the present study demonstrates clearly that the concept of neoteny is irrelevant for the pelvis. The study rather implies an accelerated evolutionary process than a retarded one."

Ruff (2003) examined the human development of femoral to humeral proportions using a longitudinal sample of 20 individuals measured radiographically at semiannual or annual intervals from 6 months of age to late adolescence and also included anthropometric data such as body weights or muscle breadths. A series of limb bone length proportion studies included ontogenetic data (Lumer 1939; Schultz 1973; Jungers and Fleagle 1980; Buschang 1982; Shea 1983; Jungers and Susman 1984). Ruff (2003) focused on other limb bone dimensions. He compared his results with a cross-sectional ontogenetic sample of 30 baboons. The results document that femoral/humeral length proportions, which are already close to those of adults, are present in human infants, while characteristically femoral/humeral diaphyseal strength proportions only develop after the adoption of bipedalism (at about 1 year of age). Between the age of one and three, a rapid increase in femoral/humeral strength occurs, and this is followed by a slow increase until mid-late adolescence (when adult proportions are reached). The femoral/humeral length ratio proportions slightly increase throughout growth. There is no apparent growth trajectory change at the initiation of walking and a small decline in late adolescence based on a later humeral growth in length. Also in early childhood, a sex difference in femoral/humeral strength proportions (but not length proportions) develops. Ruff (2003) therefore concluded that they must be largely independent of growth trajectories in strength and length proportions. Baboons (used as a baseline) show contrasting patterns of growth: much smaller age changes in proportions and particularly strength proportions. He therefore stated (p. 342): "Comparisons with an ontogenetic baboon sample highlight the specific nature of the human developmental pattern."

Returning to Adolph H. Schultz, we have an excellent example of a convert. In his youth, Schultz was stimulated by the neoteny hypothesis (see earlier). Following several studies (1953, 1973) although, he rejected Bolk's idea and the theory of man's neoteny.

Heterochrony in Human Evolution: A Compilation

Repetitio est mater studiorum or as Schwartz (1999, p. ix) commented: ". . . it would be foolhardy to cling unreservedly to a particular set of models and hypotheses without at least occasionally questioning their very bases." In *Sudden Origins*, Schwartz reconsidered and discussed inter alia the different interpretation of the Taung child. While Raymond Dart was influenced by ideas of neoteny and concluded that his fossil

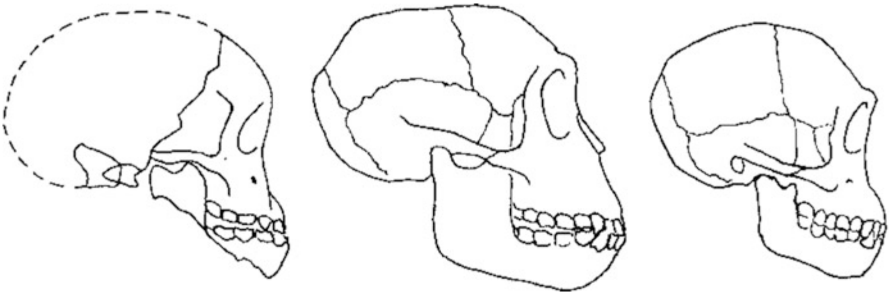

Fig. 3 The Taung child (*left*), compared to the skulls of comparably aged gorilla (*middle*) and chimpanzee (*right*). Dart's desire was to show that the apes had begun to grow away from the juvenile state. The Taung specimen has no brow ridges, small jaws, and a very large brain (Modified from Schwartz 1999, drawing by T. D. Smith, © J. H. Schwartz)

occupied a missing link position, Sir Arthur Keith drew a totally different conclusion and defined the Taung individual as an ape. Ironically, Keith's results were also based on a developmental and even a neotenic chain of ideas (Fig. 3).

Furthermore, Schwartz (1999) critically reviewed the suggestions of the Australian anthropologist Andrew Arthur Abbie, who equated neoteny and paedomorphism, and portrayed *H. sapiens* due to its long legs and a highly arched nose as gerontomorphic (more differentiated from a fetal standard), although he generally described our species as paedomorphic (little differences from a fetal standard). Abbie absorbed the heterochronic perspective but failed to sustain the argument that human morphological variability is not fixed to a limit and that any combination of features can be incorporated in the same individual.

Gould (1977, 1991, p. 2) called attention to the difference between Haeckel's heterochrony, which describes the *pathway of development in an organ relative to the pathways of other organs in the same animal*, and current usage, which defines it as "the course of a trait relative to the ontogeny of the same trait in an ancestor (or related form)." Jena's most famous zoologist was not really interested in elucidating evolutionary mechanisms as a method to explain the patterns of character states. He was rather interested in reconstructing natural history by applying biogenetic laws. Sir Gavin de Beer (1930) opened up new vistas by modifying Haeckel's concept: any change in the timing of a character is compared to the same feature in an ancestor. This established the study of heterochrony within the modern synthesis (Gould 1991).

McNamara (2002, p. 1) defined heterochrony essentially as "change to the timing and rate of development" which produces two major effects: *paedomorphosis* (if there is less growth during ontogeny, the descendant adult will resemble the juvenile condition of the ancestor) and *peramorphosis* (where the descendant undergoes greater development). Three different processes generate paedomorphosis and peramorphosis, respectively: (1) progenesis (prematurely truncated duration of growth in the descendant), neoteny (a lesser growth rate in the descendant than in the ancestor), and postdisplacement (delayed onset of growth) and (2) hypermorphosis (extension of duration of growth in the descendant), acceleration (an increase of growth rate in the descendant), and predisplacement (earlier onset of growth in the descendant). The whole organism can only be affected by progenesis and hypermorphosis, while the remaining aspects affect certain traits of the organism. McNamara (2002) further stated that peramorphosis and paedomorphosis are the products of varied processes rather than being processes in themselves. Hypermorphosis (extensions of the end of growth) and progenesis (contractions of the end of growth) are considered within a global context, "based on changes to the time of onset of sexual maturity and cessation of somatic growth, with the two frequently coinciding" (McNamara 2002, p. 105).

Different views have emerged on how large a role neoteny plays. While Gould (1977), Antón and Leigh (1998), and Montagu (1989) supported true paedomorphosis (neoteny), Shea (1988, 1989, 1992), McKinney and McNamara (1991), and McNamara (1997) favored some kind of hypermorphosis in time. Bogin (1997) suggested a new developmental stage in between (no heterochrony); Alba (2002) on the other hand characterized paedomorphosis and peramorphosis as *interpretative*, not descriptive, terms. He emphasized the importance of modifying conventional clock models based on meaningful variables. Alba (2002) called for a double standardization (initial and final developmental stages) of ontogenetic trajectories and suggests a "complete" model including absolute age (at homologous developmental stages), shape, size, and behavior. As he admitted, this is not an easy undertaking.

McKinney and McNamara (1991) have indicated that, during ontogeny, contractions and extensions can occur at transitions between particular life-history stages and that local growth fields can also be modified. The reality that heterochrony may operate at *any time during ontogeny* (from the point of fertilization until the cessation of growth) has been blurred by the comparison of the cessation of a descendant's growth with the ancestral condition (McNamara 1983; McKinney and McNamara 1991; Maier 1999). Mammals, for example, are characterized by embryonic and postembryonic (infantile, juvenile, adolescent, and adult) growth phases. In his thought experiments, McNamara (2002) showed how some authors have described paedomorphosis where it was nonexistent. Sequential hypermorphosis (defined by him in 1983 as *terminal hypermorphosis*), for instance, also effects the offset of growth and therefore implicates greater development within each growth stage based on "scaling effects and probable increase in size, either of the part, or of the whole" (2002, p. 108). Hence, the descendant is compared to the ancestor in a relatively more juvenile state. Paedomorphosis, however, should be defined by *adult* characteristics.

What kind of consequences does sequential heterochrony have for our understanding of human evolution? The list of "general neoteny supporters" is long (I have already mentioned Bolk and Gould, but see also Montagu 1989; Wolpert 1991). Montagu's (1989) favorite ancestor is a form very like the pygmy chimpanzee in order to compensate the incorrect assumption of Bolk that the hominid line has passed through an apelike stage such as the gorilla-orang type. Provided that human is "essentially neotenous," hominid evolution would have produced an organism characterized by having a smaller body size, brain, and limbs

(Shea 1989; McKinney 1998). McNamara's (2002, p. 115) summary described hominid evolution as involving "a mixture of peramorphic and paedomorphic traits." Forty years back, Starck and Kummer (1962) had come to a similar conclusion via a totally different method.

Shea (2002, p. 95) applied his working hypothesis – size diversification occurs via predominant rate changes (rate hypomorphosis and hypermorphosis) rather than by time changes (time hypomorphosis and hypermorphosis) – to human evolution and concluded that: "Certainly, at present no emergent data support any genetic or developmental basis for a global or generalized neoteny." He accused Godfrey and Sutherland (1996) of revitalizing the idea that hominid evolution has predominantly involved a generalized neotenic transformation. This accusation is problematic in that Godfrey and Sutherland (1996, p. 40) freely admitted that "Gould's neoteny hypothesis for human evolution has been criticized on a number of grounds. The thesis of this paper is that both Gould and his critics overstated their cases: *Nothing that we have said should be construed as a defense of Gould's hypothesis*. Our intention is simply to reopen the dialogue, and to propose a framework for more precise testing of heterochronic hypotheses" (my emphasis).

In contrast, Hall (2002, p. 13) attacked the one-sided concentration on heterochrony as the only way to consider development and evolution by claiming that it "seemed that everyone could find evidence for heterochrony or at least justify use of the term to explain phenotypic changes in their favourite organism. Other mechanisms linking development and evolution were ignored or not sought." He emphasized the importance of heterotopy, the *spatial pendant* of heterochrony.

In summary, I give below some important terms and definitions (see also earlier) based on Minugh-Purvis and McNamaras' (2002) summary, to present a brief synopsis:

Acceleration	A heterochronic process that involves a faster rate of development in the descendant and also produces a peramorphic trait in the descendant
Deceleration	A slower rate of developmental events in the descendant. It produces a paedomorphic trait when expressed in the adult phenotype (syn. neoteny)
Hypermorphosis	Developmental events show a delayed cessation (or offset) in the descendant. Expressed in the adult phenotype, peramorphic traits are produced. Global hypermorphosis can be caused by late sexual maturation (terminal hypermorphosis). But hypermorphosis can also be caused by a delayed cessation in local growth fields
Isomorphosis	Peramorphosis followed by paedomorphosis (or vice versa). The descendant does not show any effective morphological changes. Unusual phenomenon of paedomorphosis
Neoteny	A slower rate of developmental events in the descendant, producing paedomorphic traits when expressed in the adult phenotype (syn. deceleration)
Paedomorphosis	The descendant adult retains subadult ancestral traits
Peramorphosis	The ancestral adult shows development of traits beyond the "usual" ancestral stage

(*continued*)

Progenesis	Developmental events show an early cessation in the descendant. Expressed in the adult phenotype, peramorphosis is produced (syn. time hypomorphosis)
Sequential heterochrony	Contraction or prolongation in the descendant relative to the ancestor of life-history stages or ontogenetic growth
Sequential hypermorphosis	Life-history stages or ontogenetic growth is prolonged in the descendant relative to the ancestor (syn. proportional growth proportion)

Tolkien's Hobbits Came True: *H. floresiensis* and Heterochrony

In his first chapter of his book *The Hobbit*, "An unexpected party," J. R. R. Tolkien described these creatures as wearing ". . . no shoes, because their feet grow natural leathery soles and thick warm brown hair like the stuff on their heads; have long clever brown fingers, good-natured faces,. . ." Furthermore, and more importantly, the author characterized them as "..little people, about half of our height" (Tolkien 2007, p. 4). *Homo floresiensis* was named for Pleistocene hominid remains on the Island of Flores (Indonesia) – these fossils in many ways represent the embodiment of Prof. Tolkien's fantastic creatures. However, for some researchers insular dwarfism by natural selection seems not to be a good explanation (e.g., Jacob et al. 2006). They prefer a pathologic scenario which reminds one of the interpretation of the Neanderthal enigma àla Rudolf Virchow.

The ontogeny-phylogeny nexus might serve as a plausible model for the evolution of *Homo floresiensis*. Kubo et al. (2013) analyzed the endocranial volume of LB1 via high-resolution micro-CT scans. They finally concluded that is mechanistically possible that the dwarfs from Flores evolved from early Indonesian *Homo erectus*. Mammals such as hippos have served as a model for brain size reduction in *Homo floresiensis* (Weston and Lister 2009). However, these studies have not deeply considered the role of ontogenetic processes. Van Heteren (2008) presented an interesting evo-devo approach by adapting the model of heterochrony – that, like the pygmy elephants of Cyprus, *H. floresiensis* might have stopped growth at an earlier age. Additionally, paedomorphic features might have developed "by making the rate of ossification increase" (p. 7).

In support of his hypothesis, Van Heteren (2008) adduced various cranial paedomorphic features such as the orbital index, the mandibular angle, the endocast, and the canine fossa. The dental index also supports his view of *H. floresiensis* as an interesting case of heterochrony. Furthermore, such postcranial adaptations as the humeral and tibial torsion or the brachial index may indicate neoteny. Although the detailed interpretation of these characteristics cannot be considered in this review, the Dutch tradition of considering ontogenetic interpretations when reconstructing phylogeny remains vivid.

As I have shown earlier, the general neoteny theory of human evolution seems not to be the correct general approach to exploring our ancestry. Yet for the interpretation of particular problems of paleoanthropology such as the hobbit phenomenon, ontogenetic studies nonetheless represent powerful tools for phylogenetic research.

Conclusions

Alberch (1982) rightly pointed to the importance of developmental constraints in evolutionary processes. It is nevertheless also important to emphasize the highly informative aspects of development (e.g., Britz and Bartsch 2003; Cracraft 2005; Alemseged et al. 2006; Brakefield 2006) – we should appreciate the synergistic effects. Considering paleoanthropology, Dullemeijer (1975, p. 86) predicted that "the fundamental idea can inspire many in their future research if the foetalization theory is reduced to the right proportions, ... It seems to open great perspectives for anthropology." Two years later, Gould (1977) responded to this challenge and inspired a whole generation of biologists.

Most studies overwhelmingly reject a general neoteny phenomenon in human evolution. The conclusion of man's domination by neoteny represents a pithecocentric perspective: a fruitful but wrong hypothesis. Sophisticated techniques, such as geometric morphometrics, and more embryological data indeed improve the quality of the data sets but on the whole often verify traditional contributions. Gould's (1977) brilliant *forte*, however, was primarily to break down the language barrier and to revitalize the topics of ontogeny *and*Phylogeny. *Summa summarum*, I would like to conclude with Dullemeijer's (1975, p. 84) take-home message – not only in the figurative sense – by stating: "*Homo sapiens* has its own face."

Cross-References

- ▶ Fossil Record of Miocene Hominoids
- ▶ Fossil Record of the Primates From the Paleocene to the Oligocene
- ▶ General Principles of Evolutionary Morphology
- ▶ Historical Overview of Paleoanthropological Research
- ▶ Homology: A Philosophical and Biological Perspective
- ▶ *Homo floresiensis*
- ▶ Modeling the Past: The Primatological Approach
- ▶ Potential Hominoid Ancestors for Hominidae
- ▶ Primate Origins and Supraordinal Relationships: Morphological Evidence
- ▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms
- ▶ Species Concepts and Speciation: Facts and Fantasies
- ▶ The Evolution of Speech and Language
- ▶ Virtual Anthropology and Biomechanics

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