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The evolution of hominin ontogenies

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Abstract

Since the beginnings of paleoanthropology, immature fossil hominin specimens have marked important but highly contested cornerstones of research. Long deemed as not representative of a fossil species’ morphology, immature hominins are now in the center of scientific attention, and an increasing interest in evolutionary developmental questions has made developmental paleoanthropology a vibrant field of research. Here we report on recent advances in this field, which result from a combination of new methods to reconstruct fossil ontogenies with insights from evo-devo research on extant species.

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1. Introduction

In 1830, Belgian anatomist Philippe-Charles Schmerling recovered “… human skeletal remains … from the Cave of Engis, … associated with those of elephant, rhinoceros, and carnivore species not known from the actual creation” (cited after [1]). Among these fossil human remains was the cranium of an approximately 4-year-old child. The “Engis child” remained practically unnoticed for more than a century and was identified as a Neanderthal only in 1936 [3]. Dart’s lucid analysis of this fossil, which still represents a masterly combination of comparative developmental morphology with evolutionary thinking, was received with reservation. Taung’s young individual age (3–4 years), the apparently incipient state of development of many characteristic features as well as the lack of a comparative sample made it difficult at that time to recognize the specimen’s significance for paleoanthropology [4].

Today, we are in a more comfortable situation regarding fossil hominins (species more closely related to modern humans than to any other extant species), and particularly regarding immature specimens. Sample sizes have increased, new analytical methods are available, and comparative phenetic and genetic evidence from extant great apes as well as from our closest fossil relative – Homo neanderthalensis – are steadily accumulating. Most importantly, the evolutionary developmental perspective has influenced paleoanthropological thinking in significant ways. This is best represented by a succinct statement made by Lovejoy [5, p. 103]: “Neither
biomechanical nor cladistic analyses can now be properly conducted absent fundamental contextual structuring by modern developmental biology. . . . Issues such as the problem of redundancy in cladistic analyses, the putative role of homology in phylogenetic reconstruction, or the often wholesale adaptationism so prominent in twentieth-century hominin biomechanical analyses can now take their place in history.” This perspective is at the basis of a research direction, which we term here Evolutionary Developmental Paleoanthropology (EDPA). EDPA is best defined by the questions it asks:

- **How** are different taxon-specific morphologies of fossil hominins generated during ontogeny? Addressing how-questions has two aims: the first is to document – on the basis of the available fossil evidence – how fossil hominin species grew and developed from birth to death. The second aim is to use this evidence to infer the developmental mechanisms that generated the observed evolutionary diversity in the hominin clade, and to infer how these mechanisms constrain phenetic diversity. This permits researchers to address issues of pleiotropy, homology and homoplasy – which constantly plague taxonomic and phyletic analyses of fossil hominins – in a more comprehensive way than on a static phenetic basis [5]. Such analyses lead to the definition of ontogenetic traits, which can be treated like classical genetic and/or phenetic traits during phyletic, taxonomic and functional analyses.

- **When**-questions are asked on two different time scales: when during an individual’s lifetime does a given ontogenetic event happen, or a given mode of growth and development deploy? And when during hominin evolution did a specific pattern of ontogeny arise for the first time?

- **Why** do taxon-specific ontogenetic traits differ between paleospecies? It has long been recognized that selection not only acts on adults as the final outcome of ontogeny, but on the course of ontogeny itself [6, p. 43sq.]. Hypotheses about the function and adaptive significance of ontogeny are closely related to life history research, which asks how an individual, over its lifespan, allocates time and resources to growth, development, maturation, maintenance, and reproduction, and why the evolution of a given life history profile might have represented an adaptive advantage in a particular environmental context.

In this review, we give an overview of the theoretical and methodological foundations of EDPA, and of the fossil evidence documenting the evolution of hominin ontogeny. We then consider how theory and empiric are combined to find answers to how-, when-, and why-questions.

**2. Basic questions of hominin ontogeny and life history**

Addressing developmental questions in human evolutionary studies can be traced back to Bolk [7]. Bolk referred to a basic principle of evolutionary developmental biology, which is still valid today: natural selection never acts as a creative force generating evolutionary novelty, but only selects from a variety of forms produced by random modifications of developmental programs. Based on this principle, Bolk argued that all characteristic human features are a consequence of ontogenetic retardation, rather than of natural selection and adaptation. Today, we can no longer follow Bolk in exempting humans from natural selection, as ontogenies themselves are subject to selection. However, Bolk’s “fetalization hypothesis” set the stage for all subsequent comparative ontogenetic analyses by providing a long list of human “fetal” and/or “delayed” features. The list includes traits such as a long gestation period, helpless newborns with large brains, late eruption of the molar teeth, a long childhood (the time between weaning and sexual maturity), delayed somatic development, sparse body pelage, late onset of reproduction, a long post-reproductive life phase, and a long lifespan (see Fig. 1). Bolk also set the stage for EDPA by hypothesizing that fossil hominin species might have represented intermediate stages between chimpanzee-like and modern human-like ontogenies, and accordingly, that Neanderthals had a more rapid developmental schedule than modern humans.

The human fetalization hypothesis was restated, expanded, and embedded into an evolutionary context through Stephen Jay Gould’s influential work on Ontogeny and phylogeny [8]. Since then, arguments about hominin phylogeny almost invariably invoke some form of evolutionary shift in modes of ontogeny. Such shifts can be brought about by modification of the temporal characteristics of an ancestral mode of ontogeny (heterochrony) and/or of its spatial characteristics (heteropy). Using modern nomenclature of heterochrony, fetalization corresponds to paedomorphy, meaning that adult forms of a descendant species remain similar to immature forms of the ancestral species. Conversely, peramorphy characterizes species that develop beyond the ancestor’s ontogenetic trajectory endpoint.

**3. Comparative ontogeny of chimps and humans**

As one moves backward in evolutionary and developmental time, the hominin fossil evidence dwindles in a double sense: fossil finds documenting the early phases of ontogeny – during which an individual undergoes its most significant morphological changes – are scarce and fragmentary, and the same is true for fossil finds documenting the early phases of hominin evolution. Accordingly, we start here with a comparison of the best-documented ontogenies, those of ourselves as the only surviving hominin species, and of
our closest living relatives, the chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). Human–chimpanzee comparisons are well suited to identify basic differences between great ape and human ontogenies and thus serve as an important reference to reconstruct and interpret fossil hominin ontogenies. However, this should not lead us to think that evolution followed a straight path leading from chimpanzee-like to human-like ontogenies [9].

Fig. 1 provides a graphical comparison of human and chimpanzee ontogenic schedules. Since humans have larger body masses, and thus slower metabolisms, than chimpanzees, human ontogeny is expected to proceed at a generally slower pace. Here we use a heuristic approach to estimate the slow-down factor: Kleiber’s Law states a negative allometric relationship between body mass (BM) and mass-specific metabolic rates (BMR/BM)\[^{[10]}\],

\[
\text{BMR/BM} = \frac{\text{BM}}{\text{BM}_0 \cdot 0^{.25}}.
\]

expressing the fact that large organisms have lower mass-specific metabolic rates than small organisms. Accordingly, large organisms are less efficient in accumulating body mass than small organisms, so it is sensible to assume a similar scaling law for mass-specific growth rates,

\[
\frac{(\Delta \text{BM})/\Delta t}{(1/\text{BM})} = \text{BM}^{-0.25}.
\]

Upon integration, this yields

\[
T^{-\text{BM}^{0.25}},
\]

where \(T\) can be thought of as the time needed to reach a specific ontogenetic stage (for example, the eruption of the first molar, termination of brain growth, etc.). Using adult female average body masses for humans and chimpanzees, this yields a ratio of

\[
T_{\text{human}} / T_{\text{chimp}} = 56 \text{ kg}^{0.25} / 35 \text{ kg}^{0.25} = 1.12.
\]

Accordingly, differences in body mass are expected to account for a 12% prolongation of human relative to chimpanzee ontogeny, which is indicated in Fig. 1 by the dashed “line of metabolic equivalence” (similar values are found when regressing empirical life history data of anthropoid primates against body mass). Fig. 1 displays three groups of variables, which characterize somatic, dental and cerebral ontogeny, respectively. While several ontogenetic events seem to fall onto that line (e.g. eruption of the incisors and canine), it is obvious that most parameters exhibit significant deviations, indicating that human ontogeny and life history is not a metabolically scaled-up version of chimpanzee ontogeny and life history.

Several important “great ape rules” of ontogeny and life history are broken in humans, and not always toward paedomorphosis [11–15]: first, brain growth is extremely fast during the first few years of life in absolute terms, but slow in terms of when a given percentage of adult brain size is reached. Second, human ontogeny is characterized by late eruption of the molar teeth. Third, human somatic growth is extremely delayed; human neonates are born in a physically helpless state compared to chimpanzees (secondary altriciality; [16]), and somatic growth only “catches up” after brain growth is completed (adolescent growth spurt). Likewise, human sexual development is delayed, and there exists a uniquely human mode of “catching up” the late onset of reproductive life: infants are weaned early, and interbirth intervals are short (Fig. 1). Accordingly, unlike in great apes, modern human mothers resume reproduction long before a weaned infant becomes independent. This life history strategy implies multiple dependent offspring, which is energetically viable only because weaned infants receive alloparental support [17]. Humans are cooperative breeders [18], and for the late phases of human evolution, it is assumed that, during their extended post-reproductive life phase, grandmothers contribute substantially to sustain their grandchildren (grandmother hypothesis; [19,20]).

Fig. 1 also indicates that several ontogenetic and life history events maintain close temporal association in both chimpanzees and humans: the eruption of the first molar coincides (although loosely; [15]) with completion of brain growth, the eruption of the second molar coincides with the adolescent growth spurt, and the eruption of the third molar (the wisdom tooth) coincides with completion of somatic growth and sexual maturity [21].

Overall, the data visualized in Fig. 1 illustrate that no single overarching mechanism of retardation (be it slower rates, later onset, or later offset of ontogenetic processes) can explain the difference between chimpanzee and human ontogenies [22]. Rather, both retardation and acceleration play essential roles. Two major evolutionary developmental mechanisms are discussed in this respect: Neoteny [8] implies that developmental rates compared to sexual maturation rates are slower in a descendant species compared to its ancestor. Conversely, hypermorphosis [23] implies that the descendant species transcends the ontogeny of its ancestor as an effect of delayed sexual maturation.\(^1\)

### 4. Evolution of hominin cranial ontogeny

Is the evolution of hominin cranial ontogeny characterized by neotenic or hypermorphic shifts, or both? To compare ontogenetic trajectories, it is useful to introduce the following technical definitions: the *form* of an organism, a body part, or an organ can be decomposed into *size* (mass, length, volume, etc.) and *shape* (relationships between parts). Growth then denotes change in size over time, *development* denotes change in shape, and *ontogenetic allometry* denotes change in shape as size increases. Fig. 2 provides a visual comparison of cranial ontogeny in humans, fossil hominins, chimpanzees and bonobos. All specimens are drawn to the same scale, such that differences in cranial growth can readily be recognized. Cranial shape (y-axis of Fig. 2) is measured as the proportion between viscerocranial (facial) and neurocranial (braincase) size. This variable provides a means to recognize differences in developmental trajectories. Fig. 2 bears evidence of both neoteny and hypermorphosis in the hominin lineage: Cranial *shape* of adult modern humans and Neanderthals is similar to that of infant chimps, bonobos and australopiths (neoteny).

Conversely, neurocranial *size* of newborn modern humans and Neanderthals is similar to that of adult chimps, bonobos, and *Sahelanthropus tchadensis* (the earliest hominin found to date; [26]), and it increases after birth to approximately the fourfold of that of an adult chimpanzee (hypermorphosis). Accordingly, the paedomorphic shape of the human cranium (small face, large braincase) results from slow, neotenic cranial development combined with fast, hypermorphous brain growth. This seeming paradox, which elicited considerable controversy [22,23,27–30], is resolved when we avoid direct comparisons between heterochronous apples and oranges: slow *development* (neoteny) and fast growth (hypermorphosis) denote different ontogenetic processes, but they are correlated in the evolution of hominin ontogeny.

The cranial ontogeny of fossil hominins is best documented in the Neanderthals, our closest extinct relatives [31–35]. On genetic, developmental, and phenetic grounds Neanderthals are now gen-

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\(^1\) Concepts of neoteny and hypermorphosis used by different authors are often incommensurate and a source of major misunderstandings [24]. In the cited authors’ own words, definitions are as follows: “Maturation is retarded. size increases, and shape remains in the realm of juvenile ancestors” [8, p. 260], and “What we do is delay the offset of virtually all developmental events (growth phases) so that each phase is longer. This is hypermorphosis…” [25, p. xi].
Fig. 2. Comparative cranial ontogeny. Each species’ ontogenetic trajectory is visualized with a gray arrow. Each specimen’s position along the vertical axis indicates its cranial shape (facial size/braincase size). Extant species and Neanderthals are represented by neonates, infants (before M1 eruption) and adults, earlier hominins by those fossil specimens which best correspond to these ontogenetic stages. The following fossil specimens are visualized: *H. neanderthalensis*: Mezmaiskaya 1 neonate, Roc de Marsal 1 infant, Amud 1 adult; *H. erectus*: Mojokerto infant, KNM-ER3733 adult; *A. africanus*: Taung infant, Sts5 adult; *S. tchadensis*: TM266 adult. Numbers indicate ECV in ccm.

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erally recognized as a paleospecies, *H. neanderthalensis*, and it is thought that they diverged from our last common ancestor (LCA) between 0.5 and 0.7 ma (million years ago) and followed separate evolutionary paths [36,37] (but see [38–40] advocating morphological evidence for admixture between the two species). Using computer-assisted methods to reconstruct the fragmentary, distorted and dispersed remains of immature Neanderthals, it is now possible to follow Neanderthal cranial ontogeny from birth to adulthood [32,41]. Comparing the ontogeny of *H. neanderthalensis* and *H. sapiens* not only provides insights into the developmental foundations of the last speciation event in hominin evolution, but also permits inferences on the ontogeny of our LCA, which is still poorly identified in the fossil record. The current debate in Neanderthal-sapiens evo-devo research is marked by two opposing views: one sees the slow, “modern-style” ontogeny as uniquely human, implying that Neanderthal ontogeny was fast, thus closer to that of our LCA [42,43]. The alternative view sees ontogenetic modernity as the result of a longer evolutionary process [41,44,45]. To test these “human uniqueness” and “deep roots” hypotheses, we need to know when during evolution “modern” ontogenetic traits evolved. Neanderthals as well as modern humans exhibit various autopomorphic (i.e., unique derived) cranial features. For example, modern humans have a small face tucked under a globular braincase, with the chin being the only marked facial prominence [46]. Neanderthals, on the other hand, have a similar-sized but lower, wider and more elongate braincase, tall and projecting faces, and a prominent masticatory system [Fig. 2] [47]. Species-specific morphological differences can be traced back to early ontogenetic stages [31], and analyses using methods of geometric morphometrics show that the species-specific cranial architecture was already present in neonates, and was thus formed during prenatal ontogeny [32,41].
What can we infer about prenatal development in Neanderthals and humans? It is well known that differential activation of depositsory and resorptive bone growth fields plays a major role in bringing about species-specific cranial forms [48,49], so it is sensible to trace back Neanderthal-human differences to evolutionary modification of growth fields. For example, the human chin results from bone resorption in the frontal region of the alveolar process above the chin to accommodate the relatively small human dental arcade [50]. It is thus likely that the chin region of the Neanderthals is receding because the alveolar process overgrows the mandibular corpus [32]. Similar arguments can be applied to explain neurocranial shape differences. The wide but low braincase of Neanderthals probably results from hyper-activation of lateral endocranial resorptive growth fields, and of corresponding exocranial depository growth fields [32,51]. These fields are also present in human crania, but less active, thus giving rise to the narrow but high braincases characteristic for our species.

After birth, Neanderthals and humans essentially follow the same ancestral pattern of cranial growth and development, with the exception that humans are more neotenic [32,34]. In other words, human cranial developmental rates are slightly lower, such that adult human crania are more similar in shape to those of adolescent Neanderthals, while adult Neanderthals have considerably larger faces and, accordingly, more cranial superstructures (browridges and bony crests) than adult humans.

The ontogenetic background of the human–Neanderthal evolutionary split can thus be summarized as follows: species-specific morphologies are brought about during prenatal ontogeny, most probably through differential (heterotopic) activation of bone growth fields, while postnatal ontogeny follows a shared ancestral mode of ontogeny with some heterochronic modification. Does the Neanderthal–human split reflect a general pattern of hominin and great ape speciation through ontogenetic modification? To answer this question, it is necessary to consider a wider range of comparative ontogenetic studies, both within and between species. While there is evidence for shared postnatal patterns of ontogeny among hominins and even chimpanzees [33], other studies reveal divergent postnatal trajectories [52] even among modern human populations [53]. The latter studies are relevant, as they imply that – given sufficiently large population-specific samples, ontogenetic variation cannot be explained in terms of heterochrony alone, but also involves heterotopic modification of developmental trajectories.

Of special relevance to the human–Neanderthal evolutionary developmental split are the ontogenetic foundations of an analogous speciation event, that of chimpanzees and bonobos, which diverged approximately one million years ago [54]. Like in humans and Neanderthals, most of the species-specific differences between chimpanzees and bonobos are already established at birth, and postnatal development mainly differs in terms of heterochronic shifts [55–57]. Bonobos are more paedomorphic than chimpanzees, and likewise, they are smaller [55,58]. However, the paedomorphic aspect of adult bonobos compared to chimpanzees results from different ontogenetic mechanisms than that of humans compared to Neanderthals [58]: the human cranium is paedomorphic mainly because of hypermorphosis of brain development, while the paedomorphic shape of the bonobo cranium results from a combination of neotenic slow-down and truncation of the allometric ontogenetic trajectory. A suite of recent studies reveals additional complexity, providing evidence that postnatal differentiation between the Pan species also involves heterotopic modification of postnatal ontogenies [56,57,59,60]. Overall, thus, speciation in Homo and in Pan occurred along distinct evolutionary-developmental pathways, true to the motto of “evolutionary tinkering” [61].

Investigating the cranial ontogeny of earlier species of the genus Homo is challenging: on the one hand, the taxonomic grouping of specimens into species is constantly under discussion [62]: the earliest species, H. habilis, is often subsumed under the australopithecines (A. habilis), or under H. rudolfensis. Later species, such as H. ergaster, are often comprised under the umbrella of “H. erectus sensu lato”. Moreover, only few immature specimens are sufficiently well preserved to permit inferences on patterns of ontogeny. The most important finds are a somewhat distorted neurocranium comprising upper facial parts of a H. erectus infant from Mojokerto, Java, that died at an age of approximately 1 year (Fig. 2) [63] (but see [64] for an age estimate around 4 years), a virtually complete skeleton of a H. erectus boy from Nariokotome, Tanzania, who reached an age of 8–9 years [65,66], and a partial skeleton of an adolescent H. erectus from Dmanisi, Georgia, aged between 11 and 13 years [67,68]. Australopithecine youth are represented by the iconic A. africanaus infant from Taung, South Africa, with an estimated age at death of 3–4 years [3], and a virtually complete skeleton of a similar-aged A. afarensis infant from Dikika, Ethiopia [69]. The position of the A. africanaus and H. erectus infants and adults in Fig. 2 illustrates that the further back we go in geologic time, the more similarities can be found between inferred hominin ontogenies and those of chimpanzees and bonobos: smaller adult brains are correlated with more extended developmental trajectories, producing relatively larger faces. The earliest known hominin, Sahelanthropus [26,70], is only represented by adults, but embedding the one well-preserved cranium (Fig. 2) into a comparative analysis of great ape and human ontogenetic allometries indicates that its postnatal cranial ontogenetic trajectory likely was similar to that of chimpanzees [71].

It remains to be examined how the evolution of bipedalism, which clearly predated the evolution of large brains, constrained the evolution of hominin cranial ontogeny. Since the beginnings of the hominins, several cranial architectural features are clearly linked to upright posture: the facial skeleton is hafted to the neurocranium in a more vertical orientation than in quadrupedal apes, and the foramen magnum (the opening for the spinal cord) assumes a more basal position. Furthermore, the cranial base of hominins tends to be more flexed and anteroposteriorly shorter than in the great apes. When during hominin ontogeny do these features appear? In humans and Neanderthals, neurocranial-to-facial reorientation is already present at birth, and the aforementioned comparative study of ontogenetic allometries [71] suggests that this was already the case in the earliest hominins.

5. Evolution of brain ontogeny

What kind of information can be inferred from hominin fossils regarding brain ontogeny, and which principal limitations arise from the fact that we cannot directly observe fossil brains? The prime source of information here is the internal morphology of the braincase, the so-called endocranium. The volume of the braincase (endocranial volume, ECV) is an often-used proxy of brain size. On the other hand, changes in endocranial shape, both along ontogenetic and phylogenetic trajectories, are difficult to interpret; the inner surface of the braincase is only loosely correlated with the outer surface of the brain [72], and correlations between external brain morphology and brain function are even more loose [73,74]. For example, recent clinical studies show that modern human brain growth ceases around an age of 6–8 years [75], but brain development (typically termed “maturation”) continues toward an age of 20 years [76].

Overall, human brain development (i.e., change in shape) appears to be slow, but considering issues of growth and development mentioned earlier, we should not forget that the brain of a 3-year-old human child cognitively outperforms that of an adult chimpanzee in most respects. Hence, although there is general agreement that,
during hominin evolution, larger brains permitted higher cognitive performance, it is difficult to derive information on the evolution of cognitive development from the hominin fossil record. Here, the archaeological record might be more informative, as it represents a form of fossilized cognitive behavior. Unfortunately, however, it remains tacit about the individual age of toolmakers.

As shown in Fig. 3, there are three ways to compare chimpanzee, human, and fossil hominin brain growth trajectories. Fig. 3A graphs brain growth in terms of absolute endocranial volumes. Note that ECV of a modern human neonate (400 ccm) [77] is in the same range as that of adult chimpanzees (330–450 ccm, median value: 360 ccm) [78,79] and S. schaafensis (360–370 ccm) [70], while modern human adult ECVs range between 1150 and 1650 ccm [80]. Fig. 3B graphs brain growth as a percentage of neonate brain size. This graph shows that humans maintain high fetal-like brain growth rates well beyond birth, while growth rates drop quickly after birth in chimpanzees [81]. As an effect, human adult brains reach the 3.3-fold of neonate brain mass, while chimpanzee brains only reach the 2.5-fold. Fig. 3C graphs brain growth from the adult perspective. While chimpanzee brains have reached 40% of their adult size at birth, human brains have reached only 29%. As a consequence of the lower human ECV percentage at birth, human postnatal brain growth appears to be “delayed” during the first two years of life.

A comparison of modern human and Neanderthal trajectories shows that both species started from similar neonate ECVs (400 ccm; Fig. 3A) [41]. Neanderthal early postnatal brain growth rates were higher than in modern humans (Fig. 3A and B), but Neanderthals had to attain slightly larger average adult ECVs (Fig. 3A) [41,82], such that the time course of reaching adult brain size was similar as in modern humans (Fig. 3C). Taking into account that ECVs of late Pleistocene modern humans were in the range of contemporaneous Neanderthals (1500 ccm; [80]), we may conclude that the fossil evidence does not show significant differences in brain growth between these species. This permits several evolutionary inferences: most probably, the observed mode of brain growth – large neonate brains and high, sustained growth rates after birth – was already present in the LCA of humans and Neanderthals, i.e., at least 500,000 years ago.

When during evolution did this pattern of brain growth arise? Data on H. erectus are sparse. The Mojokerto infant’s neurocranium is fairly well preserved, but since its face is missing, its age at death is difficult to assess. A recent CT-based analysis of neurocranial ossification patterns inferred an age at death of 1 year (but see [64]), and an ECV of 663 ccm [63], thus placing Mojokerto at the lower end of modern human variation in brain growth trajectories (Fig. 3A). Using a graph similar to that of Fig. 3C, Coqueugniot et al. [63] concluded that brain growth in H. erectus was more similar to chimpanzees than to humans, and that rapid brain development left no time for modern human-like cognitive development during childhood. How reliable are these inferences? Cognitive development is difficult to correlate with early brain growth [83–86], so inferences regarding this point remain speculative. Furthermore, the position of the Mojokerto individual in Fig. 3C is in the region of overlap (±1 standard deviation) of human and chimpanzee trajectories, such that attribution of H. erectus to either trajectory remains ambiguous.

Can we express Mojokerto’s brain growth as a percentage of neonate ECV? A recent study relating maternal (adult) to neonate brain size provides a new perspective on this issue [79]. In anthropoid primates including humans, neonate brain mass scales allometrically with adult brain mass. The allometric exponent of 0.76 implies that, with increasing adult brain size, a smaller proportion of brain growth occurs before than after birth (40%/60% in chimps, 28%/72% in modern humans). Estimates for H. erectus yield 35%/65%, and an ECV at birth of 270–320 ccm. Using these estimates to place Mojokerto in Fig. 3B suggests that early brain growth rates in H. erectus were fast and modern human/Neanderthal-like, but it appears that these rates were sustained for only a short time, more like in chimpanzees. Similar estimates can be made for the australopithecines, and it is not surprising that infants of these small-brained mid-Pliocene hominins fall onto chimpanzee brain
growth trajectories. The early Pliocene hominins for which reliable adult ECV estimates are available, S. tchadensis (ECV 300–350 ccm [87]; ca. 4.5 ma), corroborate the hypothesis that high and sustained postnatal brain growth rates appeared relatively late during hominin evolution. As shown in Figs. 2 and 3, the dominant evolutionary pattern displayed by the Pleistocene hominin fossil record is an increase in neurocranial size [88] accompanied by a decrease in facial size. However, brain size evolution does not always follow the “bigger-is-better” pattern. Early H. sapiens had an average adult ECV of around 1500 ccm, which decreased to 1350 ccm over the past 50,000 years [80,89]. While most of this reduction is an effect of body size reduction, it may be speculated that smaller adult brains might have conferred a selective advantage, as they incur less energetic costs during growth.

Brain size reduction in the hominin lineage is most conspicuous in the enigmatic H. floresiensis, with an ECV of approximately 300–350 ccm [87]; ca. 1 m3). Whether this small-statured hominin (ca. 1 m) represents an offshoot of early Homo (cf. erectus?), or a pathological modern human population is still a matter of debate [92–96]. In any case, H. floresiensis has spurred a general interest in the evolutionary significance of genes associated with disorders of growth and development of the brain and the organism as a whole [97,98].

6. Evolution of dental ontogeny

Among primates the eruption of molar teeth is associated with key events of life history, such as cessation of brain growth (M1), adolescent growth spurt (M2), and onset of reproduction (M3) [21]. In accordance with the slow life history of humans, molar eruption is delayed compared to chimpanzees (Fig. 1), such that the eruption sequence has shifted from M1-I1-I2-M2-(P3,P4)-C3-M3 (apes) to M1-I1-I2-(P3,P4)-M2-M3 (genus Homo). When during hominin evolution did the transition from a great ape-like to a modern human-like sequence of dental eruption arise, what was the actual timing of eruption, and what can we infer from these data about the evolution of life history in fossil hominins? To answer these questions, we need to reconstruct tooth formation and eruption schedules in immature fossil specimens, and to estimate their ages at death. Over the past few years, important progress has been made in tackling these issues [99].

Dental hard tissues (the enamel of the crown and the dentin of the root) are formed through incremental growth, such that teeth keep a record of circadian enamel and dentine deposition patterns. Incremental growth structures are often well preserved in fossil teeth and permit detailed comparative analyses of dental development has been reported for the specimens from Gran Dolina [111], which are dated to ca. 0.8 ma, but it is unclear whether this mode implied a modern human-like (i.e., slow) timing of dental eruption [112].

Differences in dental development become more evident when we move back in evolutionary time to H. erectus, specifically to the Nariokotome boy. Based on modern human dentoskeletal developmental standards, an age at death of 11–12 years was originally suggested [65], but a detailed study of dental incremental growth patterns [112] shows that this individual died at an age of approximately 8 years. Overall, the picture emerges that dental development in H. erectus followed a chimpanzee-like (i.e., slow) sequence of dental development has been reported for the specimens from Gran Dolina [111], which are dated to ca. 0.8 ma, but it is unclear whether this mode implied a modern human-like (i.e., slow) timing of dental eruption [112].

Australopiths show us the inherent dangers of using the human-chimp polarity as a guide to assess the evolution of ontogenies. CT-based analysis of the A. africenus infant from Taung showed that the sequence of dental maturation in this individual was similar to that of chimpanzees [101]. In Paranthropus boisei [113], however, the dental eruption sequence was similar to that of modern humans, while dental root formation was similar to chimpanzees, and molar crown formation uniquely fast. Obviously, the human-like eruption sequence in P. boisei does not imply a human-like life
history. It remains to be clarified whether this ontogenetic trait is related to unique dietary or life history adaptations, or whether it results from developmental constraints imposed by a relatively vertical, orthognathic face [114].

Finally, recent data from A. ramidus indicate that the transition from a great ape-like to a modern human-like sequence of dental eruption (canines appear earlier in the sequence) was under way, suggesting that male canine prominence was no longer used as a functional signal in intrasexual competition [115].

7. Evolution of hominin somatic ontogeny

Modern human somatic ontogeny is clearly retarded relative to that of chimpanzees (Figs. 1 and 4): while humans are born with big brains and correspondingly large bodies [81], in terms of musculoskeletal maturation, human are less advanced at birth than chimpanzees and comparatively helpless. This condition was coined “secondary altriciality” to mark its derived state relative to the more precocial (i.e., independent) neonates of great apes [16]. After birth, humans remain on the slow lane of somatic ontogeny: ossification is delayed in almost all skeletal elements [116], and growth is slow until adolescence. As mentioned, deferring the costs of somatic growth to an intense adolescent growth spurt has important consequences for the human lifetime energy budget. It permits short interbirth intervals and multiple dependent offspring, but also allocation of energy to brain growth during early phases of life [18].

When and how did the characteristic human pattern evolve? As for cranial and dental ontogeny, ideas diverge about whether the human pattern is unique, i.e., represents evolutionary novelty, or whether it represents a gradual evolutionary departure from the chimpanzee trajectory, scaled up both in time and space [29].

How did somatic growth proceed in the Neanderthals compared to modern humans? Neanderthals exhibited several characteristic traits of the postcranial skeleton, which are typically seen as adaptations to arctic conditions [119], such as a relatively short tibial to femoral length, more curved long bone shafts, and general skeletal robusticity. These features are already present in newborn Neanderthal skeletons [2,41]. Taking into account these prenatal differences between species, pre-adolescent postnatal growth trajectories were similar to those of modern humans [120]. Did Neanderthals experience a late, intense growth spurt, like modern humans? In the only well-preserved adolescent Neanderthal (Le Moustier 1), the long bone epiphyses were still open; accordingly, growth was not yet completed. Applying modern human developmental standards, this individual had an age at death between 10.5 years (based on limb bone dimensions) and 13 years (based on dental development) [121], which would position it at the mid-to-low end of the range of the modern human somatic growth trajectory (Fig. 4A). Neanderthals were of comparable adult body size as their contemporary modern humans [119,122], such that an adolescent growth spurt was likely in this species.

Stature estimates for the Nariokotome boy at death vary between 147 and 159 cm [123] (corresponding to a body mass of ∼43–48 kg); this wide range indicates uncertainties of estimating body size of H. erectus on the basis of modern human comparative data. In any case, the Nariokotome boy would have been outside the 95%-range of size variation of 8-year-old modern human boys (Fig. 4A) [124]. Given these estimates, it is important to ask whether H. erectus already exhibited a modern human-like adolescent growth spurt, which would have led to the adult size of approximately 180 cm [65,123]. Like in the discourse of brain growth trajectories, the interpretation of somatic growth trajectories of fossil hominins critically depends on individual age estimates, and on estimates of adult average body size. Here, the situation is complicated through a possible latitudinal trend in H. erectus adult body size: estimates range between 160 and 180 cm for Africa, between 150 cm (China) and 160 cm (Indonesia) for Eastern Asia, and between 145 and 166 cm for Western Asia (Dmanisi) [68,123]. A well-preserved subadult H. erectus individual from Dmanisi, Georgia, which was clearly older than the Nariokotome boy at death, had an estimated stature in the same range (145–161 cm) [68]. This individual falls above the modern human average growth curve, but well within the 95%-range of variation (Fig. 4A). Together, these data can be interpreted in two ways: as evidence of absence of a modern human-like somatic growth spurt, or alternatively, as evidence of an early somatic growth spurt that was completed before the age of 10 years, as in chimpanzees [117]. Support for the latter hypothesis comes from a comparative analysis of size-independent morphological markers of femoral maturation [125], which reports features in Nariokotome that are characteristic of modern humans after the growth spurt. In any case, the current evidence indicates that H. erectus had a somatic growth trajectory more similar to chimpanzees than to modern...
humans [18,66], but that he nevertheless attained body sizes in the range of modern humans.

Overall, the evolution of delayed development (in terms of ossification) and slow growth (in terms of stature and body mass) in the hominin postcranial skeleton offers an intriguing perspective on hominin ecophysiology: while the human skeleton is typically seen as adapted to walking and endurance running [126], we must be aware that this is true for adults, but not for children: the evolution of hominin ontogeny and life history thus leads to a significant divergence between comparatively immobile young depending on parental orallopaternal support, and highly mobile post-adolescents and adults. This dichotomy raises questions regarding the evolution of social organization and cooperation within hominin groups [18].

Another aspect of somatic ontogeny concerns the evolution of bipedal locomotion. Fossil evidence suggests a rapid shift toward some form of terrestrial bipedalism very early during hominin evolution [70,127–131], and the pervasive “bipedal” organization of the skeleton of Pliocene hominins, including that of juveniles such as Taung, points toward substantial modification of early modes of ontogeny. Wild-living modern great apes exhibit arboreal and terrestrial modes of mostly hand-assisted bipedal locomotion [132,133], indicating that some form of bipedalism belonged to the basic behavioral repertoire of hominoids. Also, bipedal locomotion in African great apes occurs at higher frequencies in immature than in adult individuals [132], giving some retrospective weight to Bolk’s inclusion of bipedalism in his list of “fetal” human features. Within this context, two major evolutionary scenarios are currently discussed: one proposes that hominin bipedalism evolved via terrestrial knuckle-walking as seen in chimpanzees and gorillas [134,135], the other posits that it derived from the generalized great-ape arboreal locomotor repertoire [136] or, more specifically, from hand-assisted arboreal bipedalism as seen in orangutans [133]. Both scenarios imply substantial evolutionary modification of the ontogeny of hand and foot bones. Most notably, it is hypothesized that various features of the wrist, such as the early fusion of the scaphoid and centrale, are functionally relevant for knuckle-walkers, as they stabilize the wrist by limiting extension movements [134,135]. Accordingly, the first scenario predicts shared derived patterns of wrist ontogeny in gorillas and chimpanzees, while the second scenario predicts primitive ontogenetic patterns within a wider taxonomic scope. A recent ontogenetic analysis of wrist development in anthropoid primates provides strong evidence for the latter scenario [137]. Moreover, it indicates that modes of wrist ontogeny tend to be more informative of phylogeny than of function.

A recent series of papers dedicated to the reconstruction and comparative analysis of the A. ramidus skeleton adds significantly to our understanding of the evolution and development of early hominin postcranial morphology [9]. It appears that Ardipithecus was a facultative biped, exhibiting no evidence for knuckle-walking adaptations [131]. This essentially corroborates the hypothesis that hominin bipedalism evolved from an arboreal locomotor repertoire, and it indicates that, despite close phyletic links between hominins and chimpanzees, the evolutionary history of these groups followed highly divergent developmental, morphological and functional paths, probably brought about by minor shifts in regulatory developmental genes [131]. It is interesting to note that, following this line of thought, the Ardipithecus studies make consistent use of an evolutionary developmental approach to interpret fossil hominin morphology. Evolutionary hypotheses are stated in terms of selective pressures acting on developmental rather than functional modules, thus linking questions regarding the adaptive significance of a feature to questions of how developmental programs had to be modified during evolution to generate this feature [9].

In Section 4, we asked how the evolution of bipedal locomotion might have constrained the evolution of brain ontogeny. In fact, the fourfold increase in brain size over the past seven million years of hominin evolution led to an obstetric dilemma [138]: large adult brains imply large neonate brains [79], but efficient bipedalism implies narrow pelvies [139]. Intrauterine brain growth thus has an upper evolutionary limit imposed by female pelvic dimensions. Compared to the spacious pelvises of early Homo [140], the modern human pelvic outlet is transversally narrow, but elongate in anteroposterior direction, such that the neonate head has to perform a quarter-turn from a transverse into a posteroanterior orientation during birth [141]. When did this mode of birth evolve? The only available female Neanderthal pelvis, that from Tabun, Israel, is only partially preserved, but two independent computerized reconstructions of its transverse dimensions show that it was comparatively wide [41,142]. However, simulating the Neanderthal birth process with the neonate from Mezmaiskaya (Fig. 2) suggests that a transverse birth passage of the comparatively long Neanderthal fetal head was not possible, and that a modern human-like quarter-turn was required to deliver the baby [41]. In evolutionary terms, it is thus likely that rotational birth was already present in the LCA of humans and Neanderthals, and the recent find of a well-preserved female H. erectus pelvis indicates that neonate brain size already represented a selective constraint on female pelvic shape in this species [140].

8. Fossil ontogenies and molecular evidence

Since the first characterization of Neanderthal mitochondrial DNA by Krings et al. [143], technological innovation has led to major advances in ancient DNA (aDNA) research, such that we are now entering the era of “Neanderthal genomics” [36,37,144]. Neanderthals currently mark the deepest point in hominin evolutionary time, from which genetic information can be recovered with confidence [145]. How can ancient genomics, as well as research into the molecular basis of modern human and chimpanzee ontogenies, foster our understanding of the evolution of fossil hominin ontogenies?

After the complete sequencing of human and chimpanzee genomes, the search for genes that make us “uniquely human” has long defined the agenda of research [146–149] and has provided first insights into the evolution of the molecular basis of key “human” features [149]: brain size [97,98,150–152], facial to neurocranial size [153], and language [154–156]. Interestingly, all of the genes targeted in these studies are involved in the early development of brain and cranial structures, and it is not surprising that establishing links between brain development and brain evolution has become a major research topic [150]. A recent analysis comparing expression patterns in a large array of genes (transcriptome analysis) in the brains of young humans, chimpanzees and macaques draws a complex picture [157]: while a large number of genes displays transcriptional neoteny in humans, a smaller but still important fraction displays neoteny in chimpanzee brains. Additional complexity is added by the finding that the FOX2 “language gene” variant, which was originally thought to be a hallmark of modern human speech evolution, is also present in the Neanderthals [158].

What can we expect in this area of research in the coming decade? One direction of future research has been marked by directly testing the function of Neanderthal genes. This was already done for a gene involved in the formation of skin and hair pigmentation [159]. Another direction of research will consist in identifying the structure and function of key developmental genes in humans, chimpanzees, and possibly Neanderthals, followed by an attempt to reconstruct their structure and function in the LCA of humans.
and Neanderthals, and of humans and chimpanzees. Ultimately, this information could be used to infer differences in ontogenetic programs between long-gone fossil hominin species.

9. Conclusions and outlook

What are the future prospects and challenges of EDPA? Progress and innovation in this field depends on various factors. First of all, the empirical evidence documenting fossil hominin ontogenies needs to be broadened. New hominin-bearing sites often contain an appreciable percentage of immature remains, but the influx of new fossil prime data is not predictable and depends on the contingencies associated with field research. Nevertheless, the presently available sample of immature fossil specimens, as portrayed in this review, still contains hidden ontogenetic information, the retrieval of which will require refined analytical tools at the microstructural level, such as histological analysis, synchrotron tomography, and others. Most likely, analytical techniques from materials sciences currently not associated with paleoanthropology will also contribute to advancement of the field. This enhanced analytical tool kit may also be used to retrieve ontogenetic information contained in adult fossil specimens, such as patterns of bone growth and remodeling.

While gaps in our knowledge about fossil hominin ontogenies are being filled at a slow pace, non-invasive methods of biomedical imaging (e.g., magnetic resonance imaging, MRI) provide ideal tools to rapidly expand our comparative knowledge of the developmental morphology of humans, great apes, and other primates. It is interesting to realize that, at present, more clinical data are available on individual human ontogenetic disorders than on normal human ontogenetic change. Accordingly, “4D-anatomy” needs to be advanced, which investigates spatiotemporal patterns of ontogenetic change in humans as well as in non-human primates. The resulting phenetic data then need to be linked to comparative genomic data in order to gain insights into how mutations, developmental modifications and speciation events are linked to each other.

Because the hominin fossil record is fragmentary, and because actual processes of growth and development do not fossilize, the core task of EDPA will always be to integrate the available fossil ontogenetic “raw data” into the more complete comparative framework of actualistic data on human and primate (notably great ape) ontogenies. Like in any other evo-devo research field, the major challenge here is to combine detailed analyses at various levels of organismic scale with integrative analyses across hierarchies. Research in EDPA thus will always consist of a complex interplay of data collection, model studies, hypothesis testing, and educated guess.

At present, the results of such integrative analyses convey a complex message. While hominin evolution shows a general trend toward paedomorphic forms, especially through neoteny, each species displays its own mode of ontogeny, and within species, different organ systems display their own modes of growth and development. Evolutionary tinkering, or modular evolution, also appears to apply to the evolution of hominin ontogeny. Nevertheless, two “rules of thumb” can be formulated: (1) evolutionary modifications of prenatal modes of ontogeny are most decisive for the formation of species-specific traits, and it is unfortunate that direct evidence for these decisive early phases in a fossil hominin’s life are not available. (2) Evolutionary modifications of postnatal ontogeny are most relevant with respect to life history evolution, and they chiefly manifest themselves as heterochronic shifts.

In view of our own species, it appears that “modern human uniqueness” is less likely a result of the evolution of uniquely “modern human” modes of ontogeny and life history, but more likely the result of evolutionary contingency, i.e., the extinction of all hominin species but one.

Acknowledgements

We thank Marcelo Sánchez for inviting us to contribute to this volume. We thank the two reviewers for many valuable comments and suggestions, which greatly helped improve the manuscript.

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