Macroevolution in and Around the Hominin Clade

Bernard Wood and Mark Grabowski

Abstract In this review, we discuss the criteria for recognizing species and genera within the fossil record in general, and within the hominin clade in particular. We review the grade concept, suggest how taxa within the hominin clade can be divided into grades, and define the grade categories. We discuss the difficulties with studying macroevolution in the hominin clade but suggest that at least one trait, brain size, may provide insight into the tempo and mode of evolution. We also review evidence suggesting that stasis is the dominant signal in two early hominin taxa that have substantial and well-dated fossil records. We discuss the role of evolutionary forces in forming macroevolutionary patterns and find that while natural selection appears to be the dominant force, some well-known interspecific and intraspecific differences in hominins may have been the result of random genetic drift. Lastly, we suggest that homoplasy makes generating reliable hypotheses about relationships among early hominins more difficult than most researchers are willing to admit.

Keywords Clade · Grade · Hominin · Macroevolution · Mode · Selection · Tempo

1 Preamble

In his 1944 book *Tempo and mode in evolution,* Simpson uses the criterion of population continuity to distinguish micro- and macroevolution (Simpson 1944). He suggests that microevolution refers to "changes within potentially continuous populations" whose details can be revealed by "genetic experimentation" (ibid, p. 97).

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In contrast, he suggests that macroevolution involves the "rise and divergence of taxonomic groups that are at or near the minimum level of genetic discontinuity (species and genera)" (ibid, p. 98). Simpson (1953) later simplifies this by suggesting that macroevolution involves historical changes "from species upwards," whereas microevolution refers to historical change "within species" (ibid, p. 338).

Simpson credits Goldschmidt with introducing the term macroevolution (Simpson 1944, p. 97), but this is not correct. While it is true that Goldschmidt (1940) uses microevolution and macroevolution as the two major subheadings for his book *The material basis of evolution*, it seems that Dobzhansky (1937) introduced macroevolution into the English language 3 years before Goldschmidt's book was published. Dobzhansky, however, did not coin the term macroevolution. That distinction apparently rests with his teacher, the Russian geneticist, Filipčenko (aka Filipchenko or Philiptchenko) who used the Russian equivalent of macroevolution in 1934 in a text entitled *Genetics of soft wheats*.

Whereas Simpson (1944) had focused on genetic continuity as a criterion to distinguish micro- and macroevolution, Dobzhansky (1937) stressed the importance of temporal distinctions. Specifically, he referred to the differences between longer-term "macroevolutionary changes that require time on a geological scale" and shorter-term "microevolutionary processes" that are observable "within the span of a human lifetime" (ibid, p. 12). Levinton (2001) suggests that macroevolution is the sum of the processes that generate the "character-state transitions that diagnose evolutionary differences of major taxonomic rank" (ibid, p. 2), but Hallam's (1989) "evolution at and above the species level" (ibid, p. 59) is a more typical contemporary definition of macroevolution.

If the species category is used as the definition of what is, or is not, macroevolution, it raises problems for anyone reviewing that topic in the context of human evolution. This is because taxonomic hypotheses about the hominin clade run the gamut from those that recognize relatively few species (e.g., Wolpoff 1994) to those that are much more speciose (e.g., Wood 2010). Irrespective of their strengths and weaknesses, if the species is the rubicon that divides macroevolution from microevolution, then the type of taxonomic hypothesis that is adopted will have profound implications for what is included in a review of macroevolution in the hominin clade. This is because more inclusive interpretations of hominin species (i.e., "lumping" hypotheses) will result in substantial amounts of phenotypic evolution (e.g., an increase in brain size from *c*.600 cm^3 to *c*.>1,300 cm^3) being regarded as intraspecific, and if the definition of macroevolution is "evolution at and above the species level," then these changes would be regarded as microevolutionary and would be *outside* the purview of a review of macroevolution. In contrast, more exclusive interpretations of hominin species (i.e., "splitting" hypotheses) suggest that most phenotypic evolution within the hominin clade took place at the time of speciation, and thus, its discussion would be *within* the bailiwick of a review that focuses on macroevolution.

Thus, instead of using "evolution at and above the species level" as the definition of macroevolution, we follow Dobzhansky (1937), and especially Eldredge (1989), who suggested that macroevolution always connotes "large-scale phenotypic evolutionary change" (ibid, p. vii). We assume the following "broad-brush" distinction that macroevolution is what you can learn about evolution from the fossil record. So with respect to macroevolution in the hominin clade, we interpreted our remit as "what can be learned about human evolution from the hominin fossil record."

In this review, we focus on the hominin clade and consider the following questions. What is its comparative context? What are the criteria for recognizing species and genera within the hominin clade? Can the taxa within the hominin clade be usefully divided into grades, and if so how should they be defined? What evidence is there about the tempo and mode of evolution within the hominin clade? Are morphological trends in the hominin clade the result of selection, or can they be explained by random drift? Lastly, we consider what is known about the relationships among its constituent taxa. Inevitably, there is overlap between these questions, but they provide a structure for the task allotted to us of reviewing macroevolution in the hominin clade. Some of the topics included in the questions set out above have been addressed in our publications, so where appropriate, we point the reader to those publications rather than simply repeating arguments made elsewhere. We do not cite references listed in those publications.

2 Context

Recent attempts to use gross morphological evidence to generate hypotheses about higher primate relationships (e.g., Gibbs et al. 2002; Diogo and Wood 2011) have confirmed the close relationship between modern humans and the African apes suggested just over 150 years ago by Huxley (1863). During the first half of the twentieth century, the focus of the search for evidence about higher primate relationships shifted from evidence about gross morphology to evidence about the morphology of molecules (e.g., Grünbaum 1902; Nuttall et al. 1904). In the 1960s, two molecules, hemoglobin (Zuckerkandl et al. 1960) and albumin (Goodman 1963), were used to investigate the relationships among higher primates, and these studies concluded that chimpanzees were more closely related to modern humans than to gorillas. Sarich and Wilson (1967) came to a similar conclusion, and later, King and Wilson (1975) suggested that 99 % of the amino acid sequences of chimpanzee and modern human proteins were identical.

Initial attempts to compare the DNA of higher primates were crude (e.g., Caccone and Powell 1989); however, sequencing methods rapidly replaced hybridization as the preferred method for generating hypotheses about the relationships among extant hominoid taxa, and the number of sequence-based studies increases year by year (see Bradley 2008; Arnold et al. 2010; Perelman et al. 2011 and Prado-Martinez et al. 2014 for reviews). When DNA differences were calibrated using what was then the best paleontological evidence for the split between apes and Old World monkeys, it was predicted that the hypothetical ancestor of modern humans and chimpanzees/bonobos lived between *c*.8 and *c*.5 million years ago (Ma) (Bradley 2008). However, these predictions are likely to yield different results in light of the recent discovery of the Oligocene catarrhine *Rukwapithecus fleaglei* that may be a basal hominoid (Stevens et al. 2014). Langergraber et al. (2012) used comparative data about generation times and estimates of mutation rates and concluded that the date of the *Pan–Homo* split is probably closer to 8 than to 5 Ma, but the results of a recent analysis of a larger data set (Prado-Martinez et al. 2014) that used different assumptions suggest that it is closer to 5 Ma.

Whole genomes can now be sequenced with acceptable levels of coverage, and in the last few years, researchers have published good-quality draft sequences of the genomes of the chimpanzee (TCSAC 2005), orangutan (Locke et al. 2011), gorilla (Scally et al. 2012), and bonobo. Scally et al. (2012) sampled two western lowland and one eastern lowland gorillas and showed that when considering the entire genome, the greatest number of similarities is between modern humans and chimpanzees, but in 30 % of the genome, gorillas are closer to modern humans and chimpanzees than they are to each other. This phenomenon is known as incomplete lineage sorting (ILS). The Prüfer et al. (2012) study showed that bonobos and common chimpanzees are 99.7 % alike, yet 98.7 % of the bonobo genome resembles that of modern humans. Prüfer et al. (2012) also found evidence of ILS in their study to the extent that *c*.3 % of the modern human genome is more closely related to bonobos or to common chimpanzees than bonobos and common chimpanzees are to each other, and they suggest that 25 % of all genes contain evidence of ILS. That said, a recent comparative study of 79 great ape genomes representing all six species emphasized that the presence of genetically distinct populations within each great ape species (Prado-Martinez et al. 2014) confirms that despite the effects of ILS, chimpanzees and bonobos are more closely related to modern humans than they are to gorillas. Thus, the comparative context of the hominin clade is the one set out in Fig. 1.

3 Criteria for Including Taxa Within the Hominin Clade

The reasons for including the *c*.7 Ma remains assigned to *Sahelanthropus tchadensis* (Brunet et al. 2002; Guy et al. 2005), the *c*.6 Ma remains assigned to *Orrorin tugenensis* (Senut et al. 2001), the *c*.5.8–5.2 Ma remains assigned to *Ardipithecus kaddaba* (Haile-Selassie 2001, 2004), and the *c*.4.5–4.4 Ma remains assigned to *Ardipithecus ramidus* (White et al. 1994, 2009; White 2010) in the hominin clade, differ according to what anatomical regions are represented. However, three common lines of evidence run through the claims for the hominin status of these taxa. The first involves a reduction in size and a change in morphology of the canines, which is linked with the partial or complete loss of upper canine/P_3 honing and reduced canine sexual dimorphism. The second involves the location and orientation of the foramen magnum and inferences about posture and gait. The third involves features of the pelvis and other preserved postcranial elements that imply a dependence on bipedalism. In each case, the assumption is that these character complexes and their inferred behaviors are *only* seen in the hominin clade.

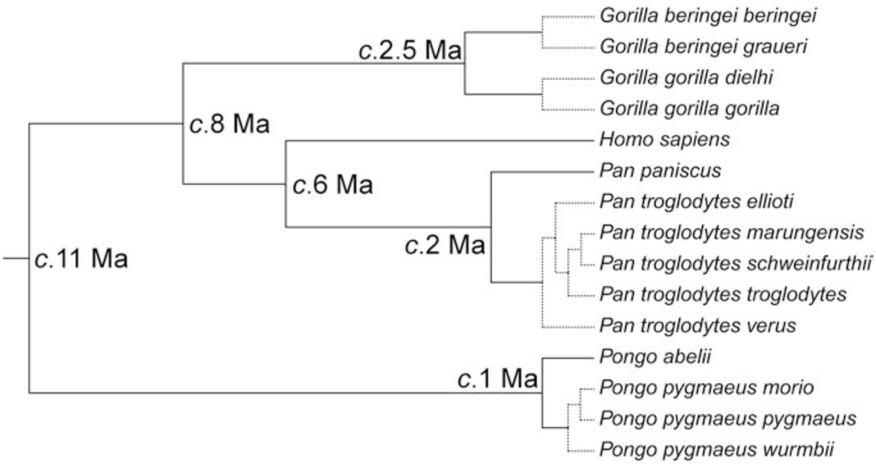

Fig. 1 Current consensus of the phylogenetic relationships and splitting times within the great ape clade. The only Asian great ape, the orangutan (*Pongo*), which is likely to have split off from the African great apes *c*.11 million years, diverged into the Bornean (*Pongo pygmaeus*) and Sumatran (*Pongo abelii*) orangs *c*.1 million years ago. There have been two major and two minor splits in the African ape clade. The first major splitting event, the one leading to gorillas, occurred *c*.8 million years ago. The second, leading to modern humans, occurred *c*.6 million years ago. The split within gorillas, into mountain (*Gorilla beringei*) and lowland (*Gorilla gorilla*), occurred *c*.2.5 million years ago. The split within chimpanzees occurred *c*.2 million years ago when the Congo River divided the ancestral chimpanzee population into bonobos (*Pan paniscus*) to the south and common chimpanzees (*Pan troglodytes*) to the north. The details of the subspecies, along with the timing of any splits, are more conjectural. Figure courtesy of Adam Gordon. Evidence for the phylogenetic relationships within the extant great ape genera is drawn from a variety of sources (*Pan*: Groves 2005; Gonder et al. 2011; *Gorilla*: Groves 2001; Scally et al. 2012; *Pongo*: Brandon-Jones et al. 2004; Singleton et al. 2004; Locke et al. 2011; Prado-Martinez et al. 2014)

The canine morphology that *Ar. ramidus* and *S. tchadensis* share with later hominins is the most convincing evidence to support their hominin status. But it is important to recognize that during the Late Miocene, a number of Eurasian hominids (e.g., *Oreopithecus*, *Ouranopithecus*, and *Gigantopithecus*) also developed smaller canines and a reduction in canine–premolar honing. Presumably, these were parallel responses linked to analogous shifts in dietary behavior and there is no a priori reason to exclude the possibility that a similar behavioral and phenotypic response could have occurred in at least one extinct African hominid clade.

The anteriorly positioned and more horizontal foramen magnum seen in modern humans and later hominins compared to the extant great apes has been assumed to relate to the upright posture and bipedal locomotion of the former. However, comparisons with other primates suggest that these features may also be linked with differences in head carriage and relative brain size rather than uniquely with bipedalism (Strait 2001) and the differences in the position and orientation of the foramen magnum seen in bonobos and chimpanzees, and the overlap between the morphology of bonobos and that of *Sahelanthropus* and *Ardipithecus* suggests that we should exercise caution before assuming that a relatively anteriorly positioned and more horizontal foramen magnum is linked exclusively with the adoption of habitual bipedalism.

The postcranial evidence for bipedalism in *Ardipithecus kadabba* mainly involves the morphology of a proximal pedal phalanx (presumed to belong to *Ar. kadabba,* but from an older geological horizon and with no associated craniodental remains), whereas in *O. tugenensis*, the evidence mainly involves the morphology of the proximal femur. The case for the femur being that of a committed biped is much stronger than the case for the pedal phalanx. The claim that *Ar. ramidus* was a biped is mainly based on highly speculative inferences about the presence of lumbar lordosis and on a few features of the pelvis and foot, but the claims are either based on questionable reconstructions, or they involve characters whose link to habitual bipedalism has yet to be convincingly demonstrated.

Researchers that support hominin status for *S. tchadensis*, *O. tugenensis*, *Ar. kaddaba*, and *Ar. ramidus* do so on the assumption that within the great apes, canine honing and bipedalism are *confined* to the hominin clade. We believe that their assumption is a logical fallacy. For even if all hominins are bipedal and lack canine honing, the converse proposition–that among the great apes bipedalism and the loss of canine honing are confined to the hominin clade–is not a logical corollary.

How strong are the cases for each of the four taxa being hominins? The argument for including *Ar. kaddaba* in the hominin clade at the present time is a particularly weak one. Its teeth are apelike, and because of the sparse fossil record, there is not enough evidence to be sure it is a committed biped. As for *O. tugenensis*, although the external morphology of the proximal femur is consistent with it being bipedal, the evidence from the internal morphology of the femoral neck is equivocal. The morphological evidence that *S. tchadensis* and *Ar. ramidus* should be included in the hominin clade is stronger, but is not compelling for either taxon. In addition, their age is against them being hominins. In the case of *S. tchadensis,* if the more recent splitting *c*.5 Ma times are correct, then if it is *c*.7 Ma it is too early for it to be the stem hominin. In the case of *Ar. ramidus*, if both it and the *c*.4.2 Ma *Australopithecus anamensis* are lineal ancestors of later hominins, as its discoverers claim, then there is simply too little time for the cranial and postcranial morphology of the former to evolve into the latter. Also, if the 3.4 Ma foot with an abducted hallux from the Burtele locality at Woranso-Mille belongs to *Ar. ramidus*, then the "ancestral" scenario is even less likely. Thus, for these reasons, one of us has referred to *S. tchadensis*, *O. tugenensis*, *Ar. kaddaba*, and *Ar. ramidus* as "possible hominins" (e.g., Wood 2010) and this is how we refer to them in this review.

4 Hominin Alpha Taxonomy

The definition of taxonomic categories is a vexed issue. With respect to the species category, Smith (2009) usefully divides contemporary species concepts into *process related* and *pattern related*, with the former emphasizing the processes involved in the generation and maintenance of species, while the latter emphasizes the methods used for recognizing species in the fossil record. The three main concepts in the process category are the biological species concept (BSC), the evolutionary species concept (ESC), and the recognition species concept (RSC). The ESC was an attempt by Simpson (1961) to add a temporal dimension to the BSC; thus, he suggested that under the ESC, a species is "an ancestral-descendant sequence of populations evolving separately from others and with its own evolutionary role and tendencies." Some use the term chronospecies to refer to a segment of the type of evolving lineage implied in the ESC definition of a species. Such segments are considered separate species because the fossil sample across time is deemed to exceed the degree or the pattern of variation that it would be reasonable to find within closely related, living species. The third concept in the process-related category, the recognition species concept, instead of emphasizing reproductive isolation, emphasizes the process that promotes interbreeding. Paterson (1985) refers to this as the "specific mate recognition system" (or SMRS), and as long as a species' SMRS signal fossilizes, the RSC can potentially be applied to the fossil record.

Given the twin impediments of having no direct evidence about interbreeding, and with only fragments of the hard tissue skeleton and the dentition as evidence, how are species recognized in the hominin fossil record? There are two main pattern-based species concepts, the phenetic species concept (PeSC) and the phylogenetic species concept (PySC). The PeSC gives equal weight to all aspects of the phenotype by assembling a matrix of characters and then uses multivariate analysis to detect clusters of individual specimens that share similar phenotypes. The PySC differs from the PeSC by emphasizing only the diagnostic aspects of the phenotype. According to Nixon and Wheeler (1990), a species defined under the PySC is "the smallest aggregation of populations diagnosable by a unique combination of character states."

In practice, most human evolution researchers use a version of the PySC in the sense that they search for the smallest cluster of individual organisms that is "diagnosable" on the basis of the preserved morphology. Because the hominin fossil record consists primarily of craniodental remains, most diagnoses of early hominin taxa inevitably emphasize craniodental morphology. Thus, using this evidence, paleoanthropologists must decide whether a collection of hominin fossils spanning several hundred thousand years consists of several samples of the same taxon, or samples of different taxa. When making these judgments, researchers should strive to neither grossly underestimate, nor extravagantly overestimate, the actual number of species represented in the hominin fossil record.

One of the many factors that paleoanthropologists must take into account in addition to the time represented in their sample is that the fossil record is predominantly confined to remains of hard tissues (i.e., bones and teeth). We know from living animals that many uncontested species are difficult to distinguish using bones and teeth (e.g., *Cercopithecus* species—see Manaster 1979); thus, there are sound, logical reasons to suspect that a hard tissue-bound fossil record is always likely to underestimate the number of species. Furthermore, if a punctuated equilibrium model of evolution is adopted along with a branching or cladogenetic interpretation of the fossil record (see below), then researchers will tend to divide the hominin fossil record into more rather than fewer species. Conversely, researchers who favor a phyletic gradualism model, which implies an anagenetic interpretation of evolution and emphasizes morphological continuity, will tend to resolve the hominin fossil record into fewer, more inclusive, longer-lived species that are more likely to show substantial changes in morphology through time.

Eldredge (1993) made a proposal about how to view the species category that is both intuitive and appealing. He suggested that species, like individuals, have a history. The history of any species begins at the point of speciation when it and its sister taxon (or taxa) arise from a common ancestor and ends when it becomes extinct or becomes the common ancestor of daughter taxa. Eldredge also acknowledges the reality that the morphological characteristics of a living species or of an evolutionary lineage are never uniformly distributed across its range, and like Sewall Wright, Eldredge is prepared to recognize the existence of distinctive local populations or demes. Related demes would share the same SMRS, but Eldredge suggests that their morphological distinctiveness could in some cases justify them being regarded as separate species. He also acknowledges that the same logic could be applied to lineage chronospecies on the basis that the number of cladogenetic events during evolutionary history is more likely to be underestimated than overestimated. Thus, within the fossil record, it may be possible to identify several paleospecies (sensu Cain, 1954) within the equivalent of a neontological BSC/RSC-type species. For many reasons, some of which are set out above, in this review, we use a relatively speciose taxonomic hypothesis (Table 1).

The genus is even more an elusive taxonomic category than the species, but for various reasons, we accept the proposal that a genus should be both a clade and a grade. To qualify as a clade, the prospective genus must consist of all the members of a monophyletic group, no more and no less. But not all of the species in the same grade have to be in the same genus, for a grade may contain species belonging to more than one monophyletic group. We have divided the species we recognize in the hominin fossil record into genera, but because we are generally skeptical about our ability to recognize subclades within the hominin clade, our genus-level distinctions are based more on evidence about grade distinctions (see below) than on hypotheses about relationships.

5 Differences Between Modern Humans and Chimpanzees/Bonobos

The features that set modern humans apart from chimpanzees and bonobos, and which can be tracked using a hard tissue-bound fossil record, are to do with craniodental morphology, axial and postcranial morphology, and life history.

With respect to dental morphology, chimpanzees and bonobos have larger canine and incisor teeth than modern humans, but if the size of the premolar and molar teeth is related to body mass, then the chewing teeth of chimpanzees/bonobos and modern humans are similar in relative size. However, the jaws of a modern human skull are generally, but not in all cases, smaller and lighter than those of chimpanzees and bonobos.

Table 1 The "old" taxonomy below reflects the pre-molecular consensus that chimpanzees and bonobos were more closely related to gorillas than to modern humans

Old
Superfamily Hominoidea (hominoids)
Family Hylobatidae (hylobatids)
Genus *Hylobates*
Family Pongidae (pongids)
Genus *Pongo*
Genus *Gorilla*
Genus *Pan*
Family Hominidae (hominids)
Subfamily Australopithecinae (possible and archaic hominins)
Genus *Ardipithecus*
Genus *Australopithecus*
Genus *Kenyanthropus*
Genus *Orrorin*
Genus *Paranthropus*
Genus *Sahelanthropus*
Subfamily Homininae (hominines)
Genus *Homo*
New
Superfamily Hominoidea (hominoids)
Family Hylobatidae (hylobatids)
Genus *Hylobates*
Family Hominidae (hominids)
Subfamily Ponginae
Genus *Pongo* (pongines)
Subfamily Gorillinae
Genus *Gorilla* (gorillines)
Subfamily Homininae (hominines)
Tribe Panini
Genus *Pan* (panins)
Tribe Hominini (hominins)
Subtribe Australopithecina (possible and archaic hominins)
Genus *Ardipithecus*
***Ardipithecus ramidus* (White et al., 1994) White et al., 1995**
***Ardipithecus kaddaba* HaileSelassie, 2001**
Genus *Australopithecus*
***Australopithecus africanus* Dart, 1925**
***Australopithecus afarensis* Johanson, 1978**
***Australopithecus anamensis* Leakey et al., 1995**
***Australopithecus bahrelghazali* Brunet et al., 1996**
***Australopithecus garhi* Asfaw et al., 1999**
***Australopithecus sediba* Berger et al., 2010**
Genus *Kenyanthropus*

(continued)

Table 1 (continued)

***Kenyanthropus platyops* Leakey et al., 2001**
Genus *Orrorin*
***Orrorin tugenensis* Senut et al., 2001**
Genus *Paranthropus*
***Paranthropus robustus* Broom, 1938**
***Paranthropus boisei* Leakey, 1959; Robinson, 1960**
***Paranthropus aethiopicus* Arambourg, 1968**
Genus *Sahelanthropus*
***Sahelanthropus tchadensis* Brunet et al., 2002**
Subtribe Hominina (hominans)
Genus *Homo*
Homo sapiens Linnaeus, 1745
***Homo neanderthalensis* King, 1864**
***Homo erectus* Dubois, 1893; Weidenreich, 1940**
***Homo heidelbergensis* Schoetensack, 1908**
***Homo habilis* Leakey, Tobias and Napier, 1964**
***Homo rudolfensis* (Alexeev, 1986) sensu Wood, 1992**
***Homo antecessor* Bermúdez de Castro et al., 1997**
***Homo floresiensis* Brown et al., 2004**

In this taxonomy, modern humans, and all of the taxa thought to be more closely related to modern humans than to any other living taxon, are distinguished at the level of the family as the Hominidae. The "new" taxonomic hypothesis set out above is one of several ways that researchers reflect the overwhelming molecular and morphological evidence that modern humans and chimpanzees and bonobos are more closely related to each other than chimpanzees and bonobos are to gorillas. In this taxonomy, modern humans, and all of the taxa thought to be more closely related to modern humans than to any other living taxon, are distinguished at the level of the tribe as the Hominini. Some researchers consider even this level of distinction too much and they prefer to reduce hominins to a subtribe as the Hominina. In this second, "new" taxonomy, we list fossil hominin species under each genus in the order they were established

With respect to the cranium, modern human brains are not just absolutely larger than those of chimpanzees/bonobos, but they are also larger relative to body mass. The modern human cranium has a relatively smaller face, and the cranium is more evenly balanced on the vertebral column. The foramen magnum is close to the middle of the cranial base in modern humans, whereas in common chimpanzees, it is situated more posteriorly, although bonobos have a more anterior foramen magnum than do common chimpanzees.

With regard to the axial skeleton, the chest is differently shaped in modern humans and in chimpanzees/bonobos. The thorax of chimpanzees/bonobos widens toward the base to accommodate their relatively large gut. The thorax of modern humans is uniform in width from top to bottom, and flatter from front to back, with the shoulder blades rotated around to the back so that they lie closer to the vertebral column. With respect to the vertebral column, there is a difference between modern humans and chimpanzees/bonobos in how thoracic and lumbar vertebrae contribute to trunk length. In modern humans, the dominant modal pattern for thoracic and lumbar vertebrae is 12:5, whereas in *P. troglodytes* and

P. paniscus, it is 13:4, with *P. troglodytes* averaging 13.1 thoracic and 3.6 lumbar vertebrae and *P. paniscus* averaging 13.4 thoracic and 3.8 lumbar vertebrae.

Postcranially, the longer and more mobile modern human thumb enables it to meet the tips of the fingers to make a precise "pinch" grip. In addition to the evident differences in the structure of the hand, it is likely that a neurological control component (e.g., motor unit size) accounts for the differences in dexterity between modern humans and chimpanzees/bonobos. Modern human adult locomotion is almost exclusively bipedal and thus contrasts with the predominantly quadrupedal locomotion of chimpanzees and bonobos. These differences are reflected in the morphology of the pelvic girdle and lower back, knee, ankle, and foot and in the disposition of the muscles connecting the lower limb to the pelvis and trunk. The modern human pelvis is arranged so that the body can be held upright with the body mass being supported on the hind limbs alone. The upper limbs of modern humans are relatively shorter than those of chimpanzees and bonobos, whereas the legs of modern humans are relatively longer than those of chimpanzees/bonobos. There are also differences in the foot, with the modern human foot creating a more stable platform than it does in chimpanzees and bonobos.

In addition, there are differences in the rate that the body grows and in the order in which structures appear. Modern humans reach maturity more slowly than do chimpanzees and bonobos, they erupt their teeth in a different order, and in modern humans, the milk, or deciduous, molars wear out before the adult molars have erupted.

6 Reconstructing Hypothetical Common Ancestors

The task of paleoanthropologists is to use the fossil record to try and trace the evolutionary history of the differences reviewed above back into the tree of life. This task is made more difficult because we can be sure that the differences between the earliest hominins and the Late Miocene ancestors of chimpanzees and bonobos are likely to have been more subtle and difficult to discern than the differences between modern humans and chimpanzees/bonobos. Some of the distinctive features of modern humans, such as those linked with obligate bipedalism, can be traced back a long way. Others, such as the relatively diminutive jaws and chewing teeth of modern humans, were acquired more recently and thus cannot be used to tell the difference between early hominins and potential ape ancestors. There is also reasonably sound evidence that at least two early hominin genera, *Australopithecus* and *Paranthropus*, had absolutely and relatively larger chewing teeth than did pre-modern *Homo*. Thus, even though absolutely and relatively larger chewing teeth (known as postcanine megadontia) may have been an important derived feature of early hominins, this trait has been reversed in the later stages of human evolution. Presently, we do not have sufficient information about the earliest stages of hominin evolution, or about fossil apes, to tell whether postcanine megadontia is confined to hominins.

So, given all of these caveats, how do we go about telling a *c*.5-6 million years old hominin from an early panin, or from a taxon that belongs to a closely related clade that has no living representative? The presumption based on parsimony is that taxa at the base of the panin clade (stem panins) would show little change from the presumed morphology of the hypothetical common ancestor of chimpanzees/bonobos and modern humans. Thus, they would have had projecting faces, jaws with relatively small chewing teeth, large, sexually dimorphic, honed canine teeth, and a locomotor system adapted for arboreal quadrupedalism. In contrast, taxa at the base of the hominin clade (stem hominins) would have been distinguished by cranial and other skeletal adaptations to a predominantly upright posture, and skeletal and other adaptations for a locomotor strategy that includes substantial bouts of bipedalism. These features would be combined with a masticatory apparatus that combines relatively large chewing teeth and modest-sized canines.

7 The Case for Grades Within the Hominin Clade

The reconstructions of the hypothetical common ancestors set out above are all working hypotheses that need to be reviewed and tested as appropriate evidence is uncovered and new methods for reconstructing ancestral states are developed. In the meantime, can we detect any trends in cranial, dental, and postcranial morphology that allow the extinct hominin taxa to be sorted into informal groupings that reflect their adaptation? In other words, can we sort them into grades?

Taxa, including extinct hominins, are put in the same grade if they share morphology that suggests they eat the same sorts of foods and share the same posture and mode of locomotion; no store is set by how they came by those behaviors. The judgment about how different two diets or two locomotor strategies have to be before the taxa being scrutinized are considered to belong to different grades is a subjective one, but until we can be sure we have access to ways of generating reliable hypotheses about the relationships among hominin taxa (i.e., about the nature of the subclades within the hominin clade), the grade concept helps sort taxa into broad functional categories. We use five grades in this review, "anatomically modern *Homo*" (the grade that includes modern humans), "pre-modern *Homo*," "transitional hominins," "archaic hominins," and "megadont and hyper-megadont archaic hominins" (Fig. 2). In the following sections, we describe each grade in terms of its characteristic regional morphology (e.g., brain volume, tooth morphology, limb proportions, and postcranial morphology). Within each grade, we describe the species in the historical order the taxa were recognized, not according to their estimated first appearance datum.

7.1 Anatomically Modern Homo

This grade includes hominin fossil evidence that is not significantly different from the morphology found in at least one regional population of modern humans. Presently, the earliest evidence of anatomically modern human

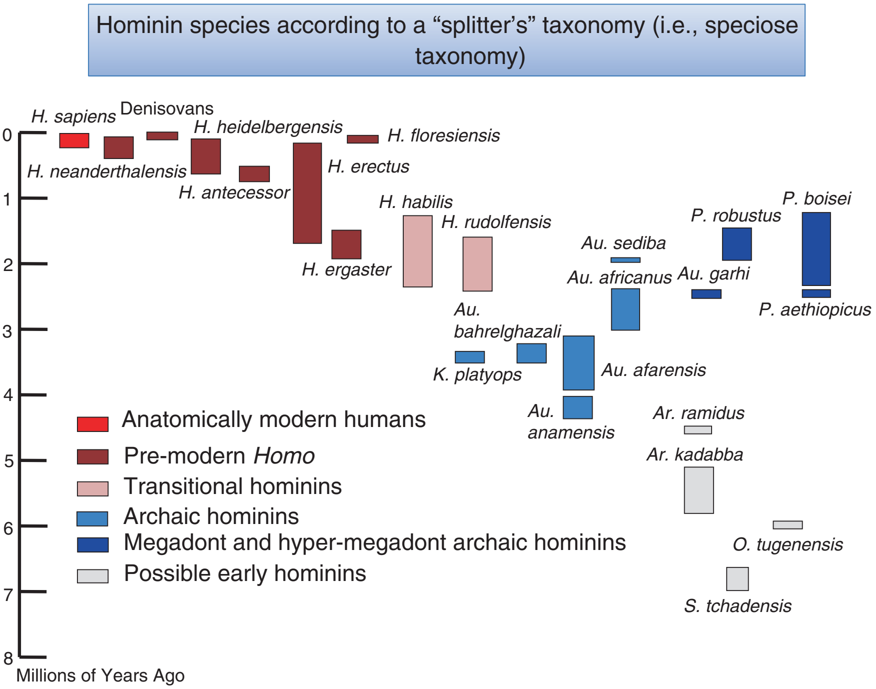

Fig. 2 Taxa recognized in a speciose hominin taxonomy sorted into six grades. In the case of taxa where there are well-dated horizons at several sites, the height of the column reflects current evidence about the earliest and the most recent fossil evidence of that taxon. For taxa known from a well-dated horizon at a single site, the height of the column reflects the age of that horizon. For some taxa, the height of the column is a reflection of uncertainty about the age of that taxon. The height of the column for the Denisovans reflects the age of the only known fossil evidence

morphology in the fossil record comes from Omo Kibish in Ethiopia. Elsewhere in Africa, there is evidence of crania (e.g., Jebel Irhoud from North Africa, Laetoli 18 from East Africa, and Florisbad and the Cave of Hearths from southern Africa) that are generally more robust and archaic looking than those of anatomically modern humans, yet they are not archaic or derived enough to justify being allocated to *Homo heidelbergensis* or to *Homo neanderthalensis*. The gradual and incremental nature of the morphological change between *Homo heidelbergensis* and anatomically modern humans makes setting the boundary between these two taxa challenging, but variation in the later *Homo* fossil record is too great to be accommodated in a single taxon (Mounier et al. 2009). Researchers who make a distinction between subrecent and living modern humans and fossils such as Florisbad and Laetoli 18 do so by formally by referring the latter specimens to a separate species, *Homo helmei* Dreyer, 1935, or informally by referring to them as "archaic *Homo sapiens*."

7.2 Pre-Modern *Homo*

This very broad grade grouping includes Pleistocene *Homo* taxa that lack the distinctive size and shape of the modern human cranium and the gracility of the modern human postcranial skeleton, but all of the included taxa have postcranial morphology that is consistent with obligate bipedalism. The teeth are generally larger and the jaws more robust than those of anatomically modern *Homo*. What makes this a particularly broad grouping is the wide range of absolute brain size (*c*.600–*c*.>1,300 cm^3).

The first fossil taxon to be recognized in the pre-modern *Homo* grade is *Homo neanderthalensis* King 1864, whose temporal range is *c*.200–28 ka (but if the Sima de los Huesos material is included, then it is *c*.>400–28 ka). The type specimen, the Neanderthal 1 skeleton, was found in 1856 at the Kleine Feldhofer Grotte in Elberfeld, Germany, and fossil evidence for *H. neanderthalensis* has since been found in Europe as well as in the Near East, the Levant and Western and Central Asia. The distinctive features of the cranium of *H. neanderthalensis* include thick, double-arched brow ridges, a face that projects anteriorly in the midline, a large nose, laterally projecting and rounded parietal bones, and a rounded, posteriorly projecting occipital bone. Mandibular and dental features include a retromolar space, distinctively high incidences of some non-metrical mandibular and dental traits, and thinner tooth enamel than in modern humans. The average endocranial volume of *H. neanderthalensis* is larger than that of living modern humans. Postcranially, *H. neanderthalensis* individuals were stout with a broad rib cage, a long clavicle, a wide pelvis, and limb bones that are generally robust, with large joint surface areas. The distal extremities tend to be short compared to most modern *Homo sapiens*, and the generally well-marked muscle attachments and robust long bone shafts point to a strenuous lifestyle. Some researchers restrict the *H. neanderthalensis* hypodigm to fossils from Europe and the Near East that used to be referred to as “Classic” Neanderthals, but others interpret the taxon more inclusively and include fossil evidence that is generally older and less distinctive (e.g., Steinheim, Swanscombe and from the Sima de los Huesos). The first DNA recovered from a fossil hominin was from the type specimen of *H. neanderthalensis*.

The next fossil hominin taxon in the pre-modern *Homo* grade to be discovered was *Homo erectus* (Dubois 1893) Weidenreich 1940. Its temporal range is *c*.1.8 Ma–*c*.30 ka. The initial discovery at Kedung Brubus was made in 1890, but the type specimen was recovered in 1891 from Trinil. *Homo erectus* is known from sites in Indonesia (e.g., Trinil, Sangiran, Sambungmachan), China (e.g., Zhoukoudian, Lantian), Africa (e.g., Olduvai Gorge, Melka-Kunturé), and possibly the Caucasus (Dmanisi). The fossil record of *H. erectus* is dominated by cranial remains, and while there is some postcranial evidence (mainly femora), there are very few hand and foot fossils. *Homo erectus* crania have a low vault, a continuous supraorbital torus, a sharply angulated occipital region, and relatively thick inner and outer tables of the cranial vault. The body of the mandible is more robust than that of *H. sapiens*, it lacks a chin, and the mandibular tooth crowns are generally larger and the roots of the premolars more complex than those of modern humans. The limb proportions of *H. erectus* are similar to those of modern humans, but the shafts of the long bones of the lower limb are flatter (the femur from front to back and the tibia from side to side) relative to those of modern humans. Overall, the cortical bone of *H. erectus* is thicker than that in modern humans. All of the dental and cranial evidence points to a modern humanlike diet for *H. erectus*, and the postcranial elements are consistent with an upright posture and obligate bipedalism. Those who support *Homo ergaster* Groves and Mazák 1975 as a separate species point to features that are more primitive (e.g., mandibular premolar root and crown morphology and, vault and cranial base morphology) than *H. erectus.* However, most researchers are not convinced that there are sufficient consistent differences between the hypodigms of *H. ergaster* and *H. erectus* to justify the former being a separate species.

After *H. erectus*, the next taxon recognized within the pre-modern *Homo* grade was *Homo heidelbergensis* Schoetensack 1908. Although the type specimen, Mauer 1, was an adult mandible found in 1907 in a sand quarry near Heidelberg, Germany, *c*.600–100 ka fossils from sites in Europe (e.g., Petralona), the Near East (e.g., Zuttiyeh), Africa (e.g., Kabwe, Bodo), China (e.g., Dali, Jinniushan, Xujiayao, Yunxian), and possibly India (Hathnora) have been included in *H. heidelbergensis*. What sets this material apart from *H. sapiens* and *H. neanderthalensis* is its cranial morphology and robusticity of the postcranial skeleton. Some *H. heidelbergensis* specimens have endocranial volumes as large as those of modern humans, but they are always more robustly built with a thickened occipital region and a projecting face and with large separate ridges above the orbits. Researchers who see the African part of this hypodigm as distinctive refer it to a separate species, *Homo rhodesiensis*. Researchers who interpret the European component of the *H. heidelbergensis* hypodigm (e.g., Sima de los Huesos) as already showing signs of *H. neanderthalensis* autapomorphies would sink it into the latter taxon.

The taxon *Homo antecessor* Bermúdez de Castro et al. 1997 was introduced for hominins recovered from the Gran Dolina site at Atapuerca, Spain. The researchers who found the remains claim that the combination of a modern humanlike facial morphology with large and relatively primitive tooth crowns and roots is not seen in *H. heidelbergensis*, and they see *H. antecessor* and not *H. heidelbergensis* as the likely recent common ancestor of *H. neanderthalensis* and *H. sapiens*.

The most recent taxon to be added to pre-modern *Homo* is *Homo floresiensis* Brown et al. 2004. It is currently only known from Liang Bua, a cave in Flores. Its published temporal range is *c*.74–17 ka, but it may be closer to 100 ka. The initial discovery and type specimen is LB1, an associated partial adult skeleton, but a second associated skeleton, and close to a hundred separate fossils representing up to 10 individuals have subsequently been recovered. This hominin displays a unique combination of early *Homo*-like cranial and dental morphology, a hitherto unknown suite of pelvic and femoral features, a small brain (*c*.417 cm^3), a small body mass (25–30 kg), and small stature (1 m). When it was first described, researchers interpreted it as *Homo erectus*, or a *Homo erectus*-like taxon that had undergone endemic dwarfing; however, more recently, researchers have suggested that it could be a dwarfed *Homo habilis*-like transitional hominin.

7.3 Transitional Hominins

For the purposes of this review, *H. habilis* and *H. rudolfensis* are retained within *Homo*, but they are treated separately from the pre-modern *Homo* grade. This is because the fossils assigned to these taxa show a mix of morphology, some of which is seen in pre-modern *Homo* and some in archaic hominins.

The taxon *Homo habilis* Leakey, Tobias and Napier 1964 was introduced for fossils recovered from Olduvai Gorge, Tanzania. The rest of the *H. habilis* hypodigm consists of other fossils found at Olduvai Gorge and of fossils from Ethiopia (Omo Shungura and Hadar) and Kenya (Koobi Fora and perhaps Chemeron), and researchers have claimed that there is also evidence of *H. habilis* in southern Africa at Sterkfontein, Swartkrans, and Drimolen. The *H. habilis* hypodigm consists of mostly cranial and dental evidence. The endocranial volume of *H. habilis* ranges from *c*.500 cm^3 to *c*.700 cm^3—but a reassessment of the endocranial volume of OH 7 suggests that it may be closer to 800 cm^3. All *H. habilis* crania are wider at the base than across the vault, but the face is broadest in its upper part. The only postcranial fossils that can be assigned to *H. habilis* with confidence are the postcranial bones associated with the type specimen, OH 7, and the associated skeleton, OH 62: isolated postcranial bones from Olduvai Gorge assigned to *H. habilis* (e.g., OH 10) could also belong to *P. boisei.* If OH 62 is representative of *H. habilis*, the skeletal evidence suggests that its limb proportions and locomotion and carpal bones were archaic hominin-like, and the curvature and well-developed muscle markings on the phalanges of OH 7 indicate that *H. habilis* was capable of powerful grasping. The size of the mandible and postcanine teeth suggests that the diet of *H. habilis* was as mechanically demanding as that of archaic hominins. The inference that *H. habilis* used spoken language is based on links between endocranial morphology and language comprehension and production that are no longer supported by comparative evidence.The temporal range of *H. habilis* would be c.2.4–1.6 Ma.

Some researchers suggest that the transitional hominin grade contains a second taxon, *Homo rudolfensis* (Alexeev, 1986) *sensu* Wood 1992, but not all researchers are convinced that the scale and nature of the variation within early *Homo* justifies the recognition of two taxa. The temporal range of *H. rudolfensis* would be *c*.2.0-1.8 Ma., and members of the proposed hypodigm include the lectotype, the KNM-ER 1470 cranium from Koobi Fora, and other fossils recovered from Koobi Fora (e.g., KNM-ER 1482, 1801, 1590, 3732, 60000, 62000, 62003). Compared to *H. habilis*, the absolute size of the brain case in *H. rudolfensis* is a little greater, and its face is widest in its mid-part, whereas the face of *H. habilis* is widest superiorly, and the dental arcades are differently shaped. Despite the mean absolute size of the *H. rudolfensis* brain (*c*.725 cm^3), when it is related to estimates of body mass based on orbit size, the brain is not substantially larger than that of the archaic hominins. At present, no postcranial remains can be reliably linked with *H. rudolfensis*. As with *H. habilis*, the size of the mandible and postcanine teeth suggests that its diet made similar mechanical demands as that of the archaic hominins.

7.4 Archaic Hominins

This grade includes all the unambiguously hominin taxa not included in *Homo* and *Paranthropus*. All archaic hominins, no matter what their absolute size is, have relatively larger chewing teeth and a more primitive postcranial skeleton than pre-modern *Homo*. They were all likely to be predominantly bipedal, but unlike pre-modern *Homo*, the anatomy of their upper limb suggests that they were still effective and regular climbers. What is known of the life history of archaic hominins suggests that it is more like that of the extant apes than modern humans.

The first taxon to be recognized in this grade was *Australopithecus africanus* Dart 1925. The type specimen, Taung 1, a juvenile skull with a partial natural endocast, was recovered in 1924 from the limeworks at Taung (formerly Taungs), now in South Africa. Most of the other fossil evidence for *Au. africanus* comes from two caves, Sterkfontein and Makapansgat, with other evidence coming from Gladysvale cave. Its temporal range is *c*.3–2.4 Ma. The cranium, mandible, and the dentition are well sampled, but the postcranial skeleton, and particularly the axial skeleton, is less well represented in the fossil record, and many of the fossils that do exist have been crushed and deformed by rocks falling on the bones before they were fully fossilized. The picture that has emerged from morphological and functional analyses suggests that although *Au. africanus* was capable of walking bipedally, it was probably more arboreally adapted (i.e., it was a facultative and not an obligate biped) than other archaic hominin taxa such as *Australopithecus afarensis*. It had relatively large chewing teeth, and apart from the reduced canines, the skull is relatively apelike. Its mean endocranial volume is *c*.460 cm^3. The Sterkfontein evidence suggests that males and females of *Au. africanus* differed substantially in body size, but probably not to the degree they did in *Au. afarensis*.

The taxon *Australopithecus afarensis* Johanson et al. 1978 is only known from East Africa, unless *Australopithecus bahrelghazali* from Chad proves to be a conspecific. The type specimen is an adult mandible, LH 4, recovered in 1974 from Laetoli, Tanzania, but the largest contribution to the *Au. afarensis* hypodigm comes from Hadar in Ethiopia and from other Ethiopian (Belohdelie, Brown Sands, Dikika, Fejej, Maka, White Sands, and Woranso-Mille) and Kenyan (Allia Bay, Koobi Fora, Tabarin and West Turkana) sites. The temporal range of *Au. afarensis* is *c*.3.8–3 Ma (*c*.4 -3 Ma if the presence of *Au. afarensis* is confirmed at Belohdelie and Fejej). The *Au. afarensis* hypodigm includes a well-preserved skull, other skulls, partial and fragmented crania, many lower jaws, sufficient limb bones to be able to estimate stature and body mass, and a specimen, A.L.-288, that preserves just less than half of the skeleton of a small adult female. Most body mass estimates range from *c*.30 to 45 kg, and the endocranial volume of *Au. afarensis* is *c*.400–550 cm^3. It has smaller incisors than those of extant chimps/bonobos, but its premolars and molars are relatively larger. Comparative evidence suggests that the forelimbs of A.L.-288 are substantially longer than those of a modern human of similar stature. The discovery at Laetoli of several trails of fossil footprints provided very graphic direct evidence that at least one contemporary hominin, presumably *Au. afarensis*, but possibly *Kenyanthropus platyops*, was capable of bipedal locomotion, but the Laetoli prints are less modern humanlike than *c*.1.5 Ma footprints from Koobi Fora presumed to be made by a pre-modern *Homo*. The upper limb of *Au. afarensis*, especially the hand and the shoulder girdle, retains morphology that most likely reflects a significant element of climbing. Although a recent study argues that sexual dimorphism in this taxon is relatively poorly developed, most researchers interpret it as showing substantial sexual dimorphism.

The taxon *Au. anamensis* (Leakey et al. 1995) is presently restricted to East Africa. The type specimen, KNM-KP 29281, was recovered in 1994 from Kanapoi, Kenya. Other sites contributing to the hypodigm are Allia Bay, also in Kenya, and the Middle Awash study area, Ethiopia. The temporal range of *Au. anamensis* is *c*.4.2–3.9 Ma. The fossil evidence consists of jaws, teeth, and postcranial elements from the upper and lower limbs. Most of the differences between *Au. anamensis* and *Au. afarensis* relate to details of the dentition. In some respects, the teeth of *Au. anamensis* are more primitive than those of *Au. afarensis* (e.g., the asymmetry of the premolar crowns and the relatively simple crowns of the deciduous first mandibular molars), but in others (e.g., the low cross-sectional profiles and bulging sides of the molar crowns), they show some similarities to *Paranthropus*. The upper limb remains are similar to those of *Au. afarensis*, and a tibia attributed to *Au. anamensis* has features associated with bipedality.

The taxon *Australopithecus bahrelghazali* Brunet et al. 1996 is most likely a regional variant of *Au. afarensis*, but the Chad discovery is significant because it substantially extends the geographical range of early hominins and reminds us that important events in human evolution (e.g., speciation, extinction) may have been taking place well away from the very small (relative to the size of the African continent) percentage of the land surface of Africa that is sampled by the existing early hominin sites.

The penultimate archaic hominin taxon to be recognized is *Kenyanthropus platyops* Leakey et al. 2001. The type specimen, KNM-WT 40000, a *c*.3.5–3.3 Ma relatively complete but distorted cranium, was found in 1999 at Lomekwi, West Turkana, Kenya. The main reasons Meave Leakey and her colleagues did not assign this material to *Au. afarensis* are its reduced subnasal prognathism, anteriorly situated zygomatic root, flat and vertically orientated malar region, relatively small but thick-enameled molars, and the unusually small M^1 compared to the size of the P^4 and M^3. Despite this unique combination of facial and dental morphology, some suggest that the new taxon is not justified because they claim that KNM-WT 40000 is a distorted *Au. afarensis* cranium, but this explanation is not consistent with the shape of the face and the small size of the postcanine teeth.

The most recent archaic hominin taxon to be recognized is *Australopithecus sediba* Berger et al. 2010 which was recovered from Malapa cave in the Blaauwbank Valley in southern Africa. The initial discoveries consisted of two associated skeletons: MH1, a juvenile, was made the holotype and MH2, an adult, the paratype. Although the lower limb of *Au. sediba* is like that of other archaic hominins, Berger et al. (2010) claim that aspects of its cranial (e.g., more globular neurocranium, gracile face), mandibular (e.g., more vertical symphyseal profile, a weak *mentum osseum*), dental (e.g., simple canine crown, small anterior and postcanine tooth crowns), and pelvic morphology (e.g., acetabulocristal buttress, expanded ilium and short ischium) are only shared with early and later *Homo* taxa. But the immaturity of one of the skeletons (MH1) plus many overall similarities to *Au. africanus* suggests that the Malapa hominins may sample *Au. africanus* at a later stage of its evolution than the existing samples from Sterkfontein and Makapansgat. The demonstration that the Malapa sample differs from the Sterkfontein and Makapansgat samples does not exclude the possibility that the three samples were drawn from the same fossil taxon, but the finding that its stable carbon isotope and phytolith signatures are predominantly C_3 does suggest that the diet of the Malapa hominins was not like that of *Au. africanus* (Henry et al. 2012).

7.5 Megadont and Hyper-Megadont Archaic Hominins

This grade includes hominin taxa conventionally included in the genus *Paranthropus*, plus *Australopithecus garhi*. As the term megadont suggests, the criterion for inclusion in this grade is large tooth size, specifically the size of the postcanine dentition. This increase is both in absolute and in relative (e.g., in relation to the anterior dentition and to estimates of body mass) terms. The genus *Paranthropus*, into which *Zinjanthropus* and *Paraustralopithecus* are subsumed, was reintroduced when cladistic analyses suggested that the first three species discussed in this section most likely formed a clade. The postcanine teeth of *Paranthropus robustus* are not much larger than those of *Au. africanus*, but those of the East African taxa in this grade are substantially larger; hence, they are referred to as hyper-megadont. The enamel of all of the taxa in this grade is thick; the enamel of the two *Paranthropus* taxa from East Africa is exceptionally thick.

The taxon *Paranthropus robustus* Broom 1938 was established to accommodate an associated skeleton, TM 1517, recovered in 1938 from the southern African site of Kromdraai B. The other sites that contribute to the *P. robustus* hypodigm, Swartkrans, Gondolin, Drimolen, and Cooper's caves, are all situated in the Blaauwbank Valley near Johannesburg, South Africa. The dentition is well represented in the hypodigm of *P. robustus*, but many of the cranial remains are crushed or distorted and the postcranial skeleton is not well represented. Research at Drimolen was only initiated in 1992, yet already more than 80 hominin specimens (many of them otherwise rare juvenile specimens) have been recovered and it promises to be a rich source of evidence about *P. robustus*. The temporal range of the taxon is *c*.2.0–1.5 Ma. The brain, face, and chewing teeth of *P. robustus* are on average larger than those of *Au. africanus*, yet the incisor teeth are smaller. The morphology of the pelvis and the hip joint is much like that of *Au. africanus*; *Paranthropus robustus* was most likely capable of bipedal walking, but it was probably not an obligate biped. It has been suggested that the thumb of *P. robustus* would have been capable of the type of grip necessary for the manufacture of simple stone tool, but this claim has not been accepted by all researchers.

In 1959, Louis Leakey suggested that a new genus and species, *Zinjanthropus boisei* Leakey, 1959, was needed to accommodate OH 5, a subadult cranium recovered in 1959 from Bed I, Olduvai Gorge, Tanzania. A year later, John Robinson suggested that *Z. boisei* be subsumed into the genus *Paranthropus* as *Paranthropus boisei*, and in 1967, Phillip Tobias suggested that it should be subsumed into *Australopithecus*, as *Australopithecus boisei*; in this review, we refer to it as *Paranthropus boisei* (Leakey, 1959) Robinson, 1960. Additional fossils from Olduvai Gorge were subsequently added to the hypodigm, plus fossil evidence from Peninj, Omo Shungura, Konso, Koobi Fora, Chesowanja, and West Turkana, all of which are in East Africa. The temporal range of the taxon is *c*.2.3–*c*.1.4 Ma. *Paranthropus boisei* has a comprehensive craniodental fossil record, comprising several skulls and well-preserved crania, many mandibles, and isolated teeth. There is evidence of both large- and small-bodied individuals, and the range of the size difference suggests a substantial degree of body size sexual dimorphism, despite the evidence for modest canine sexual dimorphism. *Paranthropus boisei* is the only hominin to combine a wide, flat face, massive premolars and molars, small anterior teeth, and a modest endocranial volume (*c*.480 cm^3). The body of the mandibles of *P. boisei* is larger and wider than that of any other hominin, and the tooth crowns grow at a faster rate than has been recorded for any other early hominin. For a long time, there was no postcranial evidence that could, with certainty, be attributed to *P. boisei*, but a fragmentary associated upper limb skeleton from Olduvai Gorge (Domínguez-Rodrigo et al. 2013) and a better preserved associated upper limb skeleton from Koobi Fora (Richmond et al. 2011) almost certainly belong to that taxon. Some of the postcranial fossils from Bed I at Olduvai Gorge currently attributed to *Homo habilis* may belong to *P. boisei.*

The taxon *Paranthropus aethiopicus* (Arambourg and Coppens, 1968) Chamberlain and Wood 1985 was introduced as *Paraustralopithecus aethiopicus* to accommodate Omo 18.18 (or 18.1967.18), an edentulous adult mandible recovered in 1967 from Omo Shungura in Ethiopia. The hypodigm is small, but it includes a well-preserved adult cranium from West Turkana (KNM-WT 17000) together with mandibles (e.g., KNM-WT 16005) and isolated teeth from Omo Shungura (some also assign the Omo 338y-6 cranium to this taxon). No published postcranial fossils have been assigned to *P. aethiopicus*, but a proximal tibia from Laetoli may belong to it. The temporal range of *P. aethiopicus* is *c*.2.5–2.3 Ma. *Paranthropus aethiopicus* is similar to *P. boisei* except that the face is more prognathic, the cranial base is less flexed, the anterior teeth are larger, and the postcanine teeth are not so large or morphologically specialized.

The most recent addition to the hyper-megadont archaic hominin hypodigm is *Australopithecus garhi* Asfaw et al. 1999. It was introduced to accommodate specimens recovered in 1997 from Aramis in the Middle Awash study area, Ethiopia. The hypodigm is presently restricted to fossils recovered from the Hata Member in the Middle Awash study area, Ethiopia. The type specimen, the *c*.2.5 Ma BOU-VP-12/130, combines a primitive cranium with large-crowned postcanine teeth, and particularly large premolars. However, unlike *Paranthropus boisei*, the incisors are small and the canines are large and the enamel apparently lacks the extreme thickness seen in the latter taxon. A partial skeleton with a long femur and forearm was found nearby, but it is not associated with the type cranium and it has not been formerly assigned to *Au. garhi*. If the type specimen of *P. aethiopicus* (Omo 18.18) belongs to the same hypodigm as the mandibles that appear to match the *Au. garhi* cranium, then *P. aethiopicus* would have priority.

8 Tempo and Mode

The study of macroevolution in hominin evolution is complicated by a number of factors unrelated to taxonomy. First, hominin remains are extremely rare in the fossil record, most fossils are frustratingly incomplete, and because of these factors, the same morphological regions are not well enough represented in the fossil records of some taxa to allow meaningful comparisons to be made among taxa. Second, the evolutionary sequence for the majority of hominin lineages is unknown. Most hominin taxa, particularly early hominins, have no obvious ancestors, and in most cases, ancestor-descendent sequences (fossil time series) cannot be reliably constructed—two possible exceptions are mentioned below. Third, error from many sources—measurement, reconstruction, sampling, and dating—can lead to spurious conclusions about evolutionary patterns. Finally, differences in scale can lead to differences in interpretation of tempo and mode of macroevolutionary change. Depending on the time separating recovered fossils, gradual steady-rate evolutionary changes can appear to be punctuated, and punctuated changes can appear to be gradual. None of these complications are limited to studying evolution within the hominin clade, but many of these issues are exacerbated in paleoanthropology given the intense scrutiny that our own lineage receives.

At one time, or another, every early hominin discussed above has been presented as “the” ancestor of later hominins, but in our opinion, only two pairs of taxa, *Au. anamensis* and *Au. afarensis* (Kimbel et al. 2006), and *P. aethiopicus* and *P. boisei* (Wood and Schroer 2013), are plausible examples of ancestor/descendant relationships (i.e., are examples of anagenesis). In the case of the former pair, *Au. anamensis* and *Au. afarensis* are most likely time-successive taxa within a single lineage with the Laetoli hypodigm of the former taxon intermediate between *Au. anamensis* and the Hadar hypodigm of *Au. afarensis*. This hypothesis has been given support by the discovery of fossil evidence from Woranso-Mille in Ethiopia that is both temporally and morphologically intermediate between *Au. anamensis* and *Au. afarensis* (Haile-Selassie et al. 2010). As for *P. aethiopicus* and *P. boisei*, although there are differences between the taxa (Suwa 1988; Wood et al. 1994), they are consistent with the older, less derived taxon being the ancestor of the younger more derived taxon. Indeed, some researchers have taken the view that the hypodigms of the two taxa are so similar they should both be included in *P. boisei* (Walker and Leakey 1988).

Another complicating factor is the history and current status of the punctuated equilibrium (Eldredge and Gould 1972; Gould and Eldredge 1977; reviewed in Sepkoski 2012) model that has provided the context for many past discussions of tempo and mode in the hominin clade. This model suggests that while stasis (i.e., lack of morphological change) is the predominant pattern of evolution within species, bursts of rapid change occur at speciation events. Further, these events occur in small isolated populations where new selection pressures and genetic drift can have a more dramatic effect than in larger populations (e.g., as in Mayr's allopatric model of speciation) (Mayr 1942). In fact, Gould and Eldredge's (1977) classic paper on punctuated equilibrium used hominin evolution as one of the primary supporting examples (see also Eldredge and Tattersall 1975). Based on the known fossil record at the time, the authors argued that stasis was predominant within hominin taxa, with each species looking much the same at the beginning and at the end of its fossil record. This interpretation stimulated a rebuttal by Cronin et al. (1981), who suggested that the apparent evidence of stasis within hominins was the result of poor samples and uncertainties about dating and taxonomy. In a recent review of the status of current evolutionary biological thought on the punctuated equilibrium hypothesis, Pennell et al. (2014) argued that current thinking on punctuated equilibrium conflates four key questions that should be addressed independently for any group such as the hominins. First, what is the relative importance of gradualistic versus punctuated evolution? Second, what is the role of speciation events versus within-lineage evolution in the group? Third, when change is due to speciation, are these changes adaptive or driven by neutral processes? Finally, how important is species selection in shaping patterns of diversity? Lieberman and Eldredge (2014) countered by suggesting that Pennell et al. (2014) did not correctly define punctuated equilibrium (or define macroevolution at all, though this is included in the glossary on their first page). Lieberman and Eldredge also suggested that Pennell et al.'s four questions were about patterns of evolution rather than processes, or conflated the two, or do not directly relate to Lieberman and Eldredge's understanding of the punctuated equilibrium hypothesis. While we do not wish to get into a debate on the merits of the punctuated equilibrium model, or the views of either set of authors, we view Pennell et al. (2014) as an attempt to show that regardless of the original intentions of its authors (see Sepkoski 2012 for the history of this idea), all four questions are ways researchers have attempted to test the validity of the punctuated equilibrium model of evolution.

The dearth of unambiguous evidence for ancestor-descendent lineages within the hominin clade means that the hominin fossil record currently does not permit useful insights into Pennell et al.'s (2014) questions two, three, and four. However, a number of studies have addressed whether within hominin taxa, the dominant signal is one of stasis or gradual change, and most have done so with reference to testing a punctuated model of evolution. In order to investigate the tempo of evolution within an early hominin taxon, (a) the taxon needs to be distinctive; (b) it must have a good, well-dated fossil record, and (c) the sample needs to span enough time (at least several hundred thousand years) for any temporal trends to manifest. One, or more, of these criteria rules out most early hominin taxa, especially those only found in the southern African cave sites, and the only early hominin taxa that comply with these criteria are *Au. afarensis* and *P. boisei*. In both cases, when researchers tracked morphology that is well represented in the fossil record [Lockwood et al. (2000) for *Au. afarensis* and Wood et al. (1994) for *P. boisei*], the predominant signal across approximately a million years was stasis. In the case of a third taxon, *H. erectus*, researchers have reached different conclusions about the likelihood of stasis (Tobias 1985; Wood et al. 1994; Ruff et al. 1997; Lockwood et al. 2000), with Rightmire (1981), suggesting that there was no consistent evidence of directional change in skull and tooth dimensions, whereas when Wolpoff (1984) analyzed a more narrowly defined sample of *H. erectus*'*s* mandibular, cranial, and dental features, he suggested that there was evidence for evolutionary change within that taxon.

Only a few traits are known from a wide enough range of fossil hominins to allow for quantitative, rather than qualitative, comparisons to be made across long periods of time. One of them, endocranial volume, has been regularly pointed out as a classic example of a macroevolutionary trend (Haldane 1949; Tobias 1971; Jerison 1973). Though current evidence on hominin brain size evolution points to an general increase over time (Holloway et al. 2004) and numerous hypotheses have been suggested as to the factors that caused this increase (e.g., Clutton-Brock and Harvey 1980; Martin 1996; Dunbar 1998), there is debate as to the tempo of brain size increase during hominin evolution. Some have argued for a gradual increase in hominin brain size over time (Lestrel and Read 1973; Lestrel 1976; but see Godfrey and Jacobs 1981; Lee and Wolpoff 2003) and others for an increasing rate of change (Tobias 1971; Holloway et al. 2004), and yet another sees evidence of stasis, followed by more rapid change (Ruff et al. 1997). A consistent theme of these interpretations is that there was a grade shift in endocranial volume *c.*1.8 Ma. One problem with past studies is that they present endocranial volume values as if they had neither dating nor measurement error. When Du et al. (in prep) analyzed a comprehensive data set on hominin brain size that took account of dating and measurement error, and which spanned the period from 3.5 to 0.5 Ma, they found that a gradual model of brain size received the strongest support.

9 Evolutionary Forces and Macroevolutionary Patterns

During the 1980s, there was a sizable backlash against portions of the punctuated equilibrium model of evolution (e.g., Lande 1980; Charlesworth et al. 1982). One of the chief reasons was because some versions of the model suggested that the causes of macroevolution are distinct from those leading to microevolution, thus suggesting that one of the central tenets of the modern synthesis is incorrect (e.g., Gould 1980). In a series of papers, population geneticists dissected various parts of the model, arguing that punctuated evolution was merely one end of a spectrum of evolutionary possibilities and likely did not play a major role in producing the patterns seen in the fossil record (Lande 1980; Charlesworth et al. 1982; Barton and Charlesworth 1984). While macroevolutionary patterns of evolution differ from microevolutionary patterns for some traits such as body mass (Uyeda et al. 2011), it is widely accepted that the idea that separate evolutionary processes are required to produce most macroevolutionary change is not supported by the evidence (reviewed in Charlesworth et al. 1982). The geological timescale is long enough that any variation in a trait, whether the result of many genes or a few, that increases fitness is likely to have been selected for and macromutations are extremely likely to be deleterious due to either their main effect or pleiotropic effects on other traits (Fisher 1930; Lande 1980; Charlesworth et al. 1982). Likewise, the recent suggestions that large morphological changes in hominin evolution were the result of a few simple changes in growth gradients or developmental fields (Lovejoy et al. 1999, 2003; Lovejoy and McCollum 2010) do not mean that one or just a few genes are at play (Lande 1980). Experimental attempts to identify the genes that control morphological changes suggest that variation in the vast majority of traits is controlled by multiple loci (i.e., it is polygenic) (Lynch and Walsh 1998).

Evolutionary forces—natural selection, random genetic drift, gene flow, and mutation—acting on heritable variation within populations, account for the majority of evolutionary change, but be that as it may, in paleoanthropology, it is nearly always assumed that macroevolutionary changes seen across the fossil record are the result of natural selection. While this is undoubtedly true for changes such as substantial increases in brain size between taxa, changes in morphology may also be due to the other three evolutionary forces, in addition to selection on other traits. Quantitative genetics (QG), which provides a mechanistic understanding of these evolutionary processes, began as an attempt to understand the inheritance of quantitative traits (height, weight, measurement of skeletal traits, etc.) (Provine 1971; Lynch and Walsh 1998), but its scope has expanded to include goals that range from understanding the nature of quantitative trait variation, the consequences of inbreeding, to developing predictive models for evolutionary change. Evolutionary quantitative genetics (EQG) takes concepts that were originally intended to look at changes in quantitative traits between generations, usually in association with livestock and crop improvement, and applies them to look at changes over evolutionary time (Roff 1997). A number of recent studies (Ackermann and Cheverud 2004; Rolian et al. 2010; Grabowski et al. 2011) have applied the theories and ideas of evolutionary quantitative genetics to the hominin fossil record in an attempt to provide insight into evolutionary forces that resulted in the patterns observed. In the next section, we focus on the first two forces, selection and drift, as these are likely the most relevant when applying evolutionary quantitative genetic methods to paleoanthropology. The results from these studies lead to the conclusion that morphological changes were likely due to a complex relationship between natural selection and random genetic drift.

9.1 *Natural Selection*

Most fossil analyses atomize the phenotype into a set of traits, observe how much a given trait differs between species, and then ascribe selection for a particular function as the cause of that change. But we know that organisms are integrated units, with many traits sharing some portion of their genetic background due to pleiotropy (i.e., the traits are integrated), and thus, natural selection on one trait leads to correlated responses in others (Olson and Miller 1958; Lande 1979; Gould and Lewontin 1979). This means that any change in morphology between fossil taxa may not be the result of direct selection for a particular trait or function, but is instead the result of a correlated response to selection on other integrated traits. Though this point is now generally accepted across much of biology, and some acceptance has occurred (Lovejoy et al. 1999, 2002, 2003; Strait 2001, Ackermann and Cheverud 2004), within paleoanthropology, atomization still reigns. Based on the work of Lande (1979), Lande and Arnold (1983), studies have reconstructed selection pressures that led to difference in morphology between species (Cheverud 1996, Marroig and Cheverud 2004, Rolian et al. 2010), including between fossil hominins (Ackermann and Cheverud 2004). The results of these studies suggest that at least some of these changes that were thought to be the result of natural selection driven by functional considerations were actually a correlated response to selection on other traits. For example, Rolian et al. (2010) found that the reduction in finger length seen during hominin evolution was likely a correlated response to selection to reduce toe length. In other words, the relatively short fingers that enable much of the manual dexterity that sets modern humans apart from other primates may not have been the result of selection on finger length. Instead, selection for shorter toes to permit habitual bipedalism led to changes in both homologous structures. Grabowski and Roseman (in press) tested the hypothesis that strong directional selection on many individual aspects of morphology was responsible for the large differences observed across a sample of fossil hominin hips spanning the Plio-Pleistocene. Their findings showed a complex and changing pattern of natural selection drove hominin hip evolution, and many, but not all, traits hypothesized to play functional roles in bipedalism evolved as a result of natural selection.

9.2 *Random Genetic Drift*

Tests for the roles of selection versus drift in producing the morphological diversity seen between worldwide modern human populations have become relatively common. For example, Betti et al. (2010) found that drift was much more important in shaping cranial diversity than selection due to climatic differences, with the exception of populations from extremely cold regions. Similarly, Betti et al. (2013) found that a combination of selection and drift explained variations in pelvic dimensions in modern human populations. With regard to fossil hominins, Ackermann and Cheverud (2004) tested whether random evolutionary processes alone could account for the morphological diversity seen in early hominin fossil crania. They also tested adaptive hypotheses about hominin facial diversity by estimating past selection pressures required to produce observed morphological change. Their results showed that though early hominin facial diversity exceeds levels expected if it had originated through random processes, diversity seen in early *Homo* did not. Weaver et al. (2007) tested the null hypothesis that morphological differences in the crania of Neanderthals and anatomically modern humans were the result of genetic drift. The researchers found that the null model could not be rejected, and thus, morphological differences between Neanderthals and modern humans could have been the result of genetic drift rather than selection.

10 Phylogenetic Relationships

For much of its history, hominin systematics was predicated on the assumption that there is a direct relationship between morphological similarity and genetic relatedness; the more hard tissue morphology two hominin taxa share, the closer their relationship. For extant taxa, this hypothesis can be tested against relationships based on molecular evidence. Such data, either on their own, or in combination with morphological evidence, have been used in efforts to try to resolve relationships among taxa, including those within large clades of medium- to large-sized mammals. But even at this “macro”-scale, it is apparent that a substantially similar skeletal phenotype does not always mean a shared recent evolutionary history. Long ago, Lankester (1870) suggested that the term homoplasy be used for morphology that is seen in what we now call sister taxa, but not in their most recent common ancestor. Such morphology gives the impression that the two taxa are more closely related than they really are. Because homoplasy can be mistaken for shared derived similarity (or synapomorphy), it complicates attempts to reconstruct phylogenetic relationships.

The confounding effects of homoplasy could be coped with if the “noise” generated by the latter was trivial compared to the strength of the phylogenetic “signal.” But in some attempts to infer relationships among extant higher primates using skeletal data (in the form of either traditional non-metrical characters or characters generated from metrical data), the ratio of “noise” to “signal” was in the order of 1:2. The results of these analyses were not only frustratingly inconclusive, but when they were compared with the pattern of relationships generated using molecular data, some were misleading (Collard and Wood 2000). Other researchers suggested that this dismal performance was due to the exclusion of character-state data from fossil taxa (Strait and Grine 2004), but this argument is moot because soft tissue characters (for which there are no fossil data) are capable of recovering a pattern of relationships among extant higher primates that is consistent with the molecular evidence (Gibbs et al. 2000, 2002; Diogo and Wood 2011).

Therefore, something about the nature of hard tissue evidence may be problematic. Thankfully, hard tissue evidence *can* produce results congruent with the relationships generated from molecular data (e.g., Lockwood et al. 2004), as long as the anatomical regions targeted have a high enough signal-to-noise ratio. The research reviewed above suggests that the problem is with either, or both, the nature of the data or the scale of the enquiry, and not with cladistic methodology. However, that the type of data the fossil record provides (i.e., mostly craniodental hard tissue morphology) seems to be particularly prone to homoplasy when used at this relatively fine taxonomic level is not the best context for paleoanthropologists attempting to reconstruct phylogenies based on fossilized hard tissue remains.

There is also comparative evidence that homoplasy needs to be taken into account when generating hypotheses about the relationships among the taxa in the higher primate part of the tree of life. Although there is overwhelming molecular and morphological evidence for a (((*Pan*, *Homo*) *Gorilla*) *Pongo*) pattern of relationships among the extant hominids, selected morphological character states can be used to infer a (((*Pongo*, *Homo*) *Pan*) *Gorilla*) pattern of relationships, but these are almost certainly homoplasies. Similarly, homoplasy complicates attempts to resolve the relationships of fossil apes such as *Sivapithecus* (Young 2003), *Morotopithecus* (Nakatsukasa 2008), and *Chororapithecus* (Suwa et al. 2007). Moreover, studies of other mammalian clades evolving in Africa during the same time period as hominins and in similar paleoenvironments point to substantial and recurrent homoplasy [e.g., bovids (Gatesy et al. 1997), equids (Bernor et al. 2010), elephantids (Todd 2010), carnivores (Van Valkenburgh 2007), and Old World monkeys (Jablonski and Leakey 2008)]. There is no reason to assume that higher primate lineages were immune from the tendency to adapt morphologically in similar, and therefore phylogenetically confounding, ways to shared ecological challenges.

The important point is that shared similarities can only take one so far in determining phylogenetic relationships because homoplasy, as well as uncertainties in determining the polarity of character transformation, has the potential to generate substantial noise that serves to confound attempts to generate reliable hypotheses about phylogenetic relationships. These considerations have clear implications for generating hypotheses about phylogenetic relationships within the hominin clade and especially for the relationships of *Sahelanthropus*, *Orrorin*, and *Ardipithecus*. Even if these taxa share *some* derived features with later Pliocene hominins, it would be rash to simply presume that those features are immune from homoplasy, especially when other aspects of their respective phenotypes are consistent with a more distant relationship with the hominin clade.

11 Conclusions

It is difficult to believe, but the second, 1964, edition of Le Gros Clark's "*Fossil evidence for Human Evolution*" was the last time a review looked at the whole of what we now call the hominin fossil record (Clark 1964). Much has happened in the ensuing half century. We now have the advantage of new dating methods, new fossil evidence, new methods for capturing (e.g., 3D landmark data) and analyzing morphology (e.g., geometric morphometrics), and new methods for extracting data from fossils (e.g., imaging, molecular evidence). We also have the advantage of quantitative methods for alpha taxonomy, methods for generating hypotheses about relationships, and the emergence of functional morphological analysis. However, we need to test many of the assumptions (e.g., selection drives observed change, morphology is homologous, climate drives evolution, and all taxa are ancestors until proved otherwise) that underly attempts to improve our understanding of macroevolution within the hominin clade.

Much progress has been made, but many of the questions raised by Le Gros Clark are still with us. More fossil evidence is crucial, but an order of magnitude increase in the fossil evidence in the absence of equivalent progress in how we analyze the fossil record would not constitute an advance. Real progress will come when evidence and analysis move forward in tandem.

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