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CROTCHETS & QUIDDITIES

A Metaphoric Rise to Stardom

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In the evolving theoretical basis of physical anthropology, genes always get the leading role. But stars are not the only members of a cast.

In 1951, Sherwood L. Washburn, a leading physical anthropologist, announced a landmark prospectus for what he called the "new physical anthropology" (Fig. 1).[1] He said that physical anthroplogy largely comprised opinions on dry metric data with little theoretical foundation. We needed that kind of foundation, and he had one to offer. Fifty-some years later, progress in the field means that it's time for a newer framework and again, one is waiting in the wings.

GENES IN PRINCIPLE

Washburn challenged us to adopt the perspective of the modern evolutionary synthesis, which, in the 1930s, had unified paleontology, Darwinian evolution, and Mendelian inheritance. The modern synthesis defined evolution as changes in the frequency of alleles (genetic variants). This resolved several knotty problems that had prevented the development of a unified theory of life.

A unifying theory had become possible for various reasons. Mendel's work had shown that discretely inherited "elements" could transmit traits from one generation to the next and the same principles were found to apply to plants and animals as well. Mendel only considered simple qualitative traits, but it was later shown mathematically that many genes acting in concert could produce the quantitative traits that were so important to Darwin's gradualistic view of evolution. Mendel's elements, dubbed "genes" in 1910, mutated occasionally, supplying the variation that could be screened by Darwin's natural selection to produce adaptive divergence and the formation of new species. Comparative anatomy, functional adaptation, taxonomy, and paleontology had been separate areas of research that sometimes seemed incompatible. But now they could all be accounted for by a single evolutionary process working on genes. Finally, we had a consistent, comprehensive, universally applicable theory of life.

The genetic theory of life was so elegant and persuasive that it was accepted even though at the time there was little knowledge of what genes actually were or how they worked. It sufficed to assume that stable, heritable something-or-others existed and were the universal cause of biological traits. A deep faith in genes justified explaining the phenotypes we cared about—the fossils in the ground and the living primates on it—in terms of adaptive genetic evolution. The theory provided a program for research as well as the confident ethnusiasm that accompanies the pursuit of fundamental truth. This perspective was enthusiastically adopted as the formal framework of biological anthropology, which it still is.

EVOLUTION ON THE OUTSIDE AND IN THE FIELD

Accounting for how humans compare to other primates was a central goal of Washburn's "new physical anthropology," which he said should be 80% concerned with heredity and only 20% with traditional approaches. In the subsequent half-century, primate studies have reflected changing currents in evolutionary thought: Attempts to elucidate our place in nature have at times stressed how we are more like and sometimes how we are less like other members of our taxonomic order. But these studies all stayed within the same theoretical framework, the fundamental belief that considering more than 60 million years and including over 200 species will provide relevant and interpretable insight into the processes responsible for changes leading to human physical and even behavioral phenotypes.[1,2] From its inception, a central objective of Evolutionary Anthropology has been to present assessments of these results, for which it has been an authoritative source.

The idea that we can use comparative studies to make broader inferences about distinct characters in different species requires accepting that the species are all subject to the same determinative processes. Thus, in the generation of primate studies following Washburn's paper, the environment was assumed to be the force driving the adaptive, presumably genetic, evolution of all sorts of physical traits, especially such traditional core interests of anthropology as skeletal and dental adaptations.

But Washburn energetically pushed his view further, on his own and in collaboration with Irv Devore at Harvard. They extended the theory to field

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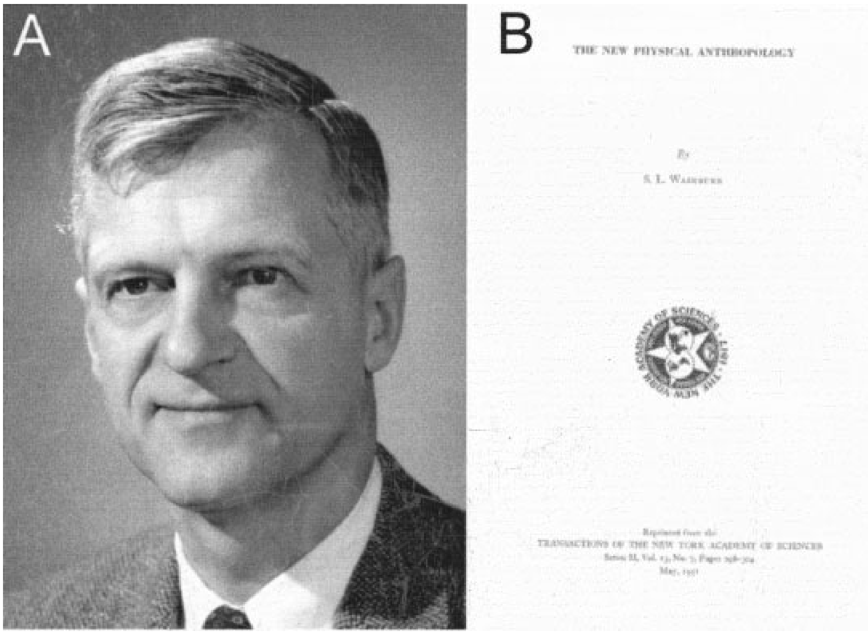

Figure 1. A. Sherwood Washburn. B. Washburn's landmark paper.[1]

studies of wild primates aimed at understanding how environmental conditions determined the adaptation of social behavior.[3,4–8] The findings of many famous primate field studies, among them ones focusing on dominance hierarchies, territoriality, harems versus monogamous pairings, and male versus female behavior, were extrapolated to humans. Physical anthropology was largely dominated by this new evolutionary approach, which made Hollywood-like stars of field workers like Jay, Goodall, Fosse, Lancaster, and Hrdy, as well as theoretical popularizers like Tiger, Fox, Ardrey, and Morris. These stars were the most visible part of a galaxy that included numerous other primatologists who more quietly made contributions at this time.

Assuming the evolutionary synthesis, these personalities made genes the implicit scientific star of the show. Primate traits were inferred to be the heritable effects of genes as the presumed targets of Darwinian evolution. But because these genes were of totally unknown number or nature, nonhuman primates served as metaphors of explanation for hominin dietary, locomotor, cultural, language, and brain evolution.[9–11] Derived from the Greek meta + pherein, which means to carry beyond or to transfer meaning between two unlikes (for example, "All the world's a stage, ..."),[12] metaphor is a type of abstraction that scientists usually try to avoid. Unlike "models" in biology, metaphors assume far more than is reliably known to be directly homologous or mechanistically relevant, often carrying many loadings, sometimes unstated, that can include value judgments, iconic simplifications, or broad applications that may, at best, be more analogous than homologous as well as very subjective.

It is engaging in metaphor to attribute what we know about a complex trait from observational studies of primates to hypothesized internal causal factors (genes) of unknown and, especially during Washburn's time, unknowable nature. But from this attribution, dominance hierarchies or nuclear family structures in wild baboons were assumed to provide biologically causal explanations of all sorts of hierarchies, from the culture of modern nation states to human kinship and marriage systems (Fig. 2). Metaphors may be built on grains of truth but, to borrow again from the Bard, is this metaphoric use of genes "a tale told by an idiot, full of sound and fury, signifying nothing," or is it truth? If the trait were not "genetic" in this hypothetical sense, what is its causal basis? How can we know?

EVOLUTION ON THE INSIDE AND IN THE LAB

The incredible recent progress in genetic technologies promises direct answers to these questions by identifying specific genes to replace those that had long been abstractly hypothesized to exist and imbued with metaphorically extended importance. One important area is developmental genetics. Development was significant evolutionary evidence to Darwin, but

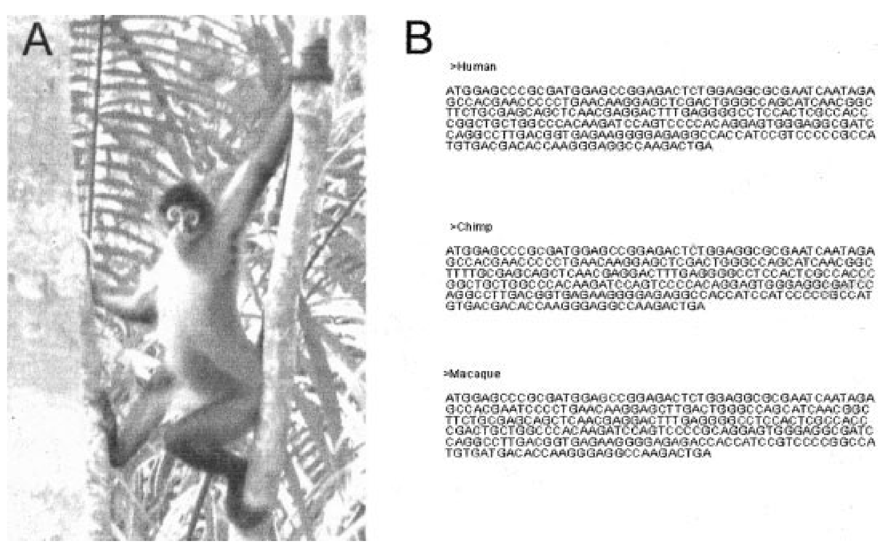

Figure 2. Metaphors old and new. A. Spider monkey, *Ateles geoffroyi,* on Barro Colorado, Panama, taken by one of us (HAL). B. Homologous sequences of a gene (GGA1) from human, chimp, and macaque (Source: GenBank).

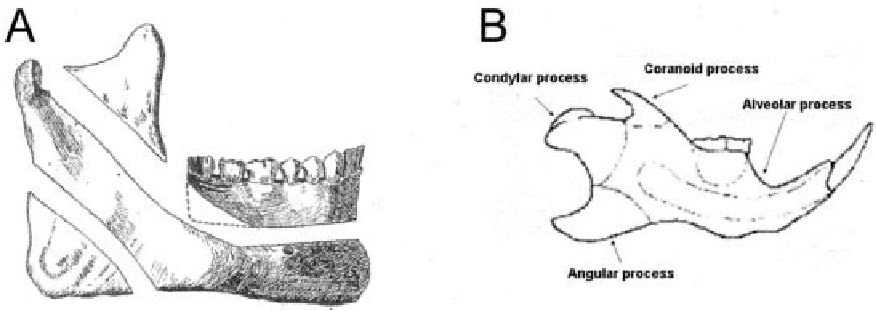

Figure 3. Guessing and testing about "evo" and "devo." A. An "evo" perspective helps identify causally independent traits. Regions of the jaw Washburn found to evolve independently.[1] B. A "devo" perspective tells us why: Each labeled region has been shown experimentally to be under independent genetic control.[20]

was largely ignored by the modern synthesis as an unimportant black box. The new physical anthropology was about introducing the population and historical dynamic among generations of individuals, but evolutionary theory was nearly silent on how the hypothesized genes made their respective traits. However, the technologies of molecular biology are giving development new vibrancy, reuniting it with evolution in a union called evo-devo, or evolutionary developmental biology.[13,14]

We can now move from metaphoric "genes" hypothesized for external traits to the inside, where real genes are, and explicitly identify what had heretofore only been implicit in statements about primate and human evolution. We can experimentally identify genes that are expressed in specific tissues and at specific times during embryogenesis; we can manipulate those genes to see how they work. These approaches connect what happens among organisms during a species' evolutionary time to what happens among cells during an organism's lifetime. Applications of this new new physical anthropology have already included studies of limb, skull, and tooth development and variation.[13,15–19]

Washburn said that combining evolution, comparison, development, variation, and experimental evidence in living and fossil primates would reveal new aspects of skeletal biology. "Evolution, in a sense, has dissected the body for us,"[1] showing that traits thought to have evolved in a unitary way were actually composed of evolutionarily independent modules. Based on present and past hominid variation, Washburn identified several areas of the jaw (Fig. 3A) that seemed to have evolved independently, each controlled by different selective forces. This meant that if his observations were "at all correct, it is theoretically impossible to make any progress in genetic understanding by taking the traditional measurements on the mandible" because they artificially confounded independently controlled traits.

We can now see the power of the new approaches. As an experimental model, Jim Cheverud and colleagues recently crossed two mouse strains with somewhat different mandibular shape.[20,21] They used gene mapping, in which they searched variable sites spread across the entire genome to find regions in which sequence differences between the parents were co-inherited with mandibular shape variation in their offspring. They found gene regions that independently affect different aspects of mandibular shape and, remarkably, these matched Washburn's earlier conjectures (Fig. 3B). What he had empirically found to be phenotypically modular they showed to be directly under modular genetic control as well. In a similar kind of study in living baboons, gene regions have been found that affect tooth size, enamel thickness, and cusp variation that resembles variation in the anthropoid fossil record.[22,23] However, this second example reverses Washburn's point because dental traits previously treated as being of independent taxonomic value turn out to develop under the control of the same genes.

"GENES" THAT BECOME GENES CAN BECOME "GENES"

In addition to "evo-devo," new technology is making possible major advances in the application of the concepts of the classical modern synthesis. The entire human, chimpanzee, and macaque genome sequences have become publicly available, with a stream of other species to follow. New genomic approaches allow us to align sequences of the same (orthologous) genes between humans and other primates and to search for changes in particular genes that occurred preferentially in the human or other lineages, paying intense interest to changes that may have been due to natural selection.[24–26] For example, sequence comparisons of the primate repertoire of olfactory receptor genes have shown, in specific genetic terms, the degradation in the ability to smell in the ape and human lineages, also confirming the long-suspected loss of pheromones for sexual attraction.[13,27,28]

Genomes, like species, evolve over time, so that Washburn's suggestion that we should begin with a framework developed from the fossil and comparative records is still relevant. But now, as then, it is important to keep in mind several cautionary points: Traits generally do not evolve in a simple linear way; most interesting traits vary continuously rather than discretely; primate evolutionary rates are generally concordant with overall mammalian evolutionary rates; most human traits are also present in other primates, especially the great apes; and many changes associated with anatomically modern humans occurred before the origin of the genus *Homo,* among them bipedalism, larger cranial capacities, and more complex mental ability than we have traditionally been willing to credit to these other brutes.[29]

We have had many warnings about this. Some early claims of primatology have not survived the subsequent fifty years of investigation. Female primates are not passive and nonhierarchical, alpha males don't have all the mating fun or mating success, chimpanzees aren't always nonviolent, and species' mating patterns are not predetermined. Extensive field work has shown that phenotypes can be fluid. Moreover, variation for most of our classical traits turns out to be polygenic, often associated with genes regulating development rather than, as per the classical idea, coding for the traits' structural proteins.[11,13,30]

From a genomic viewpoint, too, evolution of the traits we care about, both phenotypic and genetic, can be expected to be subtle and complex. However, it's a lot easier to raise cautions than resist the temptation to ignore them. Genes are enjoying a technology-driven ride to new metaphoric stardom in the genomic age. Today, perhaps more than ever, things biological are widely assumed to lie directly in the genome. If primate field studies sometimes uncritically invoked genetics as metaphors of explanation for hominin evolution, anthropological genomic studies—wholesale comparisons of the 30,000 genes in primate genomes—can slip into comparably strong genetic assumptions. Ironically, while it was formerly acceptable to invoke the role of genes in primate evolution without bothering to look at any actual genes, it is now acceptable to invoke the role of genes in primate evolution without bothering to look at any actual primates!

Unlike the original new physical anthropology, much of the recent genomics work is not being done by anthropoligists, who at least tend to give serious consideration to whole organisms. This has led to a new kind of genetic metaphor for, if not by, anthropology. Abstraction for hominin evolution has moved from the assumption of shared but unidentified internal causal elements to the reverse. Now actual genes serve as a new kind of metaphoric star on the stage of explanation. But rather than using a known trait to infer the existence of causal genes, known genes are now held to stand broadly, abstractly, metaphorically, as icons for the entire trait.

For example, there is irresistible vanity in focusing on "the brain" as the organ that made us human. It's become a cottage industry to single out individual brain-related genes from the mix of thousands of them expressed in the brain, under the implicit suggestion that a single gene is capable of explaining all of the changes resulting in the human phenotype.[9,31–36] Going Washburn's 80% solution and then some, a brain-related gene that varies between humans and chimpanzees is widely taken to represent the complexity of features that constitute human cognitive behavior, even including language and other things that clearly are not literally due to a single gene. Indeed, such features may be so complex that even calling them "genetic" may be to miss their important emergent nature. The brain has deeply symbolic value, even among scientists.

In the old "new" physical anthropology, the melodrama of dominance, territoriality, and other characters that evolution had molded into us naked apes was made famous by the popular media. Today, new genetic results also sell well in the media and in the mainline science journals, that have moved in a popularizing direction. But, like the simplistic enthusiasm for the fitness advantages of alpha male baboons or tribal headmen, the rush to the judgment that brain genes show special evidence of evolution in the human lineage has already been tempered by more thorough examination.[37,38]

A GALAXY OF GENOMIC STARS

The old anthropology was staid and needed something new. The prevailing working model is still the one adapted in Washburn's day, half a century ago. It is a strong acceptance of classical Darwinism in the study of important functional traits of primates, which extend to our own very different species, one with culture. Even many founding evolutionists, including Darwin himself, as well as Alfred Wallace and Thomas Huxley,[39] blinked when it came to humans, seeking special provisions or exceptions for our evolution. While anthropologists wouldn't want to leave humans out of nature, we can still get in trouble with oversimplified genetic explanations or theory applied uncritically, as is shown by hot debates about behavior genetics or the failure of genetic data to confirm simple dominance theories.

Generally, however, the best of the union of development with the older evolutionary perspective is truly energizing. It is also rapidly bearing fruit. Moving to the inside of the organism, we are learning a tremendous amount about how genes are used to build the animals we study and that we are. Because this work has shown that genetic developmental networks are deeply conserved and homologous, model systems like the mouse are finding a level of real rather than metaphoric anthropological relevance that we haven't seen since Washburn's day. That's why Figure 3B from the mouse tells us about Figure 3A for hominids, and can be called "anthropology." But with this progress has also come the tempering and subtle realization that so many genes are involved in the developmental networks that contribute to most traits of interest that we can't presume that a specific gene is responsible for any specific version of a trait in a particular fossil or primate. A control network provides many ways to make a short mandible.

Genes are providing an increasingly stellar cast of causal elements in life. A truly new physical anthropology that augments the genetic theory of evolution with a comparable genetic theory of development will provide a much more comprehensive view of the nature of life than the old new physical anthropology did. In that sense, the day is here when genes should no longer be used as metaphors. We're gaining the means, and hence the burden, to base genetic explanations more specificially on what genes do and don't do. That knowledge will lead to a more truly modern evolutionary synthesis.

NOTES

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REFERENCES

1 Washburn SL. 1951. The new physical anthropology. Trans NY Acad Sci Series II 13:298–304.

2 Lee PC. 2001. Primate biology and behavior: a template for human evolution? Cambridge: IOS Press.

3 Ribnick R. 1982. A short history of primate field studies: Old World monkeys and apes. In: Spencer F, editor. A history of American physical anthropology 1930–1980. New York: Academic Press.

4 Altmann SA, editor. 1967. Social communication among primates. Chicago: University of Chicago Press.

5 Jay PC, editor. 1968. Primates: studies and adaptation and variability. New York: Holt.

6 Washburn SL, DeVore I. 1961. Social behavior of baboons and early man. Viking Fund Publications in Anthropology 31:91–104.

7 DeVore I. 1965. Primate behavior: field studies of monkeys and apes. New York: Holt, Rinehart, Winston.

8 Rodman P. 1999. Whither primatology? The place of primates in comptemporary anthropology. Ann Rev Anthropol 28:311–339.

9 Isbell L, Young T. 1996. The evolution of bipedalism in homonids and reduced group size in chimpanzees: alternative responses to decreasing resource availability. J Hum Evol 30:389–397.

10 Sarringhaus LA, Stock JT, Marchant LF, McGrew WC. 2005. Bilateral asymmetry in the limb bones of the chimpanzee (*Pan troglodytes*). Am J Phys Anthropol. In press.

11 Schultz AH. 1955. Primatology in its relation to anthropology. Yearbook Anthropol 2:47–60.

12 Bremmer JB. 1980. Words on words. New York: Columbia University Press.

13 Weiss KM, Buchanan AV. 2004. Genetics and the logic of evolution. New York: Wiley-Liss, John Wiley & Sons.

14 Weiss KM. 2005. The phenogenetic logic of life. Nat Rev Genet 6:36–45.

15 Chiu C-H, Hamrick M. 2002. Evolution and development of the primate limb skeleton. Evol Anthropol 11:94–107.

16 Weiss KM. 2002. Good vibrations: the silent symphony of life. Evol Anthropol 11:176–182.

17 Weiss KM. 2002. Is the message the medium: biological traits and their regulation. Evol Anthropol 11:88–93.

18 Weiss KM, Buchanan AV. Rediscovering Darwin after a Darwinian century. Evol Anthropol 9:187–200.

19 Cohn MJ, Lovejoy CO, Wolpert L, Coates MI. 2002. Branching, segmentation and the metapterygial axis: pattern versus process in the vertebrate limb. Bioessays 24:460–465.

20 Ehrich TH, Vaughn TT, Koreishi SF, Linsey RB, Pletscher LS, Cheverud JM. 2003. Pleiotropic effects on mandibular morphology I. Developmental morphological integration and differential dominance. J Exp Zool B Mol Dev Evol 296:58–79.

21 Mezey JG, Cheverud JM, Wagner GP. 2000. Is the genotype-phenotype map modular? A statistical approach using mouse quantitative trait loci data. Genetics 156:305–311.

22 Hlusko LJ, Mahaney MC. 2003. Genetic contributions to expression of the baboon cingular remnant. Arch Oral Biol 48:663–672.

23 Hlusko LJ, Maas ML, Mahaney MC. 2004. Statistical genetics of molar cusp patterning in pedigreed baboons: implications for primate dental development and evolution. J Exp Zool B Mol Dev Evol 302:268–283.

24 Clark AG, Glanowski S, Nielsen R, Thomas PD, Kejariwal A, Todd MA, Tanenbaum DM, Civello D, Lu F, Murphy B, Ferriera S, Wang G, Zheng X, White TJ, Sninsky JJ, Adams MD, Cargill M. 2003. Inferring nonneutral evolution from human-chimp-mouse orthologous gene trios. Science 302:1960–1963.

25 Fortna A, Kim Y, MacLaren E, Marshall K, Hahn G, Meltesen L, Brenton M, Hink R, Burgers S, Hernandez-Boussard T, Karimpour-Fard A, Glueck D, McGavran L, Berry R, Pollack J, Sikela JM. 2004. Lineage-specific gene duplication and loss in human and great ape evolution. PLoS Biol 2:E207.

26 Gilad Y, Man O, Paabo S, Lancet D. 2003. Human specific loss of olfactory receptor genes. Proc Natl Acad Sci USA 100:3324–3327.

27 Gilad Y, Wiebe V, Przeworski M, Lancet D, Paabo S. 2004. Loss of olfactory receptor genes coincides with the acquisition of full trichromatic vision in primates. PLoS Biol 2:E5.

28 Weiss KM. 2004. Perfume. Evol Anthropol 13: 205–210.

29 Carroll SB. 2003. Genetics and the making of *Homo sapiens*. Nature 422:849–857.

30 Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT. 1987. Primate societies. Chicago: University of Chicago Press.

31 Stedman HH, Kozyak BW, Nelson A, Thesier DM, Su LT, Low DW, Bridges CR, Shrager JB, Minugh-Purvis N, Mitchell MA. 2004. Myosin gene mutation correlates with anatomical changes in the human lineages. Nature 428:415–418.

32 Enard W. Przeworski M, Fisher SE, Lai CS, Wiebe V, Kitano T, Monaco AP, Paabo S. 2002. Molecular evolution of FOXP2, a gene involved in speech and language. Nature 418:869–872.

33 Uddin M, Wildman DE, Liu G, Xu W, Johnson RM, Hof PR, Kapatos G, Grossman LI, Goodman. 2004. Sister grouping of chimpanzees and humans as revealed by genome-wide phylogenetic analysis of brain gene expression profiles. Proc Natl Acad Sci USA 101:2957–2962.

34 Zhang J. 2003. Evolution of the human ASPM gene, a major determinant of brain size. Genetics 165:2063–2070.

35 Chou HH, Hayakawa T, Diaz S, Krings M, Indriati E, Leakey M, Paabo S, Satta Y, Takahata N, Varki A. 2002. Inactivation of CMP-N-acetylneuraminic acid hydroxylase occurred prior to brain expansion during human evolution. Proc Natl Acad Sci USA 99:11736–11741.

36 Enard W, Khaitovich P, Klose J, Zollner S, Heissig F, Giavalisco P, Nieselt-Struwe K, Muchmore E, Varki A, Ravid R, Doxiadis GM, Bontrop RE, Paabo S. 2002. Intra- and interspecific variation in primate gene expression patterns. Science 296:340–343.

37 Khaitovich P, Weiss G, Lachmann M, Hellmann I, Enard W, Muetzel B, Wirkner U, Ansorge W, Paabo S. 2004. A neutral model of transcriptome evolution. PLoS Biol 2:E132.

38 Nielsen R, Bustamante CD, Clark AG, Glanowski S, Sackton T, Hubisz M, Fiedel-Alon A, Tanenbaum DM, Civello D, White T, Sninsky JJ, Adams MD, Cargill M. n.d. A scan for positively selected genes in the genomes of humans of chimpanzees. PLoS Biol 3. In press.

39 Weiss KM. 2004. Thomas Henry Huxley (1825–1895) puts us in our place. J Exp Zool Part B Mol Dev Evol 302:196–206.

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