32nd ALTENBERG WORKSHOP IN THEORETICAL BIOLOGY

Is Paleoanthropology an Evolutionary Science? Or, *Are Analyses of Human Evolution Biological?*

organized by
Jeffrey H. Schwartz

September 17-20, 2015

KLI Institute
Klosterneuburg, Austria

Welcome

to the 32nd Altenberg Workshop in Theoretical Biology. The Altenberg Workshops are interdisciplinary meetings organized by the KLI Institute in Klosterneuburg, Austria. The workshop themes are selected for their potential impact on the advancement of biological theory. Leading experts in their fields are asked to invite a group of internationally recognized scientists for three days of open discussion in a relaxed atmosphere. By this procedure the KLI Institute intends to generate new conceptual advances and research initiatives in the biosciences. We are delighted that you are able to participate in this workshop, and we wish you a productive and enjoyable stay.

Gerd B. Müller
Chairman

The topic

Given the pronouncements about human evolution that dominate anthropology textbooks and frequent the pages of newspapers and science e-news websites, it would seem that the major questions in paleoanthropology have been answered. Indeed, it is commonplace to read that a new fossil or molecular analysis supports fully, or tweaks only a tiny bit, scenarios of who's related to whom and how, when, where, and why one species of human relative (hominid) transformed seamlessly into another. If this is so, one may ask: Why bother trying to find more fossils, another molecule, or evidence pertaining to the life-history and persistence of any hominid, or pursue these inquiries with the latest technology, if you already know the story?

In light of the impact pronouncements on human evolution have on the public and on non-biologically savvy academics, it seems appropriate to convene a workshop that focuses on the disconnect between human evolutionary studies and the theoretical and methodological standards and practice that inform the rest of evolutionary biology. The result of this workshop will be a broad-based publication that will bring to light the assumptions and misconceptions as well as the positive and biologically viable aspects of human evolutionary studies. In turn, such wide-ranging collaboration should at the very least make apparent to scholars who assume that the study of human evolution is both biologically and theoretically sound that this is not necessarily or universally correct. More optimistically, such an endeavor – indeed, challenge – may provide a spark of intellectual curiosity among paleoanthropologists and their academic kin that could have long-lasting, positive effects on their disciplines. Although ambitious, I would also hope that some of the insights and recommendations that will emerge from this workshop will become known to the media and disseminated to the public that, after all, accepts pronouncements on human evolution as biologically sound fact.

Format

There will be 14 presentations, with 50 minutes allotted for each—roughly 30 minutes for each talk, followed by 20 minutes for questions on that talk and discussion. On Friday we kick off with an introductory statement, addressing the aims and framework of the workshop, by the organizer; on Sunday we end with a general discussion, including publication plans.

To support discussion during the sessions, we encourage all participants to send a rough draft of their presentation and/or some materials that are relevant to their topic to the organizers in advance of the workshop, to be circulated among the participants.

Manuscript preparation and publication

The Altenberg Workshops in Theoretical Biology are fully sponsored by the KLI Institute. In turn, the Institute requires all participants to contribute a paper to a volume edited by the organizer(s). Altenberg Workshop results are usually published in the *Vienna Series in Theoretical Biology* (MIT Press). The contributors are not necessarily limited to the original participants; they may be complemented by experts on those topics that emerge as important, and may include co-authors invited at the discretion of the participants.

We expect that participants will revise their drafts as a result of our discussions at the workshop and the ensuing review process. We aim for a March 2016 date for receipt of finished manuscripts for publication. The length of the contributions should be approximately 8,000 words. The use of figures and photographs is highly encouraged. All contributions will be edited for style and content, and the figures, tables, and the like will be drafted in a common format. The editor will send specific instructions after the workshop.

Jeffrey H. Schwartz

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Is Paleoanthropology an Evolutionary Science? Or, Are Analyses of Human Evolution Biological?

Thursday 17 September	Evening		
6.00 pm		Welcome reception and dinner at the KLI Institute	

Friday 18 September	Morning	Historical and Theoretical Issues I	Chair: Templeton
9.30 am – 10.00 am	Schwartz	Scope of Workshop, Hopes, Goals	
10.00 am – 10.50 am	de Vos	Man the Beast	
10.50 am – 11.20 am	Coffee		
11.20 am – 12:10 pm	Delisle	The Deceiving Search for ‘‘Missing Links,’’ 1860–2010: The Chaotic Development of Paleoanthropology	
12:10 pm – 1.40 pm	Lunch	at the KLI Institute	

Friday 18 September	Afternoon	Historical and Theoretical Issues II	Chair: DeSalle
1.40 pm – 2.30 pm	Templeton	Hypothesis Compatibility versus Hypothesis Testing of Models of Human Evolution	
2.30 pm – 3.20 pm	Macho	Referential Models for the Study of Hominin Evolution: How Many Do We Need?	
3.20 pm – 3:50 pm	Coffee		
3.50 pm – 4.40 pm	Stout	Human Brain Evolution: History or Science?	
6.30 pm		Departure for dinner at a local Heurigen	

Saturday 19 September	Morning	Underlying Assumptions I	Chair: Dennell
9.30 am – 10.20 am	DeSalle	How Real Are Genetic Data?	
10.20 am – 11.10 am	Bastir	Back to Basics: Morphological Analysis in Paleoanthropology	
11.10 am – 11.40 am	Coffee		
11.40 am – 12.30 pm	Waddell	It´s Not Evolutionary Biology Without Networks of Descent: Quantiative Phylogenetics and the Genus *Homo*	
12.30 pm – 2.00 pm	Lunch	at the KLI Institute	

Saturday 19 September	Afternoon	Underlying Assumptions II	Chair: Macho
2.00 pm – 2.50 pm	Plummer	Scope and Scale in Palaeoenvironmental Reconstructions of Early Hominin Archaeological Sites	
2.50 pm – 3.40 pm	Petraglia	Out of Africa: Can Archeological and Genetic Data Be Reconciled?	
3.40 pm – 4:10 pm	Coffee		
4.10 pm – 5.00 pm	McManus	Paleoanthropology and Human Evolution: A Philosophical and Feminist Assessment of a Complex Relationship	
5.00 pm – 5.50 pm	Cohen	Gender and Sex in Scenarios of Human Evolution	
6.00 pm		Free evening: dinner on one´s own	

Sunday 20 September	Morning	Fact versus Fiction Revisited	Chair: Cohen
9.30 am – 10.20 am	Dennell	Where Evolutionary Biology Meets History: The Appearance of *Homo sapiens* in East Asia	
10.20 am – 11.10 am	Schwartz	What´s Real about Human Evolution: Received Wisdom, Assumptions, and Scenarios	
11.10 am – 11.40 am	Coffee		
11.40 am – 12.20 pm		General discussion and publication plans	
12.20 pm – 2.00 pm	Lunch	at the KLI Institute	
2.00 pm		Departure for Danube boat trip & dinner in Dürnstein	

Abstracts

John DE VOS

Naturalis Biodiversity Center, Leiden

Man the Beast

In spite of Thomas Huxley's (1863) argument for embracing "Man's place in Nature," paleoanthropologists continue to exclude humans from the considerations that paleontologists in general bring to the study of every other group of mammals, including an understanding of their ecosystems. Hence the question: "Is paleoanthropology an evolutionary science? Or, are analyses of human evolution biological?” I must answer, definitely NOT! In this paper I demonstrate that hominins are part of the mammalian world and its ecosystems, and treat them systematically, as one would any other mammal, by comparing: 1) the footprint trails of the horse and hominin from the Tanzanian site Laetoli G, and then their evolution; 2) pigmy forms, such as the elephant and hippopotamus, from islands of the Mediterranean and the Indonesian Archipelago, with the small hominin from Flores (*Homo floresiensis*); and 3) Neanderthal with woolly mammoth and woolly rhino adaptations to the Mammoth Steppe.

Richard DELISLE
Unversity of Lethbridge, Alberta

The Deceiving Search for ''Missing Links,'' 1860–2010: The Chaotic Development of Paleoanthropology

Paleoanthropology's methods and procedures since its inception in the 19th century can be objectively characterized as loose, undisciplined, and chaotic. This is well illustrated in two main manifestations: (1) the debatable habit of so many fossil discoverers to claim they have found a "missing link" directly leading to living humans; (2) the unconstrained behavior of too many scholars (fossil discoverers or not) in expounding a bewildering disparity of views, both reasonable and unreasonable. In fact, at one time or another, virtually every imaginable viewpoint about human evolution has been proposed. Nevertheless, this "anything goes" approach to human evolution has permitted decent progress in the field, especially from the 1860s to the 1970s. Indeed, exploring all kinds of avenues eventually showed that many of them could not be supported, empirically speaking. As will be shown in a historical sketch of the discipline, the forgotten and wildly disparate viewpoints that were entertained before the 1940s, was gradually reduced to a "near consensus" that was confined to the view that a human lineage had descended from a post-mid-Miocene type of ape living in the tropical regions of the Old World. Any viewpoint that went beyond these constraints was deemed by the scientific community as unscientific and invalid. While this near-consensus perspective may allow disagreement, as will be seen, the real progress so far achieved must be appreciated in its fullest extent. This having been said, however, future progress is likely to be impeded, as it has been since the 1980s. Whereas, in the past, it was relatively easy to select one's favorite of divergent viewpoints – and thus reject many of them – in the last few decades it has been much more difficult to choose between relatively similar evolutionary hypotheses. Here, I argue that it is time to move away from the undisciplined methods and procedures of the past, by instituting "rules of engagements" that would be agreed upon by the scientific community. While such rules remain to be established, it seems reasonable to think that future progress in paleoanthropology may depend upon them.

Alan TEMPLETON
Washington University, St. Louis

Hypothesis Compatibility versus Hypothesis Testing of Models of Human Evolution

Hypothesis testing is central to most scientific endeavors, and often regarded as the single element that distinguishes science from other forms of human knowledge. Yet much of the modeling of the last 2 ma of human evolution has abandoned hypothesis testing in favor of hypothesis compatibility: i.e., gathering data that is consistent with a favored model without using the data either to test, or to distinguish it from alternatives. Even worse, hypothesis compatibility with some non-informative data has strongly been favored over hypothesis testing that would lead to the rejection of the favored model. The "Out-of-Africa" replacement model became the favored model of human evolution in much of the post-late-1980s genetic literature on the basis of hypothesis compatibility with non-informative data tests, and by ignoring clear and strong falsifications of this model by genetic data through hypothesis testing. The tendency not to test testable hypothesis continues in the human evolutionary literature.

Gabriele MACHO
The Oxford University

Referential Models for the Study of Hominin Evolution: How Many Do We Need?

Palaeoanthropological research is often predicated on assuming a direct relationship between morphological and/or behavioral, and genetic similarity. Consequently, modern chimpanzees are considered the most appropriate model for hominin evolution, and are used to understand the biology of the Last Common Ancestor of humans and apes (LCA). This is problematic. First, fossils such as *Ardipithecus ramidus*, as well as broad comparative studies, demonstrate that chimpanzee morphology and behavior is very derived. Second, the fossil record presents a high degree of homoplasy. Third, studies in other areas of evolutionary biology, i.e. those more firmly rooted in biological sciences, reveal evolutionary processes that are more complex than those promoted by the Standard Evolutionary Synthesis (SES). Whilst the SES proposes that evolution results from changes in gene frequencies, gene flow and genetic drift, mediated by natural selection, the Extended Evolutionary Synthesis (EES) recognizes the importance of complex feedback mechanisms, e.g. niche construction, developmental biases, and epigenetics.

Using chimpanzees as proxies for the LCA has clouded our understanding of hominin evolution. Although chimpanzees can sometimes be useful as hominin evolutionary models, in general, no ape serves as the ultimate resource for reconstructing the LCA. Rather, model choice should be guided by: 1) context, i.e., the environmental and selective situation in which certain features evolved; 2) developmental plasticity; 3) genetics; and 4) biomechanical 1st principles. An ecological approach that is based on a broad comparison of mammalian taxa has much to offer toward an understanding of evolutionary processes, as is illustrated by hominin postcranial morphology, dietary diversity, brain expansion, and life history.

Dietrich STOUT
Emory University, Atlanta

Human Brain Evolution: History or Science?

Is it the aim of paleoanthropology to reconstruct the uniquely contingent evolutionary history of humans, or to discover general laws of evolutionary cause and effect? Stephen J. Gould famously argued that much of what is interesting about human nature, and especially the human brain, arose from one-off contingencies of history. Matt Cartmill has championed the opposing view: Paleoanthropology must be predictive and law-based if it is to be a science at all. Here, I revisit this perennial argument in the context of recent accounts of human brain evolution that derive from the Social Brain Hypothesis. I conclude that the impulse for generalization that motivates the SBH is healthy for paleoanthropology, but caution that we should not underestimate the complexity of lawfully interacting causes that have determined the particular course of human evolution.

Rob DeSALLE
American Museum of Natural History, New York

How Real Are Genetic Data?

Large data sets now being produced are moving the study of human evolution into a new phase. In addition, and of critical importance, is the addition of the genome sequences of several fossil and subfossil specimens of *Homo*. These exciting technological advances have also changed the way in which we view evolution within our species and genus. In this presentation, I elucidate the arguments for using genome-scale data to make inferences about human evolution. I also discuss, how one makes inferences from tree-based analyses, the role of fossil-derived sequences for understanding the evolution of our genus, and whether human populational change is tree-like.

Markus BASTIR
Museo Nacional de Ciencias Naturales, Madríd

Back to Basics: Morphological Analysis in Paleoanthropology

The morphology of fossil hominin is one of the principal sources of information about human evolution. But how morphological information is extracted, analyzed and interpreted varies from one researcher to the next. Consequently, different, conflicting evolutionary models (stories, scenarios) emerge through use of disputable morphological evidence. In order to reduce storytelling in paleoanthropology, it may be useful to reflect on its epistemological, knowledge-generating processes. How do we obtain information from anatomical structures, and how do we interpret morphological variation? The first question relates to the quantification of morphological structures, its information content, and its potential for scientific communication. The second relates to hypotheses of causation of morphology. In this paper I address these problems through a critical discussion of the use of morphometrics in analyzing hominin skeletal variation. I propose that geometric morphometrics, the theory of integration, and a concept of the organism together provide a constructive framework for research in human evolutionary morphology and biology.

Peter WADDELL
Ronin Institute, Massey University

It´s not Evolutionary Biology without Networks of Descent: Quantitative Phylogenetics and the Genus *Homo*

A range of phylogenetic methodologies for analyzing different types of data extracted from specimens within the genus *Homo* are described and illustrated. The order follows an approximately historical succession, from cladistics, to distances and maximum likelihood and, finally, to the framework of Bayesian methods. A key concept is that the genus *Homo* is a species complex. That is, not only are there many lineages of descent, each with unique adaptations, they are prone to rejoin/reticulate. In order to avoid problems of trying to force such a history onto a single tree, networks need to be considered. Parsimony/cladistic methodology is particularly useful for achieving initial estimates of likely trees or networks when the data are discrete characters. Starting with mostly partial skulls, it is not always easy to describe or define characters; indeed, it is often difficult to decide to what extent these features are genetically independent. An alternative is to work with quantitative shape changes from 3D measurements of fossils. These combine well with pairwise Procrustes distances and least squares tree fitting for a model assuming a Brownian motion of genetic/shape change. Such analyses are promising and, I argue, strongly suggest the existence of a new, near-human species in Africa (*Homo iwoeleruensis*) that went extinct ~10 ka. In addition, I explore the steps to a full tree likelihood analyze and then to a full Bayesian model, as well as the kinds of key questions/hypotheses that are of topical interest.

Thomas PLUMMER
City University of New York & New York Consortium in Evolutionary Primatology

Scope and Scale in Palaeoenvironmental Reconstructions of Early Hominin Archaeological Sites

In this paper I discuss several of the major methods used to reconstruct palaeoenvironments at African Plio-Pleistocene archaeological sites, with reference to the scale of information these methods provide. Since palaeoanthropologists ask a range of questions, on different geographical levels, reconstructing the settings for human evolution and behavior at an appropriate level requires understanding the scope and scale of palaeoenvironmental data as well as the methods of analysis. I also review some of the ways in which information about hominin environments has enhanced our understanding of the context of human evolution. Since controversy frequently arises when different studies lead to conflicting reconstructions, I argue that a multi-level, multi-proxy approach is the best way in which to ensure that palaeoenvironmental reconstructions are as accurate as possible at all levels of analysis.

Michael PETRAGLIA
University of Oxford

Out of Africa: Can Archaeological and Genetic Data Be Reconciled?

The dispersal of *Homo sapiens* 'Out of Africa' is one of the hottest topics in paleoanthropology and human evolutionary studies. The prevailing view has been that *H. sapiens* reached the Levant by ~120,000 years ago, only to become extinct in Eurasia 50,000 years later. As the theory goes, successful human populations left Africa 60,000 years ago, ultimately colonizing much of the rest of the world. A great deal of this theory has rested on genetic data drawn from modern human populations, and is now also being supplemented by ancient DNA analyses of human skeletal material. In discussing human expansions into Eurasia, geneticists and archaeologists continue to favor a rapid coastal dispersal of populations around the Indian Ocean rim. However, in recent years, there has been increasing skepticism about this consensus view, due to closer examination of the archaeological and environmental record, together with re-evaluation of genetic findings. The aim of this presentation is to discuss variant views about the 'Out of Africa' theory, and to recommend new ways to consider biological and cultural data.

Jaime Fabrizzio GUERRO McMANUS
National Autonomous University of México

Paleoanthropology and Human Evolution: A Philosophical and Feminist Assessment of a Complex Relationship

How unique has human evolution been? In light of our cognitively complex minds and societies, is human history another instance of a "major transition" in evolution? Are these traits further examples of evolutionary innovations? If so, what are the epistemic consequences of this for those who study human evolution in general, and for paleoanthropologists in particular? In this paper I tackle these questions by bringing into play philosophy of biology and analytic feminism. On the one hand, I focus on epistemological considerations regarding how we should understand evolutionary theory; specifically, I claim that, if our aim is to do justice to our uniqueness, then we can, and should not construct sciences of human evolution as tout court identical in their explanatory patterns to other evolutionary sciences. On the other hand, I critically engage in a deep reconceptualization of human nature: precisely, what human beings are.

Claudine COHEN
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Gender and Sex in Scenarios of Human Evolution

Reproductive physiology and behavior play an obvious role in the evolutionary tempo and mode of sexed animals. In *The Descent of Man* (1871), Darwin considered mate choice and sexual selection of critical importance in human evolution, which was influenced by the selection of a number of anatomical, physiological, psychological, and social features. Although Darwin's endeavor was little recognized in his time, his emphasis on the role of sexual and reproductive behavior in human evolution became central to sociobiological and evolutionary psychological scenarios. In this paper, I examine and evaluate these contemporary attempts to include such parameters in scenarios of human evolution. I will also suggest that other physiological features related to human reproduction (e.g., the acquisition of concealed ovulation) are important in considerations of hominin evolution.

Robin DENNELL
University of Sheffield

Where Evolutionary Biology Meets History: The Appearance of *Homo sapiens* in East Asia

Until ca 1948, palaeoanthropology in East Asia could be regarded as a branch of evolutionary biology. In that year, Franz Weidenreich died, and Hallam Movius published his synthesis of the East and Southeast Asian Palaeolithic, which was later reified as the Movius Line. In the early years of exploration in East Asia, Matthew and Davidson Black put forward a theoretical framework of Neogene mammalian evolution, in which the uplift of the Tibetan Plateau played a major role. According to their hypothesis, Tibetan uplift not only created challenging new conditions for the existing fauna, but was also the impetus for the evolution of new forms that could adapt and for the displacement outwards of those species that could not. On this logic, eastern Asia was the powerhouse of human evolution, while places such as Africa were the recipients of the least adapted. Weidenreich’s ideas stemmed from a different, Central European intellectual tradition, as well as from his training as an anatomist and pathologist. For him, animal, and particularly human, populations were not static entities, but parts of a much larger network linked by gene exchange, movement, and interbreeding. Under his paradigm, studies that demonstrated similarities and differences between hominin fossils (e.g., as in brain or tooth size) could be explained in terms of adaptation, gene exchange, and natural selection. Movius terminated this outlook by insisting that East Asia was always isolated, backward, and irrelevant to the study of human evolution – in short, paleoanthropology was hardly a good career choice for an ambitious researcher. Under Movius' framework, East Asia lacked a palaeolithic history because it did not change.

In recent decades, palaeoanthropology in East Asia has reverted to being essentially a historical discipline, in which the main priorities are dates, and establishing when, and from where, various anatomical features became established. To some extent, this is an inevitable consequence of the incomplete, and poorly dated and documented, Asia fossil hominin record. What is missing is consideration of population dynamics, such as immigration reflecting range extension, a widening of adaptive capabilities, or population pressure in adjacent territories. Also missing is clarity in defining *Homo sapiens.* Until the quantity and quality of information improves dramatically, palaeoanthropology in East Asia will continue to be merely a historical narrative. Nevertheless, and contra Movius, paleoanthropology in East Asia now has at least a sense of history, and of its place in the broader narrative of human evolution in Eurasia.

Jeffrey H. SCHWARTZ
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What´s Real about Human Evolution: Received Wisdom, Assumptions, and Scenarios

What constitutes *Homo sapiens* (or, for that matter, any commonly accepted hominid taxon)? Has anyone really diagnosed the species, or the genus*?* Do the terms “archaic” and “anatomically modern” clarify or muddy attempts to delineate defining features of *H. sapiens* – viz., were there archaic and anatomically modern *T. rex*? Has a close relationship between extant humans and Neanderthals, even as variants of the same species, ever been justified? Or have these claims been reiterated to the point of elevating to the level of truth assumptions that then inform how human evolutionists interpret their data, whether morphological or molecular? Here, I review the history of long-held assumptions underlying assertions of hominid relationship and evolution, as well as how they have dictated the interpretation of morphological and molecular “data."