

# Preface

## “A boring story”

For several decades now, medical students at the Sackler School of Medicine at Tel-Aviv University have been meeting Professor Yoel Rak primarily as their anatomy teacher in their first year. Still equipped with his drawing chalk and classical anatomical charts, and only seldom with PowerPoint presentations, Rak's method of anatomy gained much popularity over the years, whether he was using a model of an upside-down table to illustrate the basic framework of the sphenoid bone, or leading the students through the complexities of the peritoneal ligaments. As a professor of human anatomy, he always insisted that all bodily systems and organs should be equally presented in the anatomy course curriculum, not only the ones that have unequivocal clinical significance. His students' comments at the end of the course repeat themselves every year in stating that even the duller parts of the material became fascinating topics, and that what they remember most of all are the evolutionary correlations Yoel frequently adds to his lectures. In doing so, he reminds his students that human anatomical structure is but one example of vertebrate anatomy and constantly encourages them to think beyond the definitions of their anatomy textbook. Naturally, it follows that during the long years he had served as Chair of the Department of Anatomy and Anthropology, he also insisted that anatomy should be taught to medical students mainly through dissection of the human cadaver. In his own words to first year students, “the efforts a student makes in the strenuous and often frustrating process of searching for an anatomical structure are at the heart of studying anatomy, far more than the mere act of identifying it” (AM, pers. obs.). According to Rak, there exists a reliable correlation between a student's knowledge of anatomy and how stained her laboratory coat is at the end of a dissection.

Along these lines, the physician *sensu stricto* may be thought of as a highly trained technician, who must memorize protocols for diagnosis and treatment. The physician *sensu lato* is an educated and well-informed professional, equipped with thorough knowledge of all the basic sciences, anatomy included (Marom and Tarrasch 2015). Yoel's pedagogical principles, well expressed in both his lectures and active participation in curricular committees, most certainly adhere to the latter. His approach to anatomical studies has made it feasible for scores of medical students to study, but also to love studying anatomy, echoing some beloved phrases from Anton Chekhov's “A Boring Story”, narrated by no other than an anatomy professor: “And we proceed in the following order: in front walks Nikolai with the slides or atlases, I come after him, and after me, his head humbly lowered, strides the cart horse; or else, if necessary, a cadaver is carried in first, after the cadaver walks Nikolai, and so on. At my appearance, the students rise, then sit down, and the murmur of the sea suddenly grows still. Calm ensues.<sup>1</sup>”

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<sup>1</sup>A Boring Story: From the Notebook of an Old Man. In *Selected Stories of Anton Chekhov* (R. Pevear & Larissa Volokhonsky, translators) Modern Library, New York. 2000.

## A Matter of Character

Scholars of today's academic world are highly specialized: whether their research interests are the three dimensional architecture of a trans-membrane channel or the effect of a drug on gene expression, they keep refining their line of work. In the face of a rapidly increasing rate of knowledge expansion, this tendency may very well be an unavoidable outcome, and arguably has many advantages. However, one disadvantage that must not be overlooked is the price the scientific world pays for this high level of specialization: the increasing dearth of scholars with broad-spectrum knowledge and the ensuing ability of integration within and between scientific disciplines. One study even demonstrates how scientists view broad projects as riskier and less important than deeper projects (Bateman and Hess 2015). To many students, beginning scholars and colleagues, Yoel Rak has always represented a rare example to the contrary. His broad knowledge of human anatomy and deep acquaintance with the fossil record, but also his vast knowledge of the animal world, geology, geography, and archaeology, has allowed him to explore almost any part of the skeleton: from ear ossicles and the osseous labyrinth to the pelvic girdle; from the finest details of dental anatomy to the facial masks of the robust australopiths and the Neanderthals. To put it in Hennigian terms (Cracraft and Eldredge 1979), connecting the dots of Rak's professional accomplishments reveals the central motif of his search for characters, character states, and their positions along the morphoclines of each trait. In Rak's view, every character counts (and is legitimate to use) in the process of reconstructing phylogenies. In the debate between the anagenetic and cladogenetic views of evolution, even the *adaptive values* conferred by anatomical structures – which are outcomes of one's understanding of said anatomy – were recruited by Rak *as characters* of no less significance than the anatomical traits themselves (Marom 2013). [The squamosal suture of *Australopithecus boisei* (Rak 1978) or the Neanderthal face (Rak 1986), are cases in point.] Rak's appreciation of genetic evidence in the form of DNA sequences – as additional albeit discrete characters, that are by no means superior to anatomical traits – is probably the best example for this argument. In other words, his loyalty to the scientific “game rules” and his natural curiosity are the two main driving forces behind the process of his scientific thought and academic achievements. This is in fact what enabled him to present mandibular evidence in support of the premise that *Homo neanderthalensis* does not play a role in modern human ancestry (Rak 2002). Along the same lines, he later pointed to gorilla-like anatomy in *Australopithecus afarensis*, suggesting an evolutionary link between *Au. afarensis* and the robust australopiths (Rak et al. 2007). In both cases this was done elegantly by employing the rules of cladistic analysis and the logic of parsimony. Rak's interest in characters and their status along the primitive-derived axis should be viewed here as stemming from the high potential he ascribes to them in falsifying (or corroborating) a suggested phylogeny.

## What's in the Book?

In early 2013, we embarked on the project of editing this volume, thinking that the occasion of Yoel's 70th birthday would be an excellent opportunity to celebrate his numerous achievements in science (and wish him many more), as well as to the many friendships he has struck throughout the years. This volume presents a collection of original papers contributed by many of Yoel's friends and colleagues from all over the globe, many of whom have collaborated with their students, thus keeping the flame burning, so to speak. The papers in this volume touch upon diverse ways of thinking about human evolution. Many of these approaches are among the topics that Yoel has been studying during his productive career.

The papers fall roughly into three broad categories: Reflections on some of the broad theoretical questions of evolution, and especially about human evolution; the early hominins, with special emphasis on *Australopithecus afarensis* and *Paranthropus*; and the Neanderthals, that contentious group of our closest extinct relatives. Within and across these categories, nearly every paper addresses combinations of methodological, analytical and theoretical questions that are pertinent to the whole human evolutionary time span.

Three chapters are concerned with the history of research, changing ideas about human evolution and the mechanisms that drive it. Wool (2017) reviews influential evolutionary ideas, and their particular applications to the evolution of humans to the effect that human evolution was once deemed unique compared to other species. He reiterates [as does Newman (2017) in his historical review of Darwin's and Wallace's personal and scientific interactions] Wallace's understanding of the unique evolution of humans due to "glorious qualities which raise us so immeasurably above our fellow animals" (Wallace 1891:190). It was Wallace's opinion that this process could not have occurred by blind natural selection. Some sixty years later, Dobzhansky (1962:199) promoted "intelligence, ability to use linguistic symbols, and culture which man has developed" as the leading forces in "a whole new evolutionary pattern...which is human rather than animal". Notably, in this later view the novel evolutionary pattern was formed by the combined effects of nature and nurture rather than by the invisible power that had been Wallace's driving force. Dobzhansky (1955, 1962) raised the point that cultural evolution is faster and more efficient than biological evolution, as the pathways of information transfer can take many forms within ever-broadening audiences (due to technologies of information transmission such as writing, printing, and later the radio, television, and the internet).

Tattersall's (2017) contribution takes off from this very question when he asks why human evolution was so fast. The empirical archaeological record demonstrates that human evolution started off slowly and accelerated only over the last 100,000 years. (Notably, many archaeologists may place this acceleration at somewhat earlier or later dates.). Indeed, Holloway (2017) reiterates the anatomical evidence from the *Australopithecus* endocranials that speaks to the slow pace of brain evolution in early hominins. Tattersall suggests that around 100,000 years ago the human brain switched to a different, more efficient processing algorithm, based on a connection-sensitive brain rather than sheer brain tissue volume. While the evolutionary mechanisms underlying this acceleration in human evolutionary tempo are not exclusive to this lineage and do not require that special evolutionary mechanisms be invoked in explanation, material culture must be incorporated as part of the evolutionary process in order to explain the change of pace. The operation of genes and culture in tandem, combined with the demographic structure and spatial spread of human populations, were the forces enabling the implementation and spread of novel cultural ideas and practices that we refer to as inventions. The resulting ratchet effect propelled the evolution of the genus *Homo*, specifically in *Homo sapiens*, inevitably leading to increasing levels of complexity and symbolic information processing.

Finally, Wool (2017) draws attention to a different aspect – both exciting and somber – of humans' rapidly increasing ability for cultural evolution. Galton's nineteenth century eugenics aspirations to direct human evolution have become that much more feasible with the great advances made since the mid-twentieth century in understanding the cogs and wheels of hereditary mechanisms. It is now that much (some would say, too much) easier to actively shape the direction of many biological, cognitive and social aspects of future human evolution.

A number of papers in the volume explore paradigmatic ideas about the ways in which modern research approaches key elements of the evolutionary process. Holloway's (2017) chapter is a cautionary tale about methodology and analytical tools. He reflects on state-of-the-art techniques of studying early hominin endocasts and on the contribution of such techniques to our knowledge, emphasizing the limitations of paleoneurology and the ever-growing necessity for comparative data regarding the human and ape neuroanatomical patterns. He concludes that, when applied to the early members of the hominin lineage, novel techniques of segmentation and reconstruction do not necessarily add new information or resolve old controversies, albeit they may be more informative with regard to later hominin species such as the Neanderthals. Within the framework of their study of the robust and hyper-robust hominins of the Early Pleistocene, Wood and Schroer (2017) question the ability of hard tissue morphology to recover phylogenetic relationship, and raise doubts about the assumption of non-independence of some of the traits often used in cladistics analysis.

Several papers raise questions about the epistemological implications of studies of ecological constraints, dietary preferences/restrictions, food-getting behaviors and life histories of early hominins. Harrison (2017) discusses Laetoli, where a number of faunal proxies lead to contrasting understanding of the habitats populated by *Paranthropus boisei* versus earlier ones in which *Au. afarensis* fossils were found. Harrison uses this case study to ask whether there is a direct cause-and-effect relationship between the appearance of a new hominin species and ecological change in a region of mosaic environments. The Laetoli analysis seems to demonstrate that such is not the case, although Harrison does not rule out the possibility that when studied over larger geographic regions, environmental changes may show such correspondence.

Cartmill and Brown (2017) consider in Chap. 6 one of the defining traits of the hominin lineage, assessing empirically hypotheses that link the emergence of hominin bipedality with feeding behavior. Their study of the anatomy of the gerenuk, an African gazelle that feeds bipedally, indicates that its post-cranial anatomy shows only few of the apomorphies expected to occur given the animal's feeding habits. Importantly, they do not recognize the expected diagnostic morphologies of bipedality in early hominins (*Ardipithecus* or *Australopithecus*). To them, this result argues (albeit not conclusively, in the absence of decisive fossil material) against the bipedal feeding hypothesis of hominin origins.

A number of papers in this volume contribute to the burgeoning paleoanthropological literature dedicated to mandibular morphology and dentition of the robust and hyper-robust australopiths, a group that has been a special favorite of Yoel's given their highly specialized cranial and dental morphologies. These papers ask how these traits inform us about feeding and dietary practices of robust and hyper-robust australopiths. Perhaps surprisingly, their results are not clear-cut but rather more speculative than one might expect given the current paradigm.

Wood and Schroer's contribution (2017) discusses the taxonomy and phylogeny of the megadont (*Paranthropus robustus*) and hyper-megadont hominins (*P. boisei* and geologically older *P. aethiopicus*), known from southern Africa (ca. 2.0–1.0 Ma) and eastern Africa (ca. 2.6–1.3 Ma), respectively. They accept that *P. boisei* and *P. robustus* are two separate species sharing a number of derived characters, based on the features of the mandibular bone and dentition of these hominins, yet they are concerned that these characters are not truly independent. Wood and Schroer favor homoplasy of these features in the eastern and southern robust hominins as a valid possibility because various studies of the dentition of the two species did not yield results that would be expected under the hypothesis of monophyly.

The papers by Hylander (2017); Daegling and Grine (2017); and Glowacka et al. (2017) speak to this very point when discussing dietary habits, ontogenetic processes and biomechanical forces that affect some or all the components of the masticatory system of early hominins. The implication is that such components cannot be treated as independent traits in cladistic analyses.

Current views on the diet of *P. boisei* are discordant, due to the differing inferences from tooth wear analyses and stable isotope data (from which absence of hard objects and inclusion of sedges and grasses in the diet were inferred) on the one hand, and biomechanical models and comparative studies of dental enamel (indicating specialization for hard-object feeding) on the other. In Chap. 9, Daegling and Grine (2017) ask whether the jaws of *P. boisei* can be interpreted as functionally consistent with a herbivorous diet with only an insignificant component of hard foodstuffs. They find that a “massive” mandible may represent a structural solution to either forceful biting and chewing, persistent and prolonged mastication, or both. In the case of *P. boisei*, it is plausible that the bulk processing of low quality fibrous foods was the target of natural selection in this lineage.

Hylander (2017) focuses on the vertical shortening of canines, a characteristic that makes an early appearance in hominins, and evaluates the premise that canine reduction has an impact on the mechanical efficiency of the masticatory apparatus, in particular due to its relation with the measure of gape. Based on a large catarrhine database, Hylander attempts to understand the links among gape, jaw length and canine overlap. Interestingly, reduced sexual dimorphism is associated with relatively smaller (in humans) and larger (in hylobatids) gapes, and there are considerable differences in the amount of gape relative to jaw length on the interspecific level. Hylander concludes that a major benefit for canine height reduction in early hominins was functionally linked to increased mechanical efficiency of the jaws, and he demonstrates that gape can be predicted by the independent variables of projected jaw length and canine overlap. While he hypothesizes that the driving force for canine height reduction is gape reduction, he remains cautious about the ultimate reason for this change, because this largely depends on the identification of the earliest hominins. Explanatory scenarios would differ if this role is assigned to *Australopithecus anamensis/afarensis* (in which case a hypothesis of dietary shifts is advocated), or to *Ardipithecus ramidus* [(in which case canine reduction was due to a combination of dietary shifts with social factors (e.g., mating patterns) and tool use (presumably invisible to the archaeological eye)].

Glowacka et al. (2017) focus on the importance of dynamic ontogenetic development of the mandibular corpus in *A. afarensis*, using an expanded sample from Hadar to investigate this question. They find that the pattern of mandibular corpus growth in *A. afarensis* is neither exactly human-like nor chimpanzee-like. In chimpanzees, slow canine formation and their late emergence in relation to the other permanent teeth affect the size and shape of the anterior corpus throughout most of mandibular ontogeny, and the final adult size is reached later in the individual’s life. Yet differences between chimps, humans and *A. afarensis* are more subtle for later dental emergence stages, because the growth of teeth does not appear to influence corpus morphology throughout all of mandibular ontogeny or in all parts of the mandibular corpus. Glowacka et al. (2017) propose a mechanism to explain such ontogenetically changing relationship. Although they do not dismiss hypotheses suggesting that differences in feeding behavior may have led to differences in symphyseal form [thus converging to Hylander’s (2017) discussion, although they invoke a different mechanism], they emphasize the need to consider the effect of mandibular ontogenetic growth in addition to the often-used biomechanics of the adult form.

Human evolutionary research within the time frame of the Middle and Late Pleistocene has undergone a revolution with the introduction of paleogenetic research on the Neanderthals [Pääbo (2014) is a personal account of this scientific revolution, which includes a list of many of the influential studies in the field], the identification of new hominin groups (Denisovans), and following the actual genetic, demographic, and geographic histories of hominins during the Late and even the Middle Pleistocene. This body of research has revealed a complex and rich record of dispersals, interbreeding and bottlenecks that has been hard to decipher from the fossil record alone. In this newly emerging research-scape, it is nearly too easy to forget that a fundamental requirement for these advanced analyses is the actual presence of fossils. Importantly, researchers have been able to retrieve ancient DNA from only a small fraction of the available fossils, even when dealing with relatively late extinct hominins such as the

Neanderthals or early moderns. Geographically, such fossils are constrained to Europe; in key regions such as Africa or the Levant fossils (and archaeology) are currently the only way to directly address questions about any aspects of human evolution. A number of chapters in this volume refer to the recent body of research on Neanderthal genetics [Bailey et al. (2017); Caspari et al. (2017)]. Still, most of the contributions in the group of papers that deal with the Middle and Late Pleistocene records focus on the actual fossils, using various methodologies and analytical tools to address questions of phylogeny, activity patterns and ecological adaptations. Some of these studies [Collard and Cross, (2017); Pearson and Sparacello (2017); Weinstein-Evron and Zaidner (2017); Frayer (2017)] raise – explicitly or implicitly – questions about the type of relationship that should be expected between fossil anatomy and the archaeological behavioral record.

Rightmire’s (2017) null hypothesis states that the Middle Pleistocene Eurasian (Arago, Petralona, Sima de los Huesos, Zuttiyeh, Mauer) and African (Kabwe, Bodo, Elandsfontein) lineages represent paleodemes of one species, *Homo heidelbergensis*. He uses the relatively complete Broken Hill (Kabwe 1) cranium from Zambia and Petralona cranium from Greece to test this hypothesis. Rightmire concludes from his detailed review of the anatomy, as well as of independent studies of scaling and of geometric morphometric properties of facial features, that there is little basis for distinguishing these mid-Pleistocene individuals. Additionally, neither Petralona nor Arago can be linked more closely to later European populations (i.e., Neanderthals) than can the African mid-Pleistocene hominins. Since the null hypothesis cannot be rejected, he suggests that Petralona and Kabwe be viewed as representatives of paleodemes of a single, widely spread evolutionary lineage, which split relatively late in the Middle Pleistocene. Such a conclusion is in broad agreement with the favored interpretation of an mtDNA analysis of the ~400,000 year-old Sima de los Huesos fossils (Meyer et al. 2014).

Collard and Cross (2017) revisit a consensual notion about the relationship between thermoregulation, body shape and body size in *Homo erectus* and Neanderthals, two groups believed to represent warm and cold adaptations, respectively. Their analysis is novel in that it looks at the effects of body segment differences in surface area, skin temperature, and rate of movement, in addition to the typically discussed whole-body thermoregulation. They compiled data from published material on a sample consisting of Holocene modern humans, Pleistocene *H. sapiens*, Eurasian and African *H. erectus*, and Neanderthals, and used a series of equations to model the more complex parameters in their study. Admittedly their model simplifies past conditions, as the task of estimating the thermal responses of extinct, culture-using hominins has the potential to be extremely complex, especially given the less than ideal resolution of environmental backgrounds. With this caveat in mind, Collard and Cross (2017) find that whole-body and whole-limb heat loss estimates were consistent with the consensual notions for *H. erectus* and Neanderthals, and with the notion that there are thermoregulation-related differences in body size and shape within *H. erectus* and *H. neanderthalensis*. However, differences between the proximal and distal limb segments did not follow any particular trend. Thus, the immediate conclusion from their research is that the current consensus requires some modification: while the basic idea that thermoregulation influenced the evolution of body size and shape in *H. erectus* and *H. neanderthalensis* seems to hold, differences in limb segment size may not be linked to thermoregulation. Collard and Cross point out some future studies that may be useful for checking on “assumption errors” in their current study and for explanations of these unexpected results. Interestingly, they imply that such explanations may derive from cultural as well as biological factors.

Pearson and Sparacello (2017) also direct their attention to post-cranial remains. Against a background of competing hypotheses about the levels of robusticity of long bones in Southeast Asian Neanderthals and the early moderns of the Skhul-Qafzeh group, this contribution presents an evaluation of size-adjusted strength of the limbs in the two populations. The comparison with a suite of other groups of Pleistocene fossil hominins and populations of recent humans that differ in lifeways, geographic origin, and ecogeographic adaptations results



in a mosaic pattern. In the lower limb, European and Southwest Asian Neanderthals resemble a diverse array of modern agriculturalists and intensive foragers that are generally active but not highly mobile over long distances. While disparities in the indices of Neanderthal humeri and radii may be a species-level characteristic of this group, the (well-documented) flattening of the radius mid-shaft is known from other populations sampled for this study and may well develop from intensive physical activity or activities. Of the repertoire of activities associated with Neanderthals on the basis of use-wear studies of lithics, the authors suggest that scraping rather than spear-thrusting could account for the patterns in the upper limb bones. In contrast, the people from Skhul and Qafzeh are quite distinct from recent samples but bear a degree of resemblance to Khoesan and Zulu males and females, Kebaran foragers (Ohalo 2), and also Amud 1. The bone shape and size-adjusted strength indices suggest that each of these groups had patterns of physical activity that did not place high or frequent mechanical demands on their upper limb. Pearson and Sparacello (2017) conclude that Neanderthals and the Skhul-Qafzeh humans seem to have had highly different lifeways, and that early moderns rather than Neanderthals may have faced an uncommon set of mechanical demands on their limbs. Having said that, Pearson and Sparacello (2017) caution that these differences need not necessarily reflect fixed species-level differences, given the considerable variation that exists among ethnographically documented foragers. They also remind us that archaeologists have long seen the different cultural remains of the Levantine Middle Paleolithic as a continuum of responses to environmental and ecological conditions rather than a dichotomy in behavior between the two Levantine Middle Paleolithic populations.

Weinstein-Evron and Zaidner (2017) report on the Middle Paleolithic site of Misliya Cave in Israel. Although no diagnostic human remains have been reported from this site, the authors link it to the debates about the origins of modern humans. The Middle Pleistocene chronology of the two cultural units in the site – the Lower Paleolithic Acheulo-Yabrudian and the early Middle Paleolithic (EMP) – provides a context for delineating the cultural developments that may attest to an important behavioral shift. Major collapses of the cave mask the actual boundary between the two cultural units, yet a robust TL chronology of the sequence places the boundary between them at around 250,000 years ago, in general accordance with the chronology of Tabun, Hayonim and Qesem Caves. Weinstein-Evron and Zaidner (2017) suggest that the marked technological break between the two cultural complexes could have been associated with the arrival of a new population in the Levant. They concur with previous accounts (e.g., Hovers and Belfer-Cohen 2013) that in terms of its lithic technology, toolkit composition and potentially also the settlement patterns in the EMP, this cultural phase differs from both the earlier Acheulo-Yabrudian and the later Late Middle Paleolithic (LMP), but whether the shift to the LMP is linked to the arrival of another dispersing population remains a moot point. Regardless of demographic changes (if there were any) the authors argue that in the majority of behavioral characteristics the EMP hominins of Misliya Cave were similar to their late Mousterian counterparts, even if their biological identity still eludes us. This archaeological case study raises again familiar questions (Lieberman and Bar-Yosef 2005; Hovers 2006; Hovers and Belfer-Cohen 2006) about the links between cultural and biological evolution and whether we should expect close correlations between these trajectories.

Tabun Cave is a site where such questions are most pressing, given its long and controversial Middle Paleolithic chronology and the suggestion that the two hominin specimens found within it – Tabun C1 and Tabun C2 – represent two different groups [e.g., Rak (1998) even though they had been found in – presumably – the same stratigraphic unit. In fact, Garrod (Garrod et al. 1937) herself mentions doubts about the stratigraphic origin of the Tabun C1 skeleton]. Other researchers assign this specimen to either the Neanderthals or modern humans. Harvati and Lopez (2017) tackle this problem through a 3-D geometric morphometric analysis of the Tabun C2 mandible in a comparative sample of 26 mandibles of Middle and Late Pleistocene *H. heidelbergensis*, Neanderthals, and *H. sapiens*. Despite the greater analytical rigor of this analysis, the results remain inconclusive in showing that the overall mandibular shape cannot be easily accommodated either within the Neanderthal or the early

modern human range of variation. In their analysis, Tabun C2 does not group with the Neanderthals; it differs from Upper Paleolithic modern human specimens; and its relationship to early anatomical moderns of Skhul and Qafzeh is unclear. Thus its affinities with any of the Levantine Middle Paleolithic hominins remain unresolved. Harvati and Lopez (2017) found, to their surprise, that Tabun C2 fell closest to the much older Middle Pleistocene European specimens in their sample, presenting a mosaic of traits, possibly because the large size of the specimen contributes to its archaic morphology. Finally, the authors also consider the scenario that Tabun C2 represents a hybrid between Neanderthals and early modern humans, but they are concerned that their methods are inadequate to assess this possibility. Interestingly, hybridization in the late Middle–early Late Pleistocene has come to the forefront with the recent publication of ancient DNA analyses suggesting early interbreeding in the Levant and gene flow *from* early moderns to the (eastern) Neanderthals prior to the Late Pleistocene interbreeding showing a different direction of gene flow (Kuhlwilm et al. 2016). Given the complex statistics that led to this interpretation and the complexity of the suggested interbreeding processes on the Eurasian scene throughout this time frame, the applicability of this scenario to the Tabun C2 (or any other) specimen should be validated by future paleoanthropological and paleogenetic data.

Bailey et al. (2017) examine in their contribution whether a pattern of dental trait frequencies can be used to statistically distinguish *H. sapiens* from Neanderthals. Reviewing the recent literature on hybridization, they suggest that if Neanderthals and *H. sapiens* did interbreed extensively, one might expect to find morphological evidence of such admixture in their dentition, although no specific model is offered for how this might occur. They hypothesized that if an identifiable modern human dental pattern emerged early in our lineage, then in their analysis the earliest *H. sapiens* should classify predominantly as *H. sapiens*. If, on the other hand, the earliest *H. sapiens* are characterized by a primitive dental pattern, then their classification should be ambiguous. A second prediction is that if there had been a significant admixture event in Western Asia (as suggested by some paleogenetic studies), then a higher percentage of *H. sapiens* in Western Asia would be misclassified as *H. neanderthalensis* in comparison to Africa. Their results suggest that in most cases the predominance of primitive features, rather than derived Neanderthal traits, drove the classification. Bailey et al. (2017) find a strong modern signal at two of the earliest *H. sapiens* sites (Qafzeh and Skhul), which suggests that dental modernity appeared early in our lineage. They posit that this also argues against significant admixture between Neanderthals and *H. sapiens* in this region. However, marked heterogeneity in their African sample (independent of geographic distance) suggests that Late Pleistocene Africans were not a dentally homogeneous group, such that some populations appear to have retained higher frequencies of primitive characteristics than others. In the face of a moderate frequency of African material classifying as Neanderthal, Bailey et al. (2017) conclude their contribution with some methodological reflections regarding their method's ability to test Neanderthal – *H. sapiens* admixture, especially in the absence of detailed modeling of how the dental traits may track population history and/or gene flow.

Freyer's (2017) short paper focuses on the cognitive abilities of Neanderthals, specifically those associated with speech. He reviews the osteological evidence for sound-producing abilities as reflected by the hyoid bone, the first fossil of which was discovered in Kebara Cave in the 1980s, since then augmented by additional hyoid finds. These show how the Neanderthal hyoid differed from that of earlier *A. afarensis*, with a morphology closer to that of modern apes (implying similar, limited sound-producing abilities), and how similar it was to the modern configuration. Freyer's review (2017) of studies of the auditory anatomy, base of the skull, brain lateralization and handedness, as well as the presence of the gene FOXP2 in its modern form in Neanderthals, suggests to him that in all these the Neanderthals had the modern configuration and therefore cannot be denied the ability that defines modern humans – the ability of language.



Been et al. (2017) used a 3-D model from CT scans of the Kebara 2 Neanderthal partial skeleton to provide, for the first time, a complete 3-D virtual reconstruction of the spine of an extinct hominin. This reconstruction demonstrates that the upright posture of Kebara 2 was slightly different from that of the average modern human. When compared to modern humans, the spine of Kebara 2 exhibits a combination of a vertical sacrum and a small lumbar lordosis together with a nearly average thoracic kyphosis. As a result, the spinopelvic alignment of this specimen was different from that of modern humans, suggesting locomotor and weight-bearing differences between the two groups. Neanderthals might have been better adapted to carry heavy loads and, potentially, to engage in generally more rigorous upper body activities (as is also discussed briefly by Pearson and Sparacello 2017). On the other hand, it suggests that Neanderthals potentially had a shorter stride length and slower walking speed on a flat terrain in comparison with modern humans. If validated, these observations may have important implications for understanding the organization of activities of Neanderthals and their energetic costs while moving across various types of terrain.

In the last chapter, Caspari et al. (2017) ponder the place of the Neanderthals in human evolution, looking at the evidence from the perspective of three topics. They consider body form (focusing on the pelvis); population structure (paleodemography), and breeding behavior (as seen from the genetic evidence). Their extensive review and testing of the evidence lead them to conclude that in body form, demography and population structure, Neanderthals were unlike modern humans in the Upper Paleolithic or later. In some cases (the pelvis shape, paleodemographic curves), they seem to indeed reflect the ancestral condition. Demographic factors in particular (adult survivorship, the ratio of older to younger individuals) negatively affected the resilience of Neanderthal groups to stochastic fluctuations in size and also their densities on the landscape and their ability to formulate extensive and lasting social and economic networks. The increased survivorship and longevity in the Upper Paleolithic eventually led to social pressures that Caspari et al. (2017) associate with extensive trade networks and more complex systems of cooperation and competition between groups. In that sense, “modern human behavior” (a problematic term by many archaeological accounts) is a response to demographic pressures. The Neanderthal archaeological record shows glimpses of this behavior, but it is less frequent and less sophisticated than in the Upper Paleolithic, a reflection of their archaic life history pattern. Caspari et al. (2017) tie these inferences with their long-standing view, now arguably (e.g., Holliday et al. 2014) bolstered by ancient DNA studies demonstrating hybridization between Neanderthals and moderns during the Middle and Upper Paleolithic, that phylogenetically Neanderthals do not constitute a different taxon. They represent another way of being human.

Bones, indeed, can tell a lot, if coaxed in the right way. The papers in this volume provide diverse perspectives on what it means to be human and how our present is an outcome of our evolutionary past. The papers differ in their interests, questions, methodological approaches and analytical tools and provide quite a number of take-home messages. One insight that stands out is that the discourse between ‘hard core’ human paleoanthropology and the many other disciplines that seek to understand the social and biological evolution of humans yields the most interesting results. We hope that this volume helps to promote such interdisciplinary work in the future.

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