

USQUE AD RADICES

*Indo-European studies in honour of
Birgit Anette Olsen*

Edited by

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Usque ad Radices: Indo-European Studies in Honour of Birgit Anette Olsen

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Molecular archaeology and Indo-European linguistics: Impressions from new data

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Ancient human DNA (aDNA), the molecular study of the human past, can now place ancient people within their actual mating networks, and it can reveal shifts in ancestry across generations as particular human populations expanded or died out, as well as labeling migrants and their genes as they moved across geographic space. Ten years ago these capabilities were unknown. Archaeology has never had a tool like this for the study of ancient migrations, kinship, and biological adaptation. The challenge that faces us now is to develop methods for testing genes against linguistic and archaeological evidence without reducing culture or language to biology. The results of and inferences from recent aDNA studies are reviewed in relation to the question of Indo-European language expansions, and the steppe homeland is defended.

The University of Copenhagen gave the authors of this essay our first opportunity to work directly with the faculty in an Indo-European Linguistics department in 2012, as part of their Roots of Europe project, largely through the efforts of Birgit Rasmussen. Archaeologists Kristian Kristiansen and James Mallory also have been guests at the department. So we begin by expressing our gratitude to Birgit Rasmussen in particular, and to the faculty of which she is a part, for cultivating productive exchanges between the still-too-foreign countries of linguistics and archaeology.

1 Correlating ancient DNA, language, and material culture

Between 2012 and 2015 new methods of ancient DNA (aDNA) analysis permitted geneticists to examine not just single genetic traits, but whole human

genomes, including potentially every significant variation in ancient human genotypes; and to study not just one whole genome, laboriously reconstructed for one prehistoric individual over many months, but large numbers of genomes from many individuals, sequenced hundreds of times faster. In 2015 these new whole-genome methods went through an unplanned but very public test. As Kristian Kristiansen reiterates in this volume, his desire to integrate linguistics, stable isotope studies, and other disciplines with archaeology had widened to include the evidence from aDNA, under the umbrella of a project ('The Rise') designed to develop a new framework for studying the past (Kristiansen 2014). Kristiansen's partner was geneticist Eske Willerslev at the University of Copenhagen. We were drawn into a similar project at the same time, led in our case by geneticist David Reich at Harvard University. The samples of human bone we submitted to Reich's laboratory in 2012 were collected for radiocarbon dating and dietary isotope analysis during our archaeological projects in the Russian steppes, conducted in collaboration with Russian colleagues in Samara (Anthony et al. 2005, 2016). Reich incorporated our steppe samples into a diverse set drawn from archaeological sites across western Eurasia dated to the Mesolithic, Neolithic, and Bronze Ages. Kristiansen had acquired steppe samples from Natasha Shishlina's projects in the Kalmykian steppes (Shishlina 2008), and these were incorporated into an even larger set of Eurasian archaeological samples in Copenhagen. The Harvard team did not communicate or collaborate with the Copenhagen team prior to publication. They studied independently selected samples of hunter-gatherer, Neolithic and Bronze Age humans at the whole-genome level – 101 successfully tested individuals in the Copenhagen study and 69 at Harvard. The methods used to sequence and analyze aDNA at the whole-genome scale were somewhat different, as each lab had developed its own techniques. They published simultaneously in the June 2015 issue of *Nature* (Haak et al. 2015; Allentoft et al. 2015), not knowing exactly what the other team had said. The principal findings of both teams agreed to a remarkable degree, an effective blind test of both the methods and the inferences about past population structure and migrations that were best supported by the initial 170 whole-genome sample. These conclusions are reviewed briefly, with comments on their implications for the migrations of Indo-European-speaking peoples, in the second part of this paper.

The challenge that faces us now is to think clearly about the best methods for comparing linguistic and archaeological evidence with genetic evidence without reducing culture or language to biology. Much of the pre-

vailing pessimism about correlating these very different kinds of data (Saarikivi and Lavento 2012; Campbell 2015) was rooted in the shortcomings of older genetic methods (Sims-Williams 1998), and should be reconsidered in the light of the great methodological improvements of the last decade. The geographic distribution of languages is subject to some ecological and economic constraints (Silver and Miller 1994; Smalley 1997; Nettle 1998, 1999; Hill 1996; Nichols 1992), as is the geographic distribution of subsistence strategies, public and domestic architecture, barns, field systems, and other material practices (Glassie 1965; Noble 1992; Stark 1998), so in principle the material and linguistic domains could be said to exhibit at least some shared geographic constraints (Ehret and Posnansky 1982; Sims-Williams 1998: 523–24). Whole-genome DNA analysis is showing us that ancient mating networks also exhibited regional geographic structure that was clearer, with lower gene flow between neighboring groups, than we are accustomed to seeing among modern humans. For most Western-trained archaeologists this is one of the most surprising results of the recent aDNA research: we now have clear genetic evidence for the maintenance of persistent, centuries-long resistance to intermarriage between people who were geographically proximate. These exclusive mating relations endured while material resources that are visible archaeologically were actively exchanged across genetic-economic borders. This distinction between marriage exchange and trade in material goods in prehistoric Europe is discussed in more detail in the conclusion; here we only note that it actually simplifies the genetic map by making genetic borders and mating networks clearer. The linguist William Labov (1994) noted that even in the modern world, dialect borders are correlated with reduced cross-border movement between socio-economic regions termed ‘functional zones’. Prehistoric language borders, economies, and socially constructed mating networks might exhibit some overlapping structures at the regional scale, where a comparison of linguistic, material, and genetic data could be most productive initially.

This broad picture will then be filled in at increasingly fine scales, much as happened during the initial spread of radiocarbon dates and the resulting rearrangement of cultural chronologies at increasingly fine scales after the 1960s. Radiocarbon dates allowed us to place ancient people in their correct time, with their chronological contemporaries, and to see fine-grained before-and-after relationships, leading to better cause-and-effect questions. Now aDNA permits us to place ancient people within their mating networks, to see ancestry evolve across generations as populations expanded or died

out, and to track migrants and their genes across geographic space. Genetic ancestry tells us whether and with what frequency migrants and the indigenous population mated, and identifies the traits that came under selection (cultural or natural). Archaeology has never had a tool like this for the study of ancient migrations, kinship, and biological adaptation. We will no longer be forced to use artifact styles, types, or archaeological cultures as proxies for people, a linkage we knew explicitly was unreliable and reductive at best, but nevertheless we fell back on it where we lacked a better proxy. Instead we can now consider type/style/archaeological cultures as an independent set of material variables, measured against mating networks as shown by aDNA on a case-by-case, region-by-region basis. With these new abilities we should be able to integrate linguistic, archaeological, and genetic evidence in new ways.

1.1 What genetic ancestry is and is not

Genetic ancestry is not race. Genetic ancestry is a quantitative measure of shared genetic traits, most of which are not physically visible (blood group, haplogroup) or have subtle and mixed phenotypic indicators. In popular usage, race is defined by external physical and cultural stereotypes that are maintained and recreated through cultural practice, so can vary between sub-cultures. The ‘same’ race can be defined differently by different government bureaucracies, neighborhoods, cities, classes, castes, and other social or political groups (Yudell et al. 2016; Morning 2011). The visible human traits that enter into racial stereotypes, including skin color and hair type, can be detected in aDNA, but carry little weight in a statistical analysis of the whole human genome; and in any case the genes that code for skin color interact in such complex ways that aDNA indicates only relatively ‘darker’ or ‘lighter’ skin tones (Mathieson et al. 2015). Ancient people might have regarded some of their physical differences as visible signs of Otherness, but usually we can’t say which aspects of their phenotypes they marked for salience, and the values and emotions they attached to such stereotypes necessarily were quite different from those associated with the modern history of racism. Genetic ancestry shows that all modern races share a common human origin, and all of us are admixtures resulting from extremely complex and intertwined histories of migration and adaptation. The borders of modern nations are not determined by or correlated with genetic ancestry, and the citizens of all modern nations are admixed. The new studies do show that 10,000 years ago regional human mating networks were much more isolated from each

other than they are today, so the modern regional admixtures we see around the world today were achieved recently. But the genes of the human populations of 10,000 years ago exhibit evidence of admixture events caused by even older migrations and movements. Regional mating networks did exist in the past, and people from the same region probably did look similar to each other after millennia of gene sharing, but their genetic ancestry was always mixed. Long-distance migrations continued to re-shape regional mating networks throughout human history (Pickrell and Reich 2014).

Biological anthropologists have defined modern geographic types (Caucasian, East Asian, sub-Saharan African, etc.) and prehistoric geographic types (Europoid, Mediterranean, etc.) on the basis of skeletal and dental traits, some of which are visible (cranio-facial shape) and some ordinarily not (dental morphology), some controlled by genes (dental morphology) and others (cranio-facial shape) exhibiting the blended effects of genetic inheritance and diet/activity. Geographic cranio-facial types are defined by traits that can overlap with traits used to define both genetic ancestry and popular concepts of race, but genetic ancestry is not reducible to either race or cranio-facial type, so they don't always coincide. Population groups defined by similarities in 15 standard phenotypic measurements on the skull and face can and do agree with population groups defined by thousands of shared genes, as in the spread of the Neolithic European farmers (Pinhasi and von Cramon-Taubadel 2009), but cranio-facial shape is affected by diet and masticatory loading on the jaw (Paschetta et al. 2010), and possibly by other behaviors. A significant change in food types, for example the adoption of a cultivated seed diet by hunter-gatherers in the Ohio valley (Paschetta et al. 2010), could result in changes in cranial measurements, obscuring underlying continuity in genetic ancestry. Exactly this contradiction between different cranio-facial shapes (Menk 1980) and shared genetic ancestry (Haak et al. 2015) characterizes the Yamnaya and Corded Ware populations described below, and might be explained by a change from a pastoral to an agricultural diet during the migrations that led to the creation of the Corded Ware population.

What exactly does genetic ancestry measure? If we think of the human genome as a book, and we think of genes as sentences or even pages in that book, then the individual letters that are the basic building blocks of the text are like the 3.2 billion bases in the human chromosomes, each consisting of a single nucleotide. More than 99% of the nucleotides are the same in all humans – there is little variation in liver, blood, or bone cells across humanity

(Tishkoff and Kidd 2004: 22). Genetic ancestry compares human genomes by counting the shared single-nucleotide bases in the variable or polymorphic sections of the chromosome, known as single-nucleotide polymorphisms (SNP's). The Harvard/Leipzig laboratories developed a method in 2013 that permitted them to selectively sample 390,000 targeted SNP's (390k capture) (Haak et al. 2015), later expanded to 1.24 million (1240k capture) (Mathieson et al. 2015), from the polymorphic portions of the chromosome. This targeted sample of polymorphic base-pairs is obtained and analyzed much more rapidly (more than 200x less sequencing time) than sequencing the whole genome of 3.2 billion base-pairs. While increased analytical speed will make genome-wide human aDNA data available for many more regions and time periods, we must remember that genetic ancestry is defined with little regard for exactly how differences in SNP's affected the phenotype. In contrast, both racial stereotypes and cranio-facial measurements focus on phenotypic traits with little attention to how they are coded genetically. A single, variable phenotypic trait such as skin color might be interesting because it is culturally salient among modern humans and it exhibits rapid changes in frequency through time and space, but skin color alone will not significantly affect a calculation of shared genetic ancestry based on 1.24 million targeted SNP's.

2 A brief overview of European mating networks during the Neolithic

The Haak et al. 2015 and Allentoft et al. 2015 analyses of aDNA variation suggested that European Mesolithic hunter-gatherers were divided into three regional populations when the first farmers arrived in Europe about 6500–6000 BCE. These could represent three groups extracted from what could later prove to be a cline. The western group (Western Hunter-Gatherers or WHG) was defined by shared traits appearing in forager samples from Spain, Luxembourg, Germany, Hungary, and Croatia; while the northern group (Scandinavian Hunter-Gatherers or SHG) lived in modern Sweden and Norway; and the eastern group (Eastern Hunter Gatherers or EHG) lived in the forest and forest-steppe zone of Russia from the Baltic to the Urals and extended south into the Volga-Don steppes north of the Black and Caspian Seas as far as the lower Danube valley. The foragers in the lower Danube (Bulgaria) were more similar to the EHG, while those in the middle Danube (Hungary) were WHG (Mathieson et al. 2016). Strikingly similar MtDNA haplogroups (U4, U5), inherited solely through the mother, were

shared between the women in all three forager populations, but the paternal Y-chromosome markers differed between them. This contrast perhaps suggests that long-distance wife exchanges occurred at least occasionally, but men were less mobile, a mating pattern consistent with patrilocal residence.

The EHG in the northern Russian forests and Pontic-Caspian steppes exhibited a group of traits termed Ancient North Eurasian (ANE), first detected in Upper Paleolithic individuals dated about 24,000 years ago near Lake Baikal (Raghavan et al. 2014). The ANE ancestry in the EHG was 70% or higher. A similar ANE element is found also in Native Americans, averaging 40% of their ancestry, suggesting that both were derived from a North Eurasian Upper Paleolithic mating network that eventually expanded into both eastern Siberia and what is now western Russia. The large ANE component in the EHG distinguished them from the foragers of western Europe (WHG), who had only traces of ANE ancestry; while skin color and some other traits separated the Scandinavian foragers or SHG (paler skin) from the WHG (darker skin, sometimes with blue eyes).

All three European Mesolithic populations were genetically distinct from the Neolithic Starčevo–Criș/Cardial–Impressed/LBK farmers whose ancestors migrated from western Anatolia to present-day mainland Greece and Crete about 6500 BCE and then spread across Europe and the Mediterranean (Deguilloux et al. 2012; Lacan et al. 2011). These Early European Farmers (EEF), whether in Spain (Cardial–Impressed culture), Hungary (Starčevo–Criș culture) or Germany (Linearbandkeramik or LBK), were very similar to each other genetically (Skoglund 2012; Haak et al. 2015). All shared a common genetic origin in Neolithic western Anatolia, represented by five individuals from Menteşe Höyük and 21 individuals from Barcın Höyük in the northwest. The EEF clearly were the descendants of people who lived in western Anatolia, and they had no ANE ancestry, which distinguished them from the EHG. The EEF imported into Europe a non-indigenous agricultural economy, a house-centered domestic life, and a set of domestic rituals, including female figurines, that were all equally novel. They spoke a language from Neolithic Anatolia, necessarily quite different from the languages that had evolved in Mesolithic Europe during the early Holocene. They were genetically about as different from the indigenous WHG foragers as modern Western Europeans are from East Asians (David Reich, *personal communication* 2016).

During and after their advance overland across Europe and by boat to the western Mediterranean, the EEF pioneers remained largely genetically

isolated from the indigenous hunter-gatherers. The EEF in Europe exhibited a rate of admixture with the WHG estimated to have been only about 7–11% higher (Mathieson et al. 2015: 529) than their Anatolian ancestors before the westward migration began. This low rate of intermarriage was demonstrated in samples taken from a 1500-year time span, 6000–4500 BCE, from Starčevo–Cris, Cardial–Impressed, and LBK/Lengyel contexts (Brandt et al. 2013; Bollongino et al. 2013; Szécsényi-Nagy et al. 2015; Haak et al. 2015). Farmers in the lower Danube valley showed higher admixture with local foragers (Mathieson et al. 2016), but this exceptional local rate of admixture was not typical of the expanding agricultural population in central and western Europe. The generally low level of genetic admixture between foragers and the EEF is unexpected, given that foods and raw materials were exchanged (Bogucki 2008; Oross and Bánffy 2009; Czekaj-Zastawny et al. 2013). The exchange of mates in marriage operated according to rules that were more restricted than those applying to material exchanges visible archaeologically in the initial Early Neolithic period. This resistance to intermarriage persisted for many centuries, challenging scenarios (Robb 1993; Thomas 2006) of a border-less flow of people and ideas between farmers and foragers. However, in the Haak et al. (2015) sample from the Middle Neolithic, dated to the late fifth and fourth millennia BCE, individuals from a megalithic grave in Spain, and from the Baalberge, Salzmünde, and Bernburg cultures in Germany showed higher percentages of WHG genes. The Allentoft et al. 2015 study repeated this Middle Neolithic increase in EEF and WHG ancestry. By this time – after most of the former WHG population had adopted agricultural economies – significant intermarriage between these populations began. When their economies converged so did their mating networks.

2.1 Neolithic European languages, wheels, and substrates

In the preliterate past, languages must have spread, at least to some extent, with migrants who either overwhelmed the local population demographically (thus attaining more speakers through differential growth) or introduced their languages through face-to-face contact and subsequent spread (subject to multiple cultural feedback systems). The migrations of EEF pioneers through Mediterranean and interior Europe certainly distributed Neolithic Anatolian language(s) with their genes, as Renfrew (2002; Heggarty and Renfrew 2014) and Bellwood (2013) argued. Bilingualism among children, a powerful driver of language interference, was reduced by the small num-

ber of inter-marriages with the WHG. Under these conditions the foragers' languages might have survived for many centuries (Campbell 2002) while the mating networks of WHG foragers and EEF remained largely separate. We should remember that the Bantu languages of Africa, which spread with a new kind of cattle pastoralism and iron technology, diversified in 2000 years into more than 500 languages belonging to 19 different branches (Nettle 1998). Sufficient time passed between 6500–4000 BCE that the original West Anatolian EEF language(s) probably had differentiated by the Middle Neolithic into dozens or quite possibly hundreds of languages (Ringe 2013; Mallory 2008: 16–18; Robb 1993), and a separate indigenous family (or families) of languages might still have survived on the Atlantic fringe among the former WHG.

We would argue that all of these languages, whether of foragers or farmers, were older than Proto-Indo-European (PIE) – they existed long before PIE did. PIE must be dated not to the Mesolithic but after the beginning of the Neolithic era, so after 6500 BCE in Europe, because many Indo-European (IE) cognate word roots securely assigned to PIE (Mallory and Adams 2006: 139–172) had meanings related to Neolithic economies (cow, bull, calf, ewe, ram, lamb, wool, milk products, ard/plow, domesticated grain). The speakers of the most archaic recoverable form of PIE, preserved in the Anatolian IE languages, were already familiar with agriculture and domesticated animals – and the pre-Neolithic WHG were not.

We also argue that the EEF were too early to represent the PIE-speaking community, against the views of Renfrew (2002), Bellwood (2013), Heggarty (2015) and the computational phylogenetics of Bouckaert et al. (2012), who connected the expansion of the IE languages with the expansion of the EEF agricultural economy. The most difficult chronological problem with the EEF-origin position is that late (post-Anatolian) PIE contained a vocabulary consisting of at least five roots for wheeled vehicles – one for the referent axle **h₂eḱs-*; two roots for wheel, **Hrotós* and **k^wék^wlos*; one noun for harness pole, **h₂/3éyH-os*; and a verb meaning 'to go in a vehicle', **wég^h-e-ti* (Meid 1975; Ivanov and Gamkrelidze 1995: 621–627; Fortson 2004: 36–38; Garrett 2006: 144–45; Mallory and Adams 2006: 247–25; Pereltsvaig and Lewis 2015: 171–176; Anthony and Ringe 2015).

Wheeled vehicles did not exist anywhere before 4000 BCE. Most of the oldest archaeological, textual, and pictographic evidence for wheels is dated after 3500 BCE (Bakker et al. 1999; Fansa and Burmeister 2004; Anthony 2007). The EEF Neolithic agriculturalists lived millennia before wheels were

invented, so could not have had a vocabulary referring to them. Late PIE contained such a vocabulary. Late (post-Anatolian) PIE must have existed as a single not-yet-differentiated language community after 4000 BCE and probably after 3500 BCE, too late to have spread across Europe with agriculture two to three millennia earlier. Early PIE, the archaic ancestor of the Anatolian branch (Jasanoff 2003), either lost or never contained clear reflexes of the wheel vocabulary (only the root for ‘harness pole’ occurs in Anatolian, and this could be part of a sledge or plow). The ancestor of the Anatolian IE languages could have separated from the remainder of PIE before wheels were invented, or before 4000–3500 BCE, consistent with many linguistic indications of archaism in the Anatolian branch. But it probably did not separate too long before then, probably after 4500 BCE, since the reconstruction of PIE is not problematic with Anatolian IE forms included, meaning that the Anatolian IE languages were morphologically, phonologically, and lexically similar enough to the other IE languages that they conformed to the same rules and regularities.

Gray and Atkinson (2005) and Heggarty (2015) raised the possibility that the five PIE roots listed above were as old as the Neolithic farmers, but referred to things other than wheeled vehicles in the Neolithic proto-language (PIE) and later changed their meanings: “The supposed ‘wheel’ words actually go back to more general words for *turn*, *rotate* and *walk*...” (Heggarty 2015: 13–14). They proposed that, after wheels were invented, it was natural for late IE speakers in the pre-Germanic, pre-Greek, pre-Indo-Iranian, and pre-Tocharian branches to independently select the PIE verb **k^welh₁-*, ‘turn’, as the root for **k^wék^wlos*, ‘wheel, thing that turns’, a word that could have been invented independently many times after 4000 BCE, in their view. The accepted derivation of English *wheel* from a PIE **k^wék^wlos* meaning ‘wheel’ is therefore a mirage, they suggested. A review of Indo-European origins in the popular journal *Scientific American* presented the computational phylogenetic support for this argument as ‘simply bringing linguistics into the 21st century’ and characterized the objections of ‘traditional’ linguists as ‘bitter’, ‘outraged’, and ‘wearing thin’ (Balter 2016: 64–65).

But linguists agree that late PIE contained a wheeled-vehicle vocabulary not because they are bitter traditionalists, but because the linguistic evidence is solid. Early PIE contained at least four different verb roots in the semantic field ‘turn’, ‘spin’, or ‘revolve’ (**k^welh₁-*, *h₂werg-*, **wert-*, **wel-*). Just one of these, **k^welh₁-*, was not likely to have been chosen as the verbal root for a ‘wheel’ word independently among the speakers of pre-Germanic, pre-

Greek, pre-Indo-Iranian, and pre-Tocharian two millennia after the break-up of PIE, while three other potential verb roots were ignored. Moreover, **k^wék^wlos* was formed from the verb **k^welh₁-* by reduplicating the initial **k^w* (actually the root of the verb), so that the root of the new noun sounded sort of like *kwe-kwe*, a playful bit of sound-shifting unlikely to be repeated systematically. Reduplication occurred in other PIE words, and **k^wék^wlos* followed the PIE rules for reduplication, including the expected loss of the **h₁* laryngeal in the duplicated member, which makes it likely that the word was formed in PIE itself, and not later (Adam Hyllested, *personal communication*). But no other noun in the PIE lexicon was made from a verb in this particular way (reduplication + zero-grade root + thematic vowel + nominative singular ending) which makes it a unique neologism and therefore very probably a single-origin word (Anthony and Ringe 2015: 205; Garrett 2006: 144–145). Widely separated daughter languages did not independently think up this same unique formation in each case when they needed to invent a new word for ‘wheel’.

And we must not forget that **k^wék^wlos* is just one part of a semantic field that strengthens the connection between late PIE and wheeled vehicles. ‘Axle’ has cognates that refer to the same essential part of a wheeled vehicle in Germanic, Celtic, Italic, Balto-Slavic, Greek, and Sanskrit, so the shared root **h₂éks-* from which they are demonstrably derived probably meant ‘axle’ in late PIE. The accumulated improbability of all of the daughters developing the same secondary meanings related to wheeled vehicles from the same five roots that originally meant something else, and then adding the required parallel independent coinage of **k^wék^wlos* and its secondary meaning of ‘wheel’ as just one of those words, is so large as to border on the impossible. The only rule-bound, regular explanation for **k^wék^wlos* is that it was part of the undifferentiated late PIE vocabulary, like the other four roots designating parts of wheeled vehicles assigned by most linguists to late (post-Anatolian) PIE. The languages of Neolithic western Anatolia, the parent speech community from which the language(s) of the EEF were initially derived at around 6500 BCE, were spoken 3,000 years before wheeled vehicles were invented. Late PIE was spoken during the diffusion of wheeled vehicle technology, which began, on present evidence, no earlier than 4000–3500 BCE.

Two other linguistic arguments add weight to the hypothesis that the Neolithic EEF did not speak IE languages: 1. the agricultural vocabulary in the IE languages has inconsistent and unstable semantics, and 2. some western IE terms for agricultural crops seem to have been borrowed from non-

IE languages. The unstable semantics of the agricultural vocabulary in PIE were addressed by Mallory (2015), who found nine PIE or late PIE roots that could potentially be agricultural-crop words. Each of the nine had cognates in multiple IE daughter branches with the meanings ‘unspecified food grain’, ‘wheat’, ‘barley’, or ‘millet’. But meanings differed between daughter branches, so no single root could be assigned a meaning more specific than ‘unspecified food grain’ or perhaps even ‘seed food’. Prehistoric Europeans ate several kinds of wild seeds, notably *Chenopodium* (Behre 2008), so ‘unspecified grain’ words could have referred to wild foods – they were not necessarily agricultural. The most stable meaning attached to any of the nine was for the root **yéwos*, which meant ‘barley’ in both Anatolian and Indo-Iranian. But other Indo-Iranian reflexes of this root also meant ‘millet’ and ‘unspecified grain’, the Greek reflex meant ‘wheat’, and the Baltic reflex ‘unspecified grain’ – by no means a stable referent in IE (Mallory 2015: Table 3). In contrast, the root **h₂éks-* meant ‘axle’ in the Indic, Italic, Celtic, Germanic, Baltic, and Greek branches, a stable referent. In a language family that we know did spread among agriculturalists, Semitic, the agricultural-crop terms retained stable meanings – specific phonological roots were linked to the referents ‘wheat’, ‘millet’, ‘leek’, ‘carrot’, ‘cucumber’, ‘garlic’, and ‘cumin’ across the daughter branches (Ehret 2015). The instability of the meanings attached to the potential IE agricultural-crop vocabulary suggests that agricultural crops, while known to the speakers of PIE, were not cultivated consistently as a necessary part of the food economy by all speakers of PIE, nor were they named in the same way across PIE.

In addition, Kroonen (2012a, 2012b) has shown that many western IE languages borrowed non-IE words for agricultural crops. Agricultural-crop words borrowed into the European IE languages from a non-IE substrate included the roots for ‘carrot’, ‘oat’, ‘lentil’, ‘pea’, and ‘bean’, all attested as parts of the introduced Neolithic EEF economy. The same roots seem to have been borrowed separately into Greek and Germanic, consistent with a derivation from a Neolithic substrate EEF language (Kroonen 2012a, 2012b; Leschber 2012; Schrijver 1997). If the EEF pioneers spoke IE languages, why did they adopt non-IE words for crops that they themselves imported into Europe? On the other hand, if the speakers of PIE had a limited agricultural vocabulary, partly borrowed from the EEF with their domesticated animals and crops, variation in the meaning of IE agricultural-crop terms and borrowing from non-IE agricultural vocabulary would be expected.

Although aDNA has revealed previously unknown details about immigrant Neolithic farmer and hunter–gatherer mating networks in Europe, it is not likely that the Neolithic EEF or the WHG hunter–gatherers spoke Indo-European languages. This means that when IE languages were adopted in Europe, they spread through a process of evolving bilingualism, language shift, and replacement in a complex linguistic landscape that probably included multiple non-IE Neolithic language families and hundreds of Neolithic languages.

3 The Corded Ware migrations, 3000–2500 BCE

The biggest surprise of the recent aDNA research was a genetic shift dated to the Late Neolithic in Germany, 2900–2400 BCE, when the Corded Ware horizon spread across most of northern and central Europe. Childe (1950: 133–138) and Gimbutas (1963) had earlier speculated that migrants from the steppe Yamnaya culture (3300–2600 BCE) might have been the creators of the Corded Ware culture, and that Corded Ware might have carried IE languages into Europe from the steppes. But the similarities between Yamnaya and Corded Ware were general – single graves under mounds, weapons in the grave, prominent gender distinctions in graves – rather than typologically specific, so seemed to suggest a diffusion of ideas rather than people, and the differences in skull shape between them (Menk 1980) seemed to support that. Recent studies argued persuasively that Corded Ware could be explained as an indigenous northern European Late Neolithic development without any external population component (Furholt 2003; 2014). However, aDNA from Corded Ware graves (Haak et al. 2015; Allentoft et al. 2015) provided surprising support for the largely-discarded steppe migration theory.

Four late Corded Ware individuals buried at Esperstedt, Germany, dated 2500–2300 BCE, in typical Corded Ware graves in typical poses, with typical Corded Ware pottery; and an additional Corded Ware individual buried in an atypical ritual in an older Baalberge monument at Karsdorf, exhibited genomes that were a mixture of Eastern Hunter–Gatherer (EHG) and a population best modeled as coming from the Caucasus. This EHG/Caucasus ancestry was unlike that of the local WHG, EEF, or the admixed WHG/EEF Middle Neolithic population in Europe. The new Corded Ware type was almost identical with the EHG/Caucasus mixture that characterized nine Yamnaya-culture individuals from six cemeteries in the Volga-Ural

region centered on Samara, Russia, dated 3200–2800 BCE (Haak et al. 2015), obtained during the Samara Valley Project (Anthony et al. 2005; Anthony et al. 2016). The five Corded Ware individuals in Germany were modeled as having ancestry 79% derived from Yamnaya, 4% from WHG, and 17% from EEF (Haak et al. 2015: 210). Moreover, the Copenhagen team studied an independent sample of ten Corded Ware/Battle Axe individuals from Estonia, Poland, Sweden (Battle Axe) and Germany, and found the same strong Yamnaya EHG/Caucasian ancestry, in this case using for their Yamnaya reference group five Yamnaya individuals from three kurgan cemeteries in the North Caucasus/Caspian steppes excavated by Shishlina (Allentoft et al. 2015; Shishlina 2008). These five Yamnaya individuals turned out to be very similar genetically to the nine Yamnaya individuals from the Volga-Ural steppes studied by Reich. Both were surprisingly similar to Corded Ware individuals from cemeteries across central and northern Europe, indicating that a massive migration of Yamnaya people from the steppes into central and northern Europe was responsible for about three quarters of the genetic ancestry of the Corded Ware population, a very surprising discovery.

Uniparental markers also changed suddenly as MtDNA haplogroup N1a (inherited through the matriline) and Y haplogroup G2a (inherited through the patriline), common in the EEF agricultural population, were replaced by Y haplogroups R1a and R1b and by a variety of MtDNA haplogroups typical of the steppe Yamnaya population. The uniparental markers show that the migrants included both men and women from the steppes. They passed on a substantial element of ANE (Ancient North Eurasian) ancestry that remains characteristic of most Europeans today; this ANE element was conspicuously missing from all sampled EEF.

The lack of gene flow between the EEF and the steppe people before Yamnaya operated in both directions. None of the Yamnaya individuals, whether in the Volga-Ural or the North Caucasus steppes, exhibited admixture with the EEF.¹ This was another surprising example of marriage exclusion maintained over a timespan measured in centuries or even millennia while

¹ The online community at the *Eurogenes* blog (<http://eurogenes.blogspot.com.au/2016/05/yamnaya-khvalynsk-extra-chg-maybe.html>) described a faint signal of EEF admixture barely above the ‘noise’ level in the Yamnaya samples of Haak et al. and Allentoft et al. by experimenting on the published genetic libraries with different algorithms. If this result is real and not a statistical artifact, the faintness of the signal still would indicate a very low admixture rate between EEF and Yamnaya.

exchanges of archaeologically visible material goods and innovations proceeded. Steppe communities in the Dnieper valley acquired their first domesticated cattle, sheep, and goats, possibly with some of the feasting rituals in which they were embedded, from Starčevo–Criș EEF before 5500 BCE (Anthony 2007: Chapter 8; Benecke 1997). Before 4500 BCE they learned from the EEF Cucuteni-Tripolye culture to weld and repair small copper objects, and copper ornaments were traded from EEF communities into the steppes where they became a marker of social distinction at Khvalynsk on the Volga, dated about 4500 BCE, and at other steppe cemeteries. But while the genetically sampled Khvalynsk individuals showed admixture with populations from the Caucasus and served very well as genetic ancestors of the Yamnaya population (Mathieson et al. 2015), they showed no trace of EEF admixture. Prior to the Yamnaya migrations of 3000–2500 BCE, EEF did not migrate into the steppes or marry into steppe communities that have been sampled to date. The pre-Yamnaya pastoralists of the western steppes also were excluded from the mating networks of known EEF, who showed no ANE ancestry.

The Yamnaya horizon spread across the Pontic-Caspian steppes rapidly about 3300–3000 BCE with a newly mobile pastoral economy made possible by the combination of horseback riding and bulk wagon transport. Many Yamnaya families probably lived in their wagons much of the time – no settlements are known in the Volga-Ural steppes, where there are hundreds of small Yamnaya kurgan cemeteries (Anthony 2007: chapter 13). Not long after this mobile form of pastoralism was invented it spread into the drier parts of the lower Danube valley. Hundreds of Yamnaya-type kurgans and dozens of cemeteries have been recognized in a string of sites beginning at the western edge of the steppes, north of the Danube delta, extending up the lower Danube valley in Bulgaria and Romania in the more steppe-like parts of the region; and ending in a large, spatially coherent cluster of hundreds of kurgan cemeteries in eastern Hungary north of the Körös River, with radiocarbon dates that began about 3000–2800 BCE and extended to about 2700–2600 BCE (Ecsedy 1979; Sherratt 1986; Boyadziev 1995; Harrison and Heyd 2007; Heyd 2012; Kaiser and Winger 2015).

The migration that created these cemeteries now can be seen to have continued from eastern Hungary across the Carpathians into southern Poland, where the earliest material traits of the Corded Ware horizon are dated (Furholt 2003). Corded Ware traditions in material culture first appeared in southern and central Poland in a context of cultural opposition and co-

existence between immigrant pastoralists and the indigenous people of the Globular Amphorae culture. The two groups apparently were reluctant to intermarry, in spite of continuing co-residence for centuries in the same landscape, with Corded Ware people using ceramic amphorae borrowed directly from Globular Amphorae types (Machnik 1999; Czebreszuk and Szmyt 2011). The immigrants retained salient characteristics of the steppe Yamnaya culture, including the celebration of individual distinction symbolized by single graves under mounds often containing weapons, a mobile pastoral economy, and prominent gender distinctions. They created a set of Corded Ware customs that combined local pots and axes with Yamnaya customs into a new hybrid material culture. This hybridity in material culture obscured the scale of the migration indicated by aDNA from Corded Ware graves.

The genetic effects of the Yamnaya migration lessened after the Corded Ware period. Ten Bell Beaker individuals dated 2500–2100 BCE from five cemeteries in Germany, and nine Únětice individuals dated 2100–1900 BCE from four cemeteries showed 50–70% Yamnaya-derived ancestry (Haak et al. 2015: S.I. 3). This was less than most Corded Ware individuals, indicating that mating networks with the old WHG/EEF population now were opening. Again, Allentoft et al. (2015) found the same increasing admixture between steppe-derived and EEF/WHG-derived populations in Bell Beaker and Únětice cemeteries. The admixed Bell Beaker and Únětice population was almost indistinguishable genetically from many modern Europeans. After the Bell Beaker period, the genetic composition of Europe continued to the present day without another demographic discontinuity comparable in scale to the migrations from the steppes, 3000–2500 BCE.

4 The eastward Afanasievo migrations, 3000–2500 BCE

Allentoft et al. (2015) posited a simultaneous west-to-east migration from the western steppes eastward to the Altai Mountains around 3000 BCE (Svyatko et al. 2009) by Yamnaya-culture migrants who created the Afanasievo culture in the western Altai Mountains. The Afanasievo culture introduced sheep-goat-cattle pastoralism, domesticated horses, copper metallurgy, and kurgan graves, but not cereal cultivation, to the alpine meadows of the western Altai, previously inhabited by hunter-gatherers. Most archaeologists of the region have interpreted the Afanasievo culture as derived from the west (Shul'ga 2012; Fribus 2012; Svyatko et al. 2009; Motuzaite-Matuzeviciute et al. 2016),

and most identify the Yamnaya culture specifically as its origin. According to aDNA, the Altai Afanasievo population was “genetically indistinguishable” from the Yamnaya population in the Volga-Ural region (Allentoft et al. 2015). If Yamnaya people spoke late PIE, Afanasievo carried this language to the borders of modern China, not too far from where Tocharian later appeared.

The Yamnaya migration that flowed from the Pontic-Caspian steppes westward into northern Europe beginning about 3000 BCE was mirrored by an equally significant and contemporary Yamnaya migration that streamed eastward across Kazakhstan to the western Altai. But unlike the westward migration up the Danube, the eastward migration to the Altai did not leave a string of sites and cemeteries representing sequential movements on a path leading away from the western steppes. Only a handful of Yamnaya–Afanasievo sites could represent stopping-off places in the 2000-km space between the Urals and the Altai, the best-studied being the cemetery at Karagash (Anthony 2007: 309). The eastward migration seems to have targeted the western Altai as a pre-determined destination. The reason for such a long-distance migration still puzzles archaeologists. The western Altai has gold, copper, and tin deposits that were exploited after 2000 BCE (Stollner et al. 2011) and perhaps were mined during the Yamnaya–Afanasievo period; also the grasses and herbs of the eastern mountain meadows were more nutritious forage for livestock than any pasture at lower altitudes (Frachetti 2008: 92–98). Still, how did Yamnaya people in the western steppes become aware of these distant attractions, and why did they go so far? As Kristiansen notes in this volume, the emergence of *Yersinia pestis* as a new human disease vector at a time estimated at 3800–3600 BCE, just before the Yamnaya period (Rasmussen et al. 2015), suggests that an outbreak of septicemic or pneumonic plague in the western steppes might have provided part of the ‘push’ that impelled both migrations.

5 Conclusion: migration, border maintenance, and language

Ancient DNA analysis has expanded the tools available to archaeologists, permitting us to incorporate mating networks, migration, and adaptation into archaeological interpretation in new ways, and to combine these new sources of information with linguistics. No rules yet exist for combining the data sets, so we are in uncharted territory. But aDNA already has produced new information that challenges old ideas. Two of the subjects that clearly

require re-thinking in light of the aDNA evidence are migration and cultural frontiers. Prehistoric migrations are now much more visible and amenable to demographic analysis than they were not long ago, and mating networks, previously almost invisible, are now revealing cultural borders where marriage exclusion limited cross-border marriages for centuries between tribal societies. Both of these discoveries have implications for linguistics and language affiliation.

5.1 Migration and language expansion

Large-scale migrations by agriculturalists are thought to have been the principal techno-economic driver of large-scale language expansions among state-less societies, rather than conquest or elite dominance (Renfrew 1987; van Andel and Runnels 1995; Heggarty and Renfrew 2014; Bellwood 2013). The spread of a new economy that encouraged higher demographic growth is thought to have been the principal vector that drove large-scale prehistoric migrations, resulting in the expansion of the language(s) spoken by the expanding population and the decline of languages spoken by people whose population remained stable or declined. This is the *subsistence/demography* model of language expansions, and is one of the principal arguments supporting the linkage between the spread of the IE languages and the Neolithic spread of agriculture (Renfrew 1987; Heggarty and Renfrew 2014: 39). Agricultural expansions established the most intensive, sedentary economy that humans have invented, so the initial agricultural expansions were thought to have been followed by local growth and substantial continuity in population and language until the modern era. The agricultural spread-and-stay model was supported by the ‘serial founder effect’ theory in demography, which proposed that modern human genetic variation worldwide also could best be interpreted as resulting from a series of long-distance leaps followed by local continuity (DiGiorgio et al. 2009). But the ‘serial founder effect’ model has been proved wrong by both ancient DNA and revised genetic algorithms (Pickrell and Reich 2014). In this essay we saw that the Paleolithic populations of Europe were largely replaced by Neolithic populations derived from western Anatolia, and the Neolithic agricultural population was largely replaced by a massive new migration from the steppes in the Bronze Age.

The Yamnaya expansion followed a different kind of shift in subsistence economics – the evolution of a mobile, wagon-based, equestrian form of steppe pastoralism. It is not clear that this shift permitted greater demo-

graphic growth. Rather, it facilitated the systematic exploitation of a previously under-utilized environment, the interior grasslands of the Eurasian steppes; and outside the steppes the increase in mobility associated with wagons and horse-aided herding permitted social-political networking and economic integration across larger regions. The Corded Ware networking diagram created by Furholt (2014) showed how much larger the networked area was between Corded Ware regional communities than it had been previously among the local, regionalized cultures of the Middle Neolithic in northern Europe, and Czebreszuk and Szmyt (2011) showed how much more mobile the early Corded Ware economy was in Kujavia, an early target of Corded Ware migrants, than it was for the Globular Amphorae or other indigenous archaeological cultures in the same area.

Migration and large-scale demographic shifts occurred under a variety of conditions (Anthony 1990) beyond the initial spread of agriculture. The scope of shifts that facilitated language expansion has therefore itself expanded. Large-scale migrations are not often used to explain prehistoric culture changes in Europe, but they are accepted as a regular, recurring, and significant cause of culture change in American archaeology, where understanding prehistoric migration is a central part of archaeological theory, particularly in the southwestern US (Lyons 2003; Mills 2011). The Corded Ware–Yamnaya–Afanasiovo migrations affected half of the Eurasian continent, a much larger networked region than was affected by the expansion of west Anatolian farmers, so in that sense they make the best candidate for the vector for the continent-wide distribution of IE languages; and their timing (after the invention of wheeled vehicles) makes them chronologically suitable.

5.2 Mating networks, border maintenance, and language

Cultural frontiers or borders are the second topic for which the recent aDNA studies pose challenges to mainstream archaeological thinking. Since Barth (1969) we have accepted that cultural identities, including language affiliation, are strengthened at borders where contrasts with Others are the greatest, and that people often interact across borders (including bilingualism among adults) while maintaining strongly opposed identities and domestic languages. However, most ethnographic studies of borders in the modern world emphasize the creative hybridity that often emerges in border zones, and the flow of ideas and customs across them (Donnan and Wilson 1999). In modern settings Barth's enduring frontiers seem to be ideological fictions

honored more in the breach than in actual behavioral conformity to stereotype. In prehistory, as in the modern world, we tend to seek out evidence for interdependence at border zones. But Vehik (2002) showed long ago that in the proto-historic American Southwest, where interchange between bison-hunting foragers and maize-planting pueblo dwellers inspired much of the American literature on economic interdependence, the extent of interdependence was exaggerated, and the actual exchanges were limited in scale. The pueblo/bison hunter cultural border was more like a Barth border, a persistent zone of political and economic opposition linked by limited material exchanges. Similar persistent borders are indicated by the aDNA in Neolithic and Bronze Age Europe as well as in the Neolithic Near East (Lazaridis et al. 2016).

Among modern ethnographies providing insight into the cultural maintenance of such oppositional borders, an instructive example is John Cole and Eric Wolf's neglected study (Cole and Wolf 1999) of Romance-Germanic opposition at the linguistic frontier between German and Italian-speaking parts of Italy in the southern Tyrol. Here the German-speakers were the immigrants (after the fall of the Roman empire), their economies were distinct from their Romance neighbors (mountain pastoral-focused farming versus lowland agriculture-focused farming), the Germanic/Romance relationship was punctuated historically by violence breeding mistrust, the two ethnicities maintained negative oppositional stereotypes of each other, and church records showed that marriages between neighboring Germanic and Romance villages on the cultural frontier were close to zero (less than 2% of marriages) going back almost 300 years (Cole and Wolf 1999: 256–259). The border was maintained by a persistent culture of opposition within a state (Italy) that tried but failed to encourage integration. The demographically more powerful state language (Italian) did not spread into the mountains.

The mechanisms that kept the two sides apart were centuries-long cultural (not legal) restrictions on inter-marriage, documented in church records; and, connected with that, cultural restrictions on the acquisition/alienation of land to an inheritor/buyer from the opposed group, again proven through land records (Cole and Wolf 1999: 155–156). The combination of marriage exclusion and refusal to cede land rights across the border preserved the Germanic/Romance cultural border and its defining linguistic, organizational, and economic differences for a thousand years, even while a modern nation-state incorporated territory on both sides.

This example suggests that the persistent resistance to intermarriage between people who had different economies and resources, revealed by aDNA in prehistoric Europe, is not just a surprising and interesting discovery, but also was a practice that, if sustained, could maintain and support persistently oppositional linguistic and cultural identities in a non-state political setting. Case studies like Cole and Wolf (1999), neglected because they were thought to describe special or exceptional borders, will repay a second reading as we adjust to a prehistoric Europe that challenges many of our preconceptions.

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