

Open access • Posted Content • DOI:10.1101/2020.09.18.300087

Combining Ancient DNA and Radiocarbon Dating Data to Increase Chronological Precision — Source link

Jakob Sedig, Nick Patterson, Iñigo Olalde, David Reich

Institutions: Harvard University, Massachusetts Institute of Technology

Published on: 18 Sep 2020 - bioRxiv (Cold Spring Harbor Laboratory)

Topics: Radiocarbon dating and Ancient DNA

Related papers:

- Combining ancient dna and radiocarbon dating data to increase chronological accuracy.
- Empirical calibrated radiocarbon sampler: a tool for incorporating radiocarbon-date and calibration error into Bayesian phylogenetic analyses of ancient DNA
- Challenges in sample processing within radiocarbon dating and their impact in 14C-dates-as-data studies
- Cumulative probability functions and their role in evaluating the chronology of geomorphological events during the Holocene
- Building and testing age models for radiocarbon dates in Lateglacial and Early Holocene sediments



1	COMBINING ANCIENT DNA AND RADIOCARBON DATING DATA TO
2	INCREASE CHRONOLOGICAL PRECISION
3 4 5	Jakob W. Sedig ^{1,2} , Iñigo Olade ^{1,3} , Nick Patterson ^{1,2} , David Reich ^{1,2,4,5}
5 6 7 8	 ¹ Department of Genetics, Harvard Medical School, Boston, MA 02115, USA. ² Department of Human Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA
9	³ Institute of Evolutionary Biology, CSIC-Universitat Pompeu Fabra, 08003 Barcelona,
10	Spain.
11	⁴ Broad Institute of Harvard and MIT, Cambridge, MA 02142, USA.
12 13	⁵ Howard Hughes Medical Institute, Harvard Medical School, Boston, MA 02115, USA.
14	Correspondence to: Jakob Sedig (Jakob_Sedig@hms.harvard.edu)
15	
16	
17	
18	Abstract
19	
20	This paper examines how ancient DNA data can enhance radiocarbon dating. Because
21	there is a limit to the number of years that can separate the dates of death of related
22	individuals, the ability to identify first-, second-, and third-degree relatives through
23	aDNA analysis can serve as a constraint on radiocarbon date range estimates. To
24	determine the number of years that can separate related individuals, we modeled
25	maximums derived from biological extremes of human reproduction and death ages and
26	compiled data from historic and genealogical death records. We used these estimates to
27	evaluate the date ranges of a global dataset of individuals that have been radiocarbon
28	dated and for which ancient DNA analysis identified at least one relative. We found that
29	many of these individuals could have their date ranges reduced by building in date of
30	death separation constraints. We examined possible reasons for date discrepancies of
31	related individuals, such as dating of different skeletal elements or wiggles in the

32	radiocarbon curve. Our research demonstrates that when combined, radiocarbon dating
33	and ancient DNA analysis can provide a refined and richer view of the past.
34	
35	Keywords
36	Ancient DNA; radiocarbon dating; genealogy; Bayesian analysis
37	
38	
39	1. Introduction
40	
41	This article examines how aDNA data can be used innovatively to help with a central
42	aspect of archaeological research-chronology. Ancient DNA (aDNA) data are
43	revolutionizing the field of archaeology. Within the last decade alone, aDNA analyses
44	have discovered new hominins (Reich et al., 2010), elucidated the spread of farming
45	through Europe (Lazaridis et al., 2016; Mathieson et al., 2015), shed light on the peopling
46	of the Americas and Oceania (Lipson et al., 2018; Moreno-Mayar et al., 2018; Posth et
47	al., 2018; Rasmussen et al., 2014; Skoglund et al., 2016), and more. While aDNA has
48	helped provide insight on long-standing archaeological questions, exponentially
49	increasing aDNA data has created unique opportunities for the examination of finer-
50	grained issues, and even archaeological methods.
51	The basis of the work presented here is tied to the fact that there is a maximum
52	number of years that can separate the dates of death (DOD) for two or more genetically
53	related individuals. For example, it is exceedingly rare for a mother to die 100 years

54 before her daughter, particularly in pre-modern societies. Thus, if two or more

55	individuals are identified as biological relatives through aDNA analysis and those
56	individuals are radiocarbon dated, their relatedness can be used as a prior or constraint
57	when analyzing their overlapping radiocarbon date ranges. Using these constraints, we
58	examine how the identification of genetic relatives can help identify errors and outliers in
59	radiocarbon dating, how biological relatedness can be used to constrain overlapping
60	radiocarbon date ranges and increase dating precision, and how application of the
61	methods to a large database of published ancient DNA data
62	(https://reich.hms.harvard.edu/downloadable-genotypes-present-day-and-ancient-dna-
63	data-compiled-published-papers) can reveal potential larger issues in the radiocarbon
64	record at particular times and places.
65	
66	
67	2. Materials and Methods
68	2.1 Identification of genetic relatives with ancient DNA
69	
70	Identification of genetic relatives has become standard practice in ancient DNA analysis.
71	Typically, individuals which are screened and produce working genomic data are

72 compared against each other and previously analyzed individuals from similar geographic

regions and time periods to identify unique genetic relationships. For each pair of

74 individuals in this study, we computed the mean mismatch rate using all the autosomal

75 SNPs with at least one sequencing read for both individuals in the comparison (this

76 procedure to identify genetic relatives is described in Kennett et al. (2017:156) and van

de Loosdrecht et al. (2018:15), and is similar to that in Kuhn et al. (2018:157)). In the

bioRxiv preprint doi: https://doi.org/10.1101/2020.09.18.300087; this version posted September 18, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

78	cases with more than one sequencing read at a particular SNP for a given individual, we
79	randomly sample one for analysis. We then estimate relatedness coefficients as in
80	Kennett et al (2017:156): $r = 1 - ((x-b)/b)$ with x being the mismatch rate and b the base
81	mismatch rate expected for two genetically identical individuals from that populations,
82	which we estimate by computing intra-individual mismatch-rates. We also compute 95%
83	confidence intervals using block jackknife standard errors (Olalde et al., 2019:S61).
84	While such analysis can detect relationships up to the 5th degree, we limit relationships
85	here to 3rd degree maximum, as DOD date separations become too great to be of use
86	with decreasing genetic relatedness (e.g. great-grandparents and grandchildren).
87	
88	2.2 Genetic relatives and DOD separation maximums
89	
90	Below, two approaches-biological maximums and genealogically and historically
91	derived estimates—are examined for determining the DOD separation of genetically
92	related individuals. The biological maximums serve as theoretical extremes that, while
93	biologically possible, are very rare and unlikely to occur, especially in pre-industrial
94	archaeological cultures. Genealogically and historically (GH) derived DOD separations
95	were created through the examination of genealogical records and historic data and
96	reflect more realistic estimates of the number of years between the death of two related
97	individuals.
98	
99	2.3 Biological Maximum DOD Estimates

101	Biological maximum estimates use extremes of human reproduction and lifespan to
102	produce maximum DOD separation estimates. Figures 1 and 2 (also see SM 1) are
103	diagrams of how these estimates were modeled. The start of these models is set at 0 CE.
104	At this point, a couple consisting of a 15-year-old male and female parent a male child.
105	This child dies at birth, but both parents live to be 100 years old. Thus, the DOD
106	separation between the child and parents would be 85 years. If instead the mother died
107	during childbirth, but the child lived to 100 years old, the maximum DOD separation
108	between parents-offspring would be 100 years. Siblings have an even greater potential
109	maximum DOD separation, as Figure 2 demonstrates. In this model, the 15-year-old
110	couple has a male child that dies at 0 CE. That same couple has another child 30 years
111	later (when they are 45 years old); that second child then dies 100 years later. So, the
112	maximum separation between the siblings is 130 years.



113

114 Figure 1. Model of biological maximum date of death separation for parents-offspring.



116 Figure 2. Model of biological maximum date of death separation for siblings.

Using these parameters, a number of potential biological maximums were modeled for various degrees of genetic relatedness (Table 1; see SM 1 for diagrams of models). The biological DOD maximums presented above and in Table 1 are reliant on extremes-producing children at the biologically earliest and latest possible ages and living to extreme old age. While possible, these DOD separations are not realistic, and are largely ineffective as constraints on C14 date range distributions. Thus, to more effectively examine how date of death separations for related individuals can be applied to overlapping radiocarbon ranges, we also compiled birth and death data from historical and genealogical records.

Relation	Max Years Separation
1 st (Parents-Offspring)	100
1 st (Siblings)	135
2 nd (Grandparents- Grandchildren)	180
3 rd (Cousins)	195
2 nd (Aunts/Uncles- Nieces/Nephews)	210

131 Table 1. Theoretical DOD separation biological maximums.

132

133 2.4 Genealogically and Historically Derived DOD Estimates

134

135 We began compiling data on the date of death separations for related individuals 136 by consulting the plethora of genealogical and historical data that are publicly available 137 online. Many of these databases consist primarily of people of European ancestry who 138 lived within the last two centuries. However, to create date of death estimates from 139 heterogenous data, we sought non-European focused databases for relatives' death dates. 140 Data were gathered from historic Anglo cemeteries, and online databases of birth and 141 death dates for Cherokee, Tlingit, and other Native American groups (SM 2). Data were 142 sorted by categories of relatedness: parent-offspring, sibling, grandparent-grandchild, and other 2nd-3rd degree (aunts-uncles/nieces-nephews and cousins). 143 144 The DOD separation for related individuals was compiled into a spreadsheet for 145 each genealogical database (SM 2). DOD separations were calculated by identifying 146 related individuals then subtracting the dates of death (i.e. if a mother and daughter were 147 identified, and the mother died in 1800 CE and the daughter 1850 CE, the separation

148	between the two entered in the database would be 50). For parent-child and grandparent-
149	grandchild relationships the signed value of the DOD was recorded. As will be discussed
150	later, knowing whether the child died before the parent (which would result in a negative
151	value) is useful for building constraints of parent-child and grandparent-grandchild
152	radiocarbon ranges. However, since in many instances aDNA cannot determine the
153	relatedness direction of two individuals (e.g. which is the mother and which is the
154	daughter) the absolute value of DOD separation of each relative pair was recorded for
155	each relationship type and is primarily used for the analyses below.
156	A total of 5235 relative DOD separations were recorded: 800 parent-offspring,
157	813 sibling, 485 grandparent-grandchild, and 3137 other 2nd-3rd degree. The means,
158	medians, and standard deviations of the absolute value for each relationship type were
159	then calculated; the results are provided in Table 2 (see also SM 2).

161 Table 2. Compiled genealogical and historical data for DOD absolute value separation

	Parent- Offspring	Sibling	Grandparent- Grandchild	Other 2 nd -3 rd relationships
Mean	28.84	26.33	35.00	34.94
Median	26	20	39	30
Standard Dev.	18.94	22.41	31.93	25.6

The data in Table 2 demonstrate that the biologically maximum DOD separation
estimates in Table 1 are truly extremes. The largest mean separation in the GH dataset
was 35.00 years between grandparents-grandchildren. The single greatest DOD
separation in all the data was 117 years between Cherokee 2nd/3rd degree relatives—still

168	93 years short of the $2^{nd}/3^{rd}$ degree maximum theoretical estimate (210 years). The mean
169	GH DOD separation estimates for parents-offspring, siblings, and grandparents-
170	grandchildren are 71.16, 108.67, and 145.00 less than the biological maximum separation
171	estimates (Table 1), respectively.
172	The DOD separations above were produced by manual collection from online,
173	publicly available resources. However, in a 2018 study Kaplanis and colleagues
174	developed software and an analysis pipeline to examine genealogies of millions of
175	individuals downloaded from the online genealogical database geni.com. Kaplanis et al.
176	(2018) used this data to construct family trees (sometimes containing millions of
177	individuals); the anonymized data from this study were made available to download
178	(https://familinx.org/). Significantly, the data contained information on which individuals
179	had parent-offspring relationships, and the death date for each individual. We therefore
180	downloaded these data and found the DOD separation for over 8 million parents and
181	offspring (SM 3). We removed pairs with data errors (for example a death date of 3500)
182	and used the biological DOD separations defined above for parent-offspring as
183	constraints (i.e. 85 years for children dying before parents and 100 years for parents
184	dying before children). The mean absolute value DOD separation for these 8 million
185	parent-offspring pairs was 31.43 years, slightly higher than the mean value we manually
186	collected (28.84; SM 2); however, this should be expected as the geni.com data is heavily
187	weighted toward modern, European individuals who likely had longer life spans. Overall,
188	the similarity between the Kaplanis et al. 2018 data and the genealogical and historical
189	data we manually curated demonstrates that the DOD separations we obtained represent
190	more realistic DOD separations for related individuals than the biological maximums.

191	Although the DOD separation estimates derived from GH data are more reflective
192	of separations between genetic relatives than the biologically possible maximums, the
193	GH data presented here should be viewed only as rough estimates. More precise
194	estimates could be tailored for particular types of social organization, such as hunter-
195	gatherers, pastoralists, agriculturalists, city-dwellers, nomads, etc. However, should
196	researchers wish to create new models, the GH estimates above likely will not be
197	exceeded, as many of the separations were derived from individuals who lived after the
198	industrial revolution and likely had longer lifespans than ancient individuals.
199	
200	
201	3. Application and analysis
202	3.1 Applications of relatedness data to radiocarbon dated individuals
203	
204	We examined the ancient DNA database of published individuals from geographic
205	locales across the globe spanning more than 30,000 years (although there is bias towards
206	the last 10000 years in western Eurasia; see Marciniak and Perry, 2017; Reich, 2018) to
207	test how DOD separation estimates can be applied to related individuals and examine if
208	any new insights can be revealed. As of May 2020, 3,965 published individuals were in
209	the database, with 1,127 ancient individuals having at least one identified relative. Of
210	those, 190 pairs (231 unique individuals, SM 4) had both individuals C14 dated (all dates
211	generated with AMS and calibrated two-sigma), allowing for analysis of DOD
212	separations and constraints.
213	

216 The most basic example of how genetic relatedness can help refine radiocarbon dating is 217 through the identification of anomalies. Archaeologists have long recognized that C14 218 sample contamination can occur and that other issues, such as the marine reservoir effect, 219 can cause dates to be skewed (Taylor and Bar-Yosef, 2014). Genetic relatedness is a new 220 independent measurement that can be used to test the validity of radiocarbon date ranges, 221 particularly for samples that might not be obvious outliers. For example, if five skeletons 222 from the same stratigraphic layer in a cemetery were dated, and four of those individuals 223 had calibrated ranges of approximately CE 1-500, while one had a calibrated date range 224 of approximately 2500-2000 BCE, that one sample would seem suspicious and would 225 likely be redated (Figure 3). However, if that outlier instead had a range of approximately 226 CE 600-1000, the skeleton might not be redated, as it is relatively close to the range of 227 the other four skeletons (Figure 3). But, if it was determined that the outlier was actually 228 the father of skeleton 3, then it would be highly suspicious that skeleton 5 could be older 229 than skeleton 3, as the DOD separation between father and offspring cannot biologically 230 be more than 100 years, and more realistically is around 29 years from GH DOD 231 estimates (Table 1). Such an example was discovered in the database.



Figure 3. Examples of clear outliers in radiocarbon dating (L) and an individual that is anoutlier but does have overlap with other dates (R).

236	Two individuals, I2457 and I2600 (Olalde et al., 2018), were excavated from two
237	sites, Amesbury Down and Porton Down, Britain, separated by approximately 5km. The
238	samples had been previously radiocarbon dated; prior to aDNA analysis and the dates did
239	not seem suspect (I2457= 3890 <u>+</u> 30; 2480-2280 calBCE, SUERC-36210;
240	I2600=3646+27; 2140-1940 calBCE, SUERC-43374; Figure 4). Ancient DNA analysis
241	of the samples revealed that I2600 was the daughter of I2457, but there was thus no
242	overlap in the calibrated distributions of the father-daughter pair. The minimum DOD
243	separation between the father and daughter was 140 years, which exceeds even maximum
244	biological estimates. Individual I2457 (the father) was therefore redated and the new date
245	(3717+28; 2200-2031 calBCE; SUERC-69975) fit within the expected DOD spread
246	(Figure 5).



Figure 4. Original AMS dates for I2457 and I1600.







Figure 6. AMS ranges for I2457 and I2600 with relative constraints added.

281

282 Not all date ranges can be constrained as significantly as with these relatives, as
283 demonstrated by individuals I1054 and I1053 (Narasimhan et al., 2019), two siblings

- from the Russian Sintashta archaeological culture. Their date ranges overlap almost
- entirely (Figure 7). Thus, using the 26-year GH DOD separation estimate for siblings,

only a minor reduction can be made for their individual and combined 2-sigma date





Figure 7. AMS ranges for I1054 and I1053 with relative constraints added.

290

288



292

293 We applied the date range distribution tail trimming approach outlined above to the 190

- dated relative pairs in the database (we used separations of 29 years for parent-offspring,
- 295 26 for siblings, and 35 years for 2nd-3rd degree of unknown specificity as constraints).
- 296 We focus below on GH DOD derived constraints, as the biologically maximal DOD
- 297 constraints often exceeded the overlap of the related pairs' C14 distributions. As
- 298 mentioned above, since the type and directionality of relationships often cannot be
- 299 precisely determined through aDNA analysis, we used the largest mean absolute values

300	for DOD separations derived from GH data. In other words, if a pair could only be
301	distinguished as 1st degree relatives (either parent-offspring or siblings), the largest mean
302	GH DOD separation for first degree relatives was used, which is 29 years (for parent-
303	offspring, not 26 years for siblings).
304	After applying GH DOD constraints to the dataset, we removed 21 pairs because
305	their 2-sigma calibrated date ranges did not overlap and exceeded the GH DOD
306	estimates, suggesting dating error/a need for redating (uncorrected marine reservoir
307	effect, sample contamination, etc). This left a total of 169 pairs and 219 unique
308	individuals (SM 4). Applying the GH constraints, we were able to reduce the 2-sigma
309	calibrated ranges of 132 individuals, with a mean reduction of 54.47 years (Table 3 and
310	SM 4.2); 77 individuals had even more of a reduction than this. Figure 8 is a graph of the
311	difference between the original 2-sigma calibrated range and the GH constrained range
312	for each individual.

Table 3. Date ranges for all individuals in relative pairs.

	Original Range ¹	GH Range ²	(O)- (GH) Change ³
Mean	203.44	149.00	54.47
Standard Deviation	95.89	86.60	75.82

¹Original range is the 2-sigma calibrated range for the individual. ²GH range builds in the constraints derived from ethnographic/historic records for each individual (Table 2).

³(O)-(GH) Change is the original range minus the constrained biological range for each

individual, which reveals how many years of the original range are removed from the tail

319 ends of the 2-sigma distributions when GH estimate constraints are applied.



320

Figure 8. Difference between original 2 sigma calibrated date range and GH constrained
range for all 219 individuals, ordered from most recent date BP to oldest.

324 One possible reason for large date range reductions is if different skeletal 325 elements were radiocarbon dated for each individual in the relative pairs. Studies have 326 demonstrated that different skeletal elements have different rates of remodeling and 327 carbon uptake (Calcagnile et al., 2013; Cook et al., 2015; Hansen et al., 2017; Pinhasi et 328 al., 2015); for example, a long bone (tibia, femur, etc.) remodels throughout an 329 individual's life and therefore regularly uptakes new carbon, whereas the otic capsule 330 completes formation in utero and does not remodel during an individual's lifetime. Thus, 331 if a femur and otic capsule from the same individual are radiocarbon dated, two different 332 dates may be generated, particularly in advanced-age individuals. This could potentially 333 lead to discrepant date ranges for related individuals—if the otic capsule of an adult 334 female who died giving childbirth was dated, while the femur of her daughter was used, 335 there could in theory be a difference of more than 100 years. We therefore compiled data 336 on which element of each individual was radiocarbon dated; information on which 337 skeletal element was radiocarbon dated for each individual is provided in SM 4.1. 338 Unfortunately, in many instances no information on which element was dated was 339 available in the published literature. Additionally, if information was provided, it was 340 sometimes imprecise or vague. An element might be listed as "petrous", but with no 341 information on if the otic capsule, cochlea, or ossicles were radiocarbon dated-these 342 could generate earlier dates than the surrounding petrous pyramid or temporal bone. 343 We hypothesized that there would be a higher number of individuals above the 344 54.47 GH mean reduction for individuals in a related pair that had different skeletal 345 elements C14 dated. Table 4 provides counts of whether the skeletal element dated for 346 each individual was different or the same (or if no information was available) as their 347 relative. While there does seem to be a higher proportion of individuals with reductions 348 above the 54.47 year GH mean in instances where different elements were radiocarbon 349 dated, this is not statistically significant (chi-square test; $x^2=1.96$, p value= 0.3755, df=2; 350 SM 4.4), suggesting that dating different elements of related pairs does not significantly 351 impact the reductions made with GH constraints. This likely is due to the fact that despite 352 different elements being dated, most relatives were relatively close in age (likely because 353 few individuals in pre-modern societies reached advanced age), or that the different 354 elements dated had similar bone remodeling/carbon uptake rates. Despite this, it is likely 355 that some instances of large discrepancies can be explained by the C14 dating of different 356 skeletal elements.

357

Table 4. Counts and percentage of whether the same or different skeletal elements wereused to date an individual in a relative pair.

Comparison of skeletal element dated for each related pair	N individuals	% above 54.47 year mean GH reduction per element category
Different elements	26	50.0
Same element	138	30.9
No information	55	34.1

³⁶¹

362

363 We next examined whether applying GH constraints could reveal larger patterns 364 in the dataset. To explore if there were any periods which had a higher number of 365 relatives that exceeded the mean reduction than others, we binned into 500-year intervals 366 all 3965 published individuals in the database and the 219 dated individuals with 367 genetically identified relatives. This allowed us to examine if periods with high numbers 368 of individuals above the 54.47 year mean GH reduction were indicative of anomalies in 369 the radiocarbon record (i.e. calibration curve issues, uncorrected marine reservoir effects, 370 etc) at a particular date interval, or merely an artifact of sampling the database. Figures 9a 371 and 9b qualitatively demonstrate that periods with a high number of individuals with a 372 reduction above the 54.47 year mean roughly corresponds with the 500-year intervals that have been most densely sampled for aDNA. We performed a x^2 test to test the null 373 374 hypothesis that the number of individuals above the 54.47 year mean GH reductions per 375 500-year interval correlates with the total number of individuals sampled per 500-year 376 interval. We found a x^2 value of 57.43 (df=20), giving a p value= 1.76717E-05 (SM 4.5), 377 rejecting the null hypothesis and suggesting that the number of individuals above the 378 54.47 mean GH reduction per 500-year interval is not simply due to the overall number 379 of individuals sampled per 500-year interval. The most notable intervals were 7999-7500

- 380 BP, 7499-7000 BP, 4999-4500 BP, and 4499-4000 BP (Figure 9.C), which had residual
- 381 values of 4.86, 5.07, 11.59, and 1.65, respectively (SM 4.5).
- 382
- 383



384

Figure 9. Data from the database and 219 individuals with relatives binned in 500-year intervals. A) #of individuals total in each 500-year interval. B) # of relatives per interval that exceed the 54.47-year mean GH reduction C) Residuals from x^2 test.



plateaus. MX 190's 2-sigma range falls on a curve plateau and is much larger than MX
188's (Figure 14; 2861-2342 calBCE, ETH-19935 and 2495-2399 calBCE, BE-7995.1.1,
respectively). However, because these individuals are known to be 1st degree relatives the
29 year GH constraint could be applied, reducing MX 190's range by 365 years (to 25242370 calBCE, SM 4.1).



403

404 Figure 10. Original 2-sigma calBCE date ranges for individuals from the 4500-4999

405 calBP interval that had GH reductions about the 54.47 mean.



Figure 11. Original 2-sigma calBCE date ranges for individuals from the 7499-7000calBP interval that had GH reductions about the 54.47 mean.





- 413 Figure 12. Original 2-sigma calBCE date ranges for individuals from the 7500-7999
- 414 calBP interval that had GH reductions about the 54.47 mean.



417 Figure 13. Original 2-sigma calBCE date ranges for individuals from the 4000-4499 BP

418 calBP interval that had GH reductions about the 54.47 mean.





3.6 Building Bayesian Models

42	4
----	---

425	The range tightening described above is a "manual" method for constraining the tail ends
426	of radiocarbon date distributions using estimates for the number of years that can separate
427	the dates of death of genetic relatives. While date ranges can be constrained with this
428	manual method, we also tested how other statistical modeling could refine the date
429	ranges. Bayesian analysis to increase precision in a series of radiocarbon dates has
430	become standard practice amongst archaeologists (Bronk Ramsey, 2009; Taylor and Bar-
431	Yosef, 2014). Thus, we examined how effective knowledge of genetic relatedness and
432	date of death estimates are as priors to refine radiocarbon dates.
433	To test this, we started by importing the raw calibrated date probability
434	distributions for I2600 and I2457 from OxCal 4.3 (data provided in SM 5). We next
435	sorted the GH DOD values into 5-year intervals and produced a probability distribution.
436	The raw data were smoothed to give estimates of DOD by year (SM 5). The posterior
437	joint distribution of the datasets was then computed. Figures 15 and 16 are the marginal
438	estimates of these distributions for the father and daughter. Due to a plateau in the
439	radiocarbon curve, the date distributions for the father and daughter are bimodal with an
440	additional, lower probability "peak" (demonstrated with the purple curve). For each,
441	building in the relative information significantly reduces the probability of one of the
442	original probability peaks. And while the distribution for I2600 essentially remains
443	bimodal, the most likely probability for both I2600 and I2457 is between 2100-2000
444	BCE. This result demonstrates that building the constraints in to statistical modeling can
445	help refine date ranges. Future work building these constraints into Bayesian modeling
446	available in OxCal could provide additional refinements.



449 Figure 15. Joint probability distribution for I2457. Original AMS date probability

450 distribution in purple, new joint distribution in green.



451

452 Figure 16. Joint probability distribution for I2600. Original AMS date probability

- 453 distribution in purple, new joint distribution in green.
- 454



457	In sum, knowledge of genetic relatedness can be used to constrain radiocarbon date
458	distributions, either by applying DOD separations to the tail ends of the distributions, or
459	through Bayesian modeling. These refinements are not universally applicable; related
460	pairs often have date distributions that overlap, sometimes almost entirely, limiting the
461	extent to which DOD estimates can refine date ranges. Yet, overlap is what should be
462	expected; related individuals should not have large date separations. Date distributions of
463	related individuals that do not overlap could reveal an error in radiocarbon dating (such
464	as I2600 and I2457) or genetic analysis, or other issues, such as an uncorrected marine
465	reservoir effect. In other words, the more substantially DOD separation estimates can
466	constrain C14 date ranges, the more likely a significant issue exists in dating for any of a
467	variety of reasons (unaccounted marine reservoir effect, curve plateau, etc).

4. Discussion

Combining previously independent lines of data-knowledge of genetic relatedness derived from ancient DNA; biological and estimated DOD separations for relatives; and radiocarbon dates-creates potential benefits for researchers examining the ancient past. Perhaps the most apparent is evaluation of data generated through disparate methods. As discussed above, relatedness often confirms radiocarbon dates (and vice-versa, Saag et al., 2019:5). Using genetic relatedness and DOD separation estimates to evaluate radiocarbon dates can also help attend to some of the most common pitfalls in radiocarbon dating. According to Taylor and Bar-Yosef (2014:132), "the most common

480 reason why C14 dating evidence is considered to be anomalous can be traced to failures 481 to clearly establish and document the physical relationship between a C14 dated sample 482 and a specific targeted event or cultural expression." Somewhat counterintuitively, 483 incorporating genetic relationship DOD-separations addresses Taylor and Bar-Yosef's 484 concerns by circumventing taphonomic processes. Instead of focusing on potential 485 confounding factors of when individuals were buried, removed, reburied, etc., date ranges 486 are examined with an independent line of evidence that is not prone to contamination 487 issues associated with taphonomic processes and archaeological context. 488 Analyzing the radiocarbon record with knowledge of genetic relatives also 489 provides archaeologists an opportunity to move beyond traditional interpretations of 490 radiocarbon dates. C14 dating of skeletal remains typically provides an estimate of when 491 an individual died (although it could also reflect when a particular element ceased carbon 492 uptake during an individual's lifetime, as discussed above). The combined and 493 constrained date ranges discussed above provide minimum and maximum boundaries of 494 when two related individuals died; therefore, the overlap of the two ranges likely contains 495 the plausible period of time when the individuals were *alive* together. It is entirely 496 possible, of course, that one individual died at the minimum boundary and the other at the 497 maximum. In such instances the two related individuals would have no lifetime overlap. 498 Even in such cases, considering the combined C14 ranges of related individuals can turn 499 archaeological thinking away from incipient or terminal dates of archaeological periods, 500 but instead toward changes that happened during lifetimes. 501 Considering lifespan ranges also helps elucidate cultural plasticity, and reveal the

arbitrariness of archaeological boundaries. Archaeologists had initially suspected the

503	English Bell Beaker father-daughter pair were part of separate archaeological cultures
504	due to their initial dates. Knowing that these two individuals were related not only helped
505	in identifying an error in the initial radiocarbon dates, but also speaks to the subjective
506	nature of chronological and cultural boundaries archaeologists establish, which were of
507	no consequence for the father-daughter pair.
508	The approaches outlined above represent only a small number of applications for
509	how knowledge of genetic relatedness can help with radiocarbon dating. The potential for
510	further applicability needs to be explored; one promising application could be the use of
511	extended families for radiocarbon curve "wiggle matching."
512	
513	
514	5. Conclusion
515	
516	This research is a first step in combining two discrete analytical methods to add
517	refinement to interpretation of the archaeological record and is meant to demonstrate that
518	knowledge of genetic relatedness can be used to augment radiocarbon dating. As ancient
519	DNA databases continue to grow, and more relatives are identified and radiocarbon
520	dated, researchers will likely feel compelled to refine GH and DOD estimates as they see
521	fit, as some have already done (Kennett et al., 2017; Saag et al., 2019). Levels of social
522	organization (e.g. hunter-gatherer vs. agriculturalist), age of skeletons (adult vs. juvenile),
523	and lifespan estimate could also all be incorporated into estimates. Additionally, once
524	enough related individuals are identified and dated, specific regions, sub-regions, or even
525	sites can be examined for anomalies in the associated radiocarbon records.

526	Ancient DNA innovations are providing archaeologists with unprecedented
527	insight into the past. As ancient DNA becomes increasingly integral to archaeological
528	studies, researchers should explore novel applications of genetic data to archaeological
529	studies. This paper used ancient DNA to identify radiocarbon outliers, refine date
530	distribution ranges for related pairs, and delineate potential issues unaccounted for in the
531	radiocarbon record of particular eras and locales. Such studies should help integrate the
532	two fields and move ancient DNA and archaeology forward together into the next era of
533	research on the human past.
534	
535	Declaration of Competing Interests
536	None
537	
538	Acknowledgements
539	This work was funded by NIH grant GM100233, the Paul Allen Foundation, John
540	Templeton Foundation (grant number 6122), and David Reich is an Investigator of the
541	Howard Hughes Medical Institute. We thank Melissa Gymrek for providing assistance
542	with familinx data from the Kaplanis et al. 2018 study, Greg Hodgins for reviewing an
543	early draft of the paper, Iain Mathieson and Vagheesh Narasimhan for statistical
544	assistance, and members of our laboratory for feedback on the study during its
545	development.
546 547 548 549 550 551	

552	
553	
554	References Cited
555	
556 557	Bronk Ramsey, C., 2009. Bayesian Analysis of Radiocarbon Dates. Radiocarbon 51, 337–360. https://doi.org/10.1017/S0033822200033865
558	Calcagnile, L., Quarta, G., Cattaneo, C., D'Elia, M., 2013. Determining ¹⁴ C Content in
559	Different Human Tissues: Implications for Application of ¹⁴ C Bomb-Spike
560	Dating in Forensic Medicine. Radiocarbon 55, 1845–1849.
561	https://doi.org/10.1017/S003382220004875X
562	Cook, G.T., Ainscough, L.A.N., Dunbar, E., 2015. Radiocarbon Analysis of Modern
563	Skeletal Remains to Determine Year of Birth and Death—A Case Study.
564	Radiocarbon 57, $327-336$, https://doi.org/10.2458/azu.rc. 57, 18394
565	Hansen H B Damgaard P B Margaryan A Stenderun I Lynnerun N Willersley
566	E Allentoft M E 2017 Comparing Ancient DNA Preservation in Petrous Bone
567	and Tooth Cementum PLOS ONE 12 e0170940
568	https://doi.org/10.1371/journal.pone.0170940
569	Kaplanis I Gordon A Shor T Weissbrod O Geiger D Wahl M Gershovits M
570	Markus B Sheikh M Gymrek M Bhatia G MacArthur D.G Price A I
570	Frlich V 2018 Quantitative analysis of nonulation-scale family trees with
572	millions of relatives. Science 360, 171–175
573	https://doi.org/10.1126/science.aam9309
574	Kennett D I Plog S George R I Culleton B I Watson A S Skoglund P
575	Rohland N Mallick S Stewardson K Kistler L LeBlanc S A Whiteley
576	P.M., Reich, D., Perry, G.H., 2017. Archaeogenomic evidence reveals prehistoric
577	matrilineal dynasty. Nature Communications 8, 14115.
578	https://doi.org/10.1038/ncomms14115
579	Kuhn, J.M.M., Jakobsson, M., Günther, T., 2018. Estimating genetic kin relationships in
580	prehistoric populations. PLOS ONE 13, e0195491.
581	https://doi.org/10.1371/journal.pone.0195491
582	Lazaridis, I., Nadel, D., Rollefson, G., Merrett, D.C., Rohland, N., Mallick, S.,
583	Fernandes, D., Novak, M., Gamarra, B., Sirak, K., Connell, S., Stewardson, K.,
584	Harney, E., Fu, Q., Gonzalez-Fortes, G., Jones, E.R., Roodenberg, S.A., Lengyel,
585	G., Bocquentin, F., Gasparian, B., Monge, J.M., Gregg, M., Eshed, V., Mizrahi,
586	AS., Meiklejohn, C., Gerritsen, F., Bejenaru, L., Blüher, M., Campbell, A.,
587	Cavalleri, G., Comas, D., Froguel, P., Gilbert, E., Kerr, S.M., Kovacs, P., Krause,
588	J., McGettigan, D., Merrigan, M., Merriwether, D.A., O'Reilly, S., Richards,
589	M.B., Semino, O., Shamoon-Pour, M., Stefanescu, G., Stumvoll, M., Tönjes, A.,
590	Torroni, A., Wilson, J.F., Yengo, L., Hovhannisyan, N.A., Patterson, N., Pinhasi,
591	R., Reich, D., 2016. Genomic insights into the origin of farming in the ancient
592	Near East. Nature 536, 419–424. https://doi.org/10.1038/nature19310
593	Lipson, M., Skoglund, P., Spriggs, M., Valentin, F., Bedford, S., Shing, R., Buckley, H.,
594	Phillip, I., Ward, G.K., Mallick, S., Rohland, N., Broomandkhoshbacht, N.,
595	Cheronet, O., Ferry, M., Harper, T.K., Michel, M., Oppenheimer, J., Sirak, K.,
596	Stewardson, K., Auckland, K., Hill, A.V.S., Maitland, K., Oppenheimer, S.J.,
597	Parks, T., Robson, K., Williams, T.N., Kennett, D.J., Mentzer, A.J., Pinhasi, R.,

598	Reich, D., 2018. Population Turnover in Remote Oceania Shortly after Initial
599	Settlement. Current Biology 28, 1157-1165.e7.
600	https://doi.org/10.1016/j.cub.2018.02.051
601	Marciniak, S., Perry, G.H., 2017. Harnessing ancient genomes to study the history of
602	human adaptation. Nature Reviews Genetics 18, 659–674.
603	https://doi.org/10.1038/nrg.2017.65
604	Mathieson, I., Lazaridis, I., Rohland, N., Mallick, S., Patterson, N., Roodenberg, S.A.,
605	Harney, E., Stewardson, K., Fernandes, D., Novak, M., Sirak, K., Gamba, C.,
606	Jones, E.R., Llamas, B., Dryomov, S., Pickrell, J., Arsuaga, J.L., de Castro,
607	J.M.B., Carbonell, E., Gerritsen, F., Khokhlov, A., Kuznetsov, P., Lozano, M.,
608	Meller, H., Mochalov, O., Moiseyev, V., Guerra, M.A.R., Roodenberg, J., Vergès,
609	J.M., Krause, J., Cooper, A., Alt, K.W., Brown, D., Anthony, D., Lalueza-Fox, C.,
610	Haak, W., Pinhasi, R., Reich, D., 2015. Genome-wide patterns of selection in 230
611	ancient Eurasians. Nature 528, 499–503. https://doi.org/10.1038/nature16152
612	Moreno-Mayar, J.V., Vinner, L., de Barros Damgaard, P., de la Fuente, C., Chan, J.,
613	Spence, J.P., Allentoft, M.E., Vimala, T., Racimo, F., Pinotti, T., Rasmussen, S.,
614	Margaryan, A., Iraeta Orbegozo, M., Mylopotamitaki, D., Wooller, M., Bataille,
615	C., Becerra-Valdivia, L., Chivall, D., Comeskey, D., Devièse, T., Grayson, D.K.,
616	George, L., Harry, H., Alexandersen, V., Primeau, C., Erlandson, J., Rodrigues-
617	Carvalho, C., Reis, S., Bastos, M.Q.R., Cybulski, J., Vullo, C., Morello, F., Vilar,
618	M., Wells, S., Gregersen, K., Hansen, K.L., Lynnerup, N., Mirazón Lahr, M.,
619	Kjær, K., Strauss, A., Alfonso-Durruty, M., Salas, A., Schroeder, H., Higham, T.,
620	Malhi, R.S., Rasic, J.T., Souza, L., Santos, F.R., Malaspinas, AS., Sikora, M.,
621	Nielsen, R., Song, Y.S., Meltzer, D.J., Willerslev, E., 2018. Early human
622	dispersals within the Americas. Science 362, eaav2621.
623	https://doi.org/10.1126/science.aav2621
624	Narasimhan, V.M., Patterson, N., Moorjani, P., Rohland, N., Bernardos, R., Mallick, S.,
625	Lazaridis, I., Nakatsuka, N., Olalde, I., Lipson, M., Kim, A.M., Olivieri, L.M.,
626	Coppa, A., Vidale, M., Mallory, J., Moiseyev, V., Kitov, E., Monge, J., Adamski,
627	N., Alex, N., Broomandkhoshbacht, N., Candilio, F., Callan, K., Cheronet, O.,
628	Culleton, B.J., Ferry, M., Fernandes, D., Freilich, S., Gamarra, B., Gaudio, D.,
629	Hajdinjak, M., Harney, É., Harper, T.K., Keating, D., Lawson, A.M., Mah, M.,
630	Mandl, K., Michel, M., Novak, M., Oppenheimer, J., Rai, N., Sirak, K., Slon, V.,
631	Stewardson, K., Zalzala, F., Zhang, Z., Akhatov, G., Bagashev, A.N., Bagnera,
632	A., Baitanayev, B., Bendezu-Sarmiento, J., Bissembaev, A.A., Bonora, G.L.,
633	Chargynov, T.T., Chikisheva, T., Dashkovskiy, P.K., Derevianko, A., Dobeš, M.,
634	Douka, K., Dubova, N., Duisengali, M.N., Enshin, D., Epimakhov, A., Fribus,
635	A.V., Fuller, D., Goryachev, A., Gromov, A., Grushin, S.P., Hanks, B., Judd, M.,
636	Kazizov, E., Khokhlov, A., Krygin, A.P., Kupriyanova, E., Kuznetsov, P.,
637	Luiselli, D., Maksudov, F., Mamedov, A.M., Mamirov, T.B., Meiklejohn, C.,
638	Merrett, D.C., Micheli, R., Mochalov, O., Mustafokulov, S., Nayak, A., Pettener,
639	D., Potts, R., Razhev, D., Rykun, M., Sarno, S., Savenkova, T.M., Sikhymbaeva,
640	K., Slepchenko, S.M., Soltobaev, O.A., Stepanova, N., Svyatko, S., Tabaldiev, K.,
641	Teschler-Nicola, M., Tishkin, A.A., Tkachev, V.V., Vasilyev, S., Velemínský, P.,
642	Voyakin, D., Yermolayeva, A., Zahir, M., Zubkov, V.S., Zubova, A., Shinde,
643	V.S., Lalueza-Fox, C., Meyer, M., Anthony, D., Boivin, N., Thangaraj, K.,

644 Kennett, D.J., Frachetti, M., Pinhasi, R., Reich, D., 2019. The formation of human 645 populations in South and Central Asia. Science 365, eaat7487. 646 https://doi.org/10.1126/science.aat7487 647 Olalde, I., Brace, S., Allentoft, M.E., Armit, I., Kristiansen, K., Booth, T., Rohland, N., 648 Mallick, S., Szécsényi-Nagy, A., Mittnik, A., Altena, E., Lipson, M., Lazaridis, I., 649 Harper, T.K., Patterson, N., Broomandkhoshbacht, N., Diekmann, Y., Faltyskova, 650 Z., Fernandes, D., Ferry, M., Harney, E., de Knijff, P., Michel, M., Oppenheimer, 651 J., Stewardson, K., Barclay, A., Alt, K.W., Liesau, C., Ríos, P., Blasco, C., 652 Miguel, J.V., García, R.M., Fernández, A.A., Bánffy, E., Bernabò-Brea, M., 653 Billoin, D., Bonsall, C., Bonsall, L., Allen, T., Büster, L., Carver, S., Navarro, 654 L.C., Craig, O.E., Cook, G.T., Cunliffe, B., Denaire, A., Dinwiddy, K.E., 655 Dodwell, N., Ernée, M., Evans, C., Kuchařík, M., Farré, J.F., Fowler, C., 656 Gazenbeek, M., Pena, R.G., Haber-Uriarte, M., Haduch, E., Hey, G., Jowett, N., 657 Knowles, T., Massy, K., Pfrengle, S., Lefranc, P., Lemercier, O., Lefebvre, A., Martínez, C.H., Olmo, V.G., Ramírez, A.B., Maurandi, J.L., Majó, T., McKinley, 658 659 J.I., McSweeney, K., Mende, B.G., Mod, A., Kulcsár, G., Kiss, V., Czene, A., 660 Patay, R., Endrődi, A., Köhler, K., Hajdu, T., Szeniczey, T., Dani, J., Bernert, Z., 661 Hoole, M., Cheronet, O., Keating, D., Velemínský, P., Dobeš, M., Candilio, F., Brown, F., Fernández, R.F., Herrero-Corral, A.-M., Tusa, S., Carnieri, E., Lentini, 662 663 L., Valenti, A., Zanini, A., Waddington, C., Delibes, G., Guerra-Doce, E., Neil, 664 B., Brittain, M., Luke, M., Mortimer, R., Desideri, J., Besse, M., Brücken, G., 665 Furmanek, M., Hałuszko, A., Mackiewicz, M., Rapiński, A., Leach, S., Soriano, 666 I., Lillios, K.T., Cardoso, J.L., Pearson, M.P., Włodarczak, P., Price, T.D., Prieto, P., Rey, P.-J., Risch, R., Rojo Guerra, M.A., Schmitt, A., Serralongue, J., Silva, 667 A.M., Smrčka, V., Vergnaud, L., Zilhão, J., Caramelli, D., Higham, T., Thomas, 668 669 M.G., Kennett, D.J., Fokkens, H., Heyd, V., Sheridan, A., Sjögren, K.-G., 670 Stockhammer, P.W., Krause, J., Pinhasi, R., Haak, W., Barnes, I., Lalueza-Fox, 671 C., Reich, D., 2018. The Beaker phenomenon and the genomic transformation of 672 northwest Europe. Nature 555, 190-196. https://doi.org/10.1038/nature25738 673 Olalde, I., Mallick, S., Patterson, N., Rohland, N., Villalba-Mouco, V., Silva, M., Dulias, K., Edwards, C.J., Gandini, F., Pala, M., Soares, P., Ferrando-Bernal, M., 674 675 Adamski, N., Broomandkhoshbacht, N., Cheronet, O., Culleton, B.J., Fernandes, 676 D., Lawson, A.M., Mah, M., Oppenheimer, J., Stewardson, K., Zhang, Z., Jiménez Arenas, J.M., Toro Moyano, I.J., Salazar-García, D.C., Castanyer, P., 677 678 Santos, M., Tremoleda, J., Lozano, M., García Borja, P., Fernández-Eraso, J., 679 Mujika-Alustiza, J.A., Barroso, C., Bermúdez, F.J., Viguera Mínguez, E., Burch, 680 J., Coromina, N., Vivó, D., Cebrià, A., Fullola, J.M., García-Puchol, O., Morales, 681 J.I., Oms, F.X., Majó, T., Vergès, J.M., Díaz-Carvajal, A., Ollich-Castanyer, I., 682 López-Cachero, F.J., Silva, A.M., Alonso-Fernández, C., Delibes de Castro, G., 683 Jiménez Echevarría, J., Moreno-Márquez, A., Pascual Berlanga, G., Ramos-684 García, P., Ramos-Muñoz, J., Vijande Vila, E., Aguilella Arzo, G., Esparza 685 Arroyo, A., Lillios, K.T., Mack, J., Velasco-Vázquez, J., Waterman, A., Benítez de Lugo Enrich, L., Benito Sánchez, M., Agustí, B., Codina, F., de Prado, G., 686 687 Estalrrich, A., Fernández Flores, Á., Finlavson, C., Finlavson, G., Finlavson, S., 688 Giles-Guzmán, F., Rosas, A., Barciela González, V., García Atiénzar, G., 689 Hernández Pérez, M.S., Llanos, A., Carrión Marco, Y., Collado Benevto, I.,

690	López-Serrano, D., Sanz Tormo, M., Valera, A.C., Blasco, C., Liesau, C., Ríos,
691	P., Daura, J., de Pedro Michó, M.J., Diez-Castillo, A.A., Flores Fernández, R.,
692	Francès Farré, J., Garrido-Pena, R., Goncalves, V.S., Guerra-Doce, E., Herrero-
693	Corral, A.M., Juan-Cabanilles, J., López-Reves, D., McClure, S.B., Merino Pérez,
694	M., Oliver Foix, A., Sanz Borràs, M., Sousa, A.C., Vidal Encinas, J.M., Kennett,
695	D.J., Richards, M.B., Werner Alt, K., Haak, W., Pinhasi, R., Lalueza-Fox, C.,
696	Reich, D., 2019. The genomic history of the Iberian Peninsula over the past 8000
697	vears. Science 363, 1230–1234, https://doi.org/10.1126/science.aav4040
698	Pinhasi, R., Fernandes, D., Sirak, K., Novak, M., Connell, S., Alpaslan-Roodenberg, S.,
699	Gerritsen, F., Moisevev, V., Gromov, A., Raczky, P., Anders, A., Pietrusewsky,
700	M., Rollefson, G., Jovanovic, M., Trinhhoang, H., Bar-Oz, G., Oxenham, M.,
701	Matsumura, H., Hofreiter, M., 2015, Optimal Ancient DNA Yields from the Inner
702	Ear Part of the Human Petrous Bone, PLOS ONE 10, e0129102.
703	https://doi.org/10.1371/journal.pone.0129102
704	Posth, C., Nakatsuka, N., Lazaridis, I., Skoglund, P., Mallick, S., Lamnidis, T.C.,
705	Rohland, N., Nägele, K., Adamski, N., Bertolini, E., Broomandkhoshbacht, N.,
706	Cooper, A., Culleton, B.J., Ferraz, T., Ferry, M., Furtwängler, A., Haak, W.,
707	Harkins, K., Harper, T.K., Hünemeier, T., Lawson, A.M., Llamas, B., Michel, M.,
708	Nelson, E., Oppenheimer, J., Patterson, N., Schiffels, S., Sedig, J., Stewardson,
709	K., Talamo, S., Wang, CC., Hublin, JJ., Hubbe, M., Harvati, K., Nuevo
710	Delaunay, A., Beier, J., Francken, M., Kaulicke, P., Reyes-Centeno, H.,
711	Rademaker, K., Trask, W.R., Robinson, M., Gutierrez, S.M., Prufer, K.M.,
712	Salazar-García, D.C., Chim, E.N., Müller Plumm Gomes, L., Alves, M.L., Liryo,
713	A., Inglez, M., Oliveira, R.E., Bernardo, D.V., Barioni, A., Wesolowski, V.,
714	Scheifler, N.A., Rivera, M.A., Plens, C.R., Messineo, P.G., Figuti, L., Corach, D.,
715	Scabuzzo, C., Eggers, S., DeBlasis, P., Reindel, M., Méndez, C., Politis, G.,
716	Tomasto-Cagigao, E., Kennett, D.J., Strauss, A., Fehren-Schmitz, L., Krause, J.,
717	Reich, D., 2018. Reconstructing the Deep Population History of Central and
718	South America. Cell 175, 1185-1197.e22.
719	https://doi.org/10.1016/j.cell.2018.10.027
720	Rasmussen, M., Anzick, S.L., Waters, M.R., Skoglund, P., DeGiorgio, M., Stafford,
721	T.W., Rasmussen, S., Moltke, I., Albrechtsen, A., Doyle, S.M., Poznik, G.D.,
722	Gudmundsdottir, V., Yadav, R., Malaspinas, AS., V, S.S.W., Allentoft, M.E.,
723	Cornejo, O.E., Tambets, K., Eriksson, A., Heintzman, P.D., Karmin, M.,
724	Korneliussen, T.S., Meltzer, D.J., Pierre, T.L., Stenderup, J., Saag, L., Warmuth,
725	V.M., Lopes, M.C., Malhi, R.S., Brunak, S., Sicheritz-Ponten, T., Barnes, I.,
726	Collins, M., Orlando, L., Balloux, F., Manica, A., Gupta, R., Metspalu, M.,
727	Bustamante, C.D., Jakobsson, M., Nielsen, R., Willerslev, E., 2014. The genome
728	of a Late Pleistocene human from a Clovis burial site in western Montana. Nature
729	506, 225–229. https://doi.org/10.1038/nature13025
730	Reich, D., 2018. Who We Are and How We Got Here: Ancient DNA and the New
731	Science of the Human Past. Pantheon, New York.
732	Reich, D., Green, R.E., Kircher, M., Krause, J., Patterson, N., Durand, E.Y., Viola, B.,
733	Briggs, A.W., Stenzel, U., Johnson, P.L.F., Maricic, T., Good, J.M., Marques-
734	Bonet, T., Alkan, C., Fu, Q., Mallick, S., Li, H., Meyer, M., Eichler, E.E.,
735	Stoneking, M., Richards, M., Talamo, S., Shunkov, M.V., Derevianko, A.P.,

736	Hublin, JJ., Kelso, J., Slatkin, M., Pääbo, S., 2010. Genetic history of an archaic
737	hominin group from Denisova Cave in Siberia. Nature 468, 1053–1060.
738	https://doi.org/10.1038/nature09710
739	Saag, Lehti, Laneman, M., Varul, L., Malve, M., Valk, H., Razzak, M.A., Shirobokov,
740	I.G., Khartanovich, V.I., Mikhaylova, E.R., Kushniarevich, A., Scheib, C.L.,
741	Solnik, A., Reisberg, T., Parik, J., Saag, Lauri, Metspalu, E., Rootsi, S.,
742	Montinaro, F., Remm, M., Mägi, R., D'Atanasio, E., Crema, E.R., Díez-del-
743	Molino, D., Thomas, M.G., Kriiska, A., Kivisild, T., Villems, R., Lang, V.,
744	Metspalu, M., Tambets, K., 2019. The Arrival of Siberian Ancestry Connecting
745	the Eastern Baltic to Uralic Speakers further East. Current Biology
746	S0960982219304245. https://doi.org/10.1016/j.cub.2019.04.026
747	Skoglund, P., Posth, C., Sirak, K., Spriggs, M., Valentin, F., Bedford, S., Clark, G.R.,
748	Reepmeyer, C., Petchey, F., Fernandes, D., Fu, Q., Harney, E., Lipson, M.,
749	Mallick, S., Novak, M., Rohland, N., Stewardson, K., Abdullah, S., Cox, M.P.,
750	Friedlaender, F.R., Friedlaender, J.S., Kivisild, T., Koki, G., Kusuma, P.,
751	Merriwether, D.A., Ricaut, FX., Wee, J.T.S., Patterson, N., Krause, J., Pinhasi,
752	R., Reich, D., 2016. Genomic insights into the peopling of the Southwest Pacific.
753	Nature 538, 510–513. https://doi.org/10.1038/nature19844
754	Taylor, R.E., Bar-Yosef, O., 2014. Radiocarbon dating: an archaeological perspective,
755	Second edition. ed. Left Coast Press, Inc, Walnut Creek, California.
756	van de Loosdrecht, M., Bouzouggar, A., Humphrey, L., Posth, C., Barton, N., Aximu-
757	Petri, A., Nickel, B., Nagel, S., Talbi, E.H., El Hajraoui, M.A., Amzazi, S.,
758	Hublin, JJ., Pääbo, S., Schiffels, S., Meyer, M., Haak, W., Jeong, C., Krause, J.,
759	2018. Pleistocene North African genomes link Near Eastern and sub-Saharan
760	African human populations. Science 360, 548–552.
761	https://doi.org/10.1126/science.aar8380
762	
763	