Human Population Genetics and Genomics
https://doi.org/10.47248/hpgg2505030005

Review

Working with Luca Cavalli-Sforza on the Neolithic Transition in Europe: The Research and our Publications

Albert J. Ammerman

Instituto Veneto di Science, Lettere ed Arti. Campo San Stefano 2945, Venice 30124, Italy; Email: ammermsnalbert@gmail.com

Abstract

In 1970, Luca Cavalli-Sforza and I began to work on the question of the Neolithic transition in Europe. We started by measuring the rate of spread of first farming over the continent as a whole and in three of its regions. In turn, we went on to put forward the wave of advance model as a new way to explain the shift from hunting and gathering in a mobile way of life to the production of food in the context of sedentism. The aim here is to review our collaboration and what we wrote on the subject over a span of 50 years. The work will be developed in six main sections: (1) the initial studies, (2) the synthesis in 1984, (3) the widening harvest, (4) the analysis of ancient DNA in the bones of first farmers, (5) the discovery of the petrous bone and (6) Discussion.

Keywords: Neolithic transition; Europe; wave of advance model; interdisciplinary research; archaeology; genetics

Cite This Article:
Ammerman AJ. Working with Luca Cavalli-Sforza on the Neolithic Transition in Europe: The Research and our Publications. Hum Popul Genet Genom. 2025;5(3):0005. https://doi.org/10.47248/hpgg2505030005

Received: 28 Nov 2024
Accepted: 2 Jun 2025
Published: 16 Jul 2025

1. Introduction

What I would like to do here is to present an overview on the research and the publications on the Neolithic transition in Europe that arose from my collaboration with Luca Cavalli-Sforza, which brought archaeology and genetics together at the time. Written for scholars who already have some background in both fields of study, the review will be developed essentially in chronological order. In addition, this article will serve as an updated compendium of our publications on the Neolithic transition. To begin with, what we were trying to do was interdisciplinary research of a kind that had not been done before. For us at the time, it seemed to be the obvious and natural thing to do. In retrospect, our interests happened to come together at just the right point in time. It all began at the University of Pavia in November of 1970, and we then went on to work in close collaboration at Stanford University for five years (1972–1976), where I taught in its new Program in Human Biology. This was the pioneering work in archaeology and human population genetics that bought these two fields of study together for the first time. In turn, our collaboration set in motion work that would continue to develop over the course of the next five decades.

During the long, tedious years of Covid 19, I had the chance to write three pieces that return to our research on the Neolithic transition in Europe (see Ammerman 2020, Ammerman 2021, Ammerman 2022) [1-3]. Of course, this is not the place to repeat at length what is said in them. On the other hand, a few brief words need to be said at this point about each of them by way of introduction. The first is "The Neolithic transition in Europe at 50 years," a pre-print available online since 2020, which was written for *Walking among ancient Trees*, the festschrift in honor of Ryszard Grygiel and Peter Bogucki. It would eventually be presented to them in 2023. Most of the publications that will be cited here appear in it (see Ammerman 2020) [1] with its wider circulation than the festschrift (see Ammerman 2023) [4]. The title of the second publication is "Returning to the rate of spread of early farming in Europe: comment on the article by Manen et al. (2019) in Radiocarbon," and it came out in *Radiocarbon* two years later (see Ammerman 2021) [2]. Here, there was the chance to respond to several of their misrepresentations of our work over the years. For instance, they claimed that we were only interested in what is happening at the continental level and not the regional one. However, from the very beginning in 1971, we had measured three regional rates as well as the one for Europe as a whole, and without going into details here, we had recently published a major regional study on the West Mediterranean (see Isern et al. 2017) [5]. It was time to clean house and reply to our detractors, some of whom were not well versed in the early literature, or had missed part of the literature on the subject. The third publication, "The transition to early farming in Europe" (see Ammerman 2022) [3], was written when the editors of *Simulating the Transition to Agriculture* invited me to write the last chapter of their book for Springer after they read "The Neolithic transition in Europe at 50 Years." Again, this chapter forced me to take stock of the current literature in a broader sense. And this literature likewise included references of considerable interest when it comes to where the study of the Neolithic transition stands today. In other words, it happened to be a good time to write such a chapter.

In the scientific fields of physics, astronomy, geology, genetics and even archaeology, one commonly works by steps of approximation. Knowledge and ideas do not sit still for long. For instance, smashing the atom for the first time at Berkeley in the late 1940s; finding room for plate tectonics and asteroids in the earth sciences. Some might call such major changes a paradigm shift. In doing research in these fields of study, there is no end point when all the answers will come in. In the due course of time, there will be innovations and changes when it comes to equipment, methods and ideas. This holds for the study of the Neolithic transition and its contribution to a better understanding of human genetics. In this respect, the literature constitutes a series of stepping-stones that bring us to the time and place where we stand today. To illustrate such a sequence of approximations, it is instructive to return to the question of measuring the rate of spread of early farming in Europe. In our original study, there were just 53 archaeological sites (see Ammerman and Cavalli-Sforza 1971) [6]. This number then continued to rise from one year to the next until there were a total of 753 early

Neolithic sites with dates some three decades later (see Pinhasi, Fort and Ammerman 2005) [7]. In addition, the quality of the dates would improve with the advent of the new radiocarbon method based on accelerator mass spectrometry (AMS). To cite another example of change, the treatment of time in the original model of the wave of advance put forward by Fisher (1937) [8] was based on continuous random motion as in the diffusion of heat. However, in the case of the spread of early farming the relocation of a household or settlement takes place at discrete time intervals. In terms of mathematics, there was the considerable challenge of incorporating in the model a discrete treatment of time. It would take years before the proper mathematical treatment of the time-delay model was achieved by Fort and Mendez in 1999 [9]. On yet another front, scant attention had been paid to the role of voyaging in the Neolithic transition in the Mediterranean world for years. A pioneering attempt to do so would later be made by Zilhão (2001) [10], drawing upon his contribution to the Wenner Gren Workshop on the Neolithic Transition held in 1998 (see Ammerman and Biagi 2003) [11]. Then there would be the further development of his ideas in "Modeling the role of voyaging in the coastal spread of the Early Neolithic in West Mediterranean" (see Isern et al. 2017) [5]. As we shall see below, three of the unsung heroes in the annals of the Neolithic transition in Europe are Pinhasi, Fort, and Zilhão.

2. The Initial Studies

As mentioned before, the plan is to present this profile in chronological order for the most part, starting with the first studies in the 1970s. The next three sections will involve respectively: (3) the synthesis in 1984, (4) the widening harvest and (5) the genes of first farmers that now support the demic hypothesis more directly. In the context of where the story will end, the issue of whether or not we were on the right track, which appeared to be up in the air for years when the paradigm of indigenism was in fashion, has been resolved in recent years. In retrospect, it would all appear to be smooth sailing from the start. On the contrary, there was endless debate in the literature for years up until the last twelve years when the study of the DNA in the bones of first farmers in Europe turned to the petrous bone in the ear, the densest bone in the human body (more on this below). To begin with, we wrote two short papers linked with one another. The first was "Measuring the rate of spread of early farming in Europe" (see Ammerman and Cavalli-Sforza 1971) [6] that came out in the journal *Man* with its focus on Anthropology. "A population model for the diffusion of early farming in Europe" was presented at a conference held at the University of Sheffield in December of 1971 and published in the book entitled *The Explanation of Culture Change: Models in Prehistory*, which was edited by Renfrew. Now the new fashion for models in prehistory was in vogue both in the UK and America. In addition, there was an enthusiasm for taking a more quantitative approach to archaeology, and this is what had first brought Luca and I together at a conference on the Black Sea in the summer of 1970 (for more on all of this, see Ammerman 2020 [1]). In hindsight, what is presented in this profile might never have happened without the conference on *Mathematics in the Archaeological and Historical Sciences* (see Hodson, Kendall and Tautu 1971) [12]. In short, we learned that the spread of early farming over Europe as a whole took place at an average rate of about 1 km per year, and we put forward the concept of demic diffusion to explain the spread drawing upon the model of the wave of advance model put forward by Fisher in 1937 [8]. The alternative to demic diffusion that we also considered was the traditional idea of cultural diffusion: that is, local populations of hunters and gatherers picked up this new form of subsistence on their own (without the movement or local relocation of first farmers). Thus, the concept that human genes are at the heart of the matter when it comes to sorting out the relative importance of cultural diffusion and demic diffusion was introduced for the first time. This was the seminal intuition of Luca that now led to our further exploration of the matter.

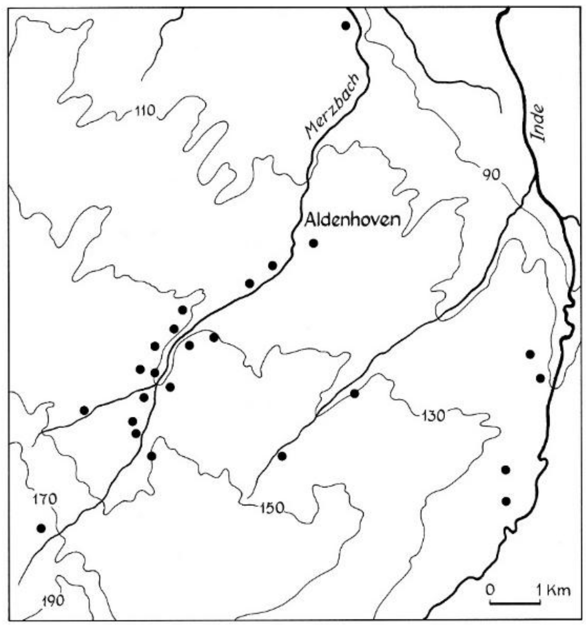

Figure 1 The map of Aldenhoven. Distribution map of Bandkeramik sites on the Aldenhovener Platte in Germany: note the concentration of sites along the stream called the Merzbach (see Ammerman and Cavalli-Sforza 1984 [13]).

Here it is worth mentioning briefly four related studies done in the 1970s that enlarged the scope of our research on the Neolithic transition. The first was a simulation study of LBK settlement patterns in central Europe (for the pattern on the Aldenhovener Platte in Germany, see **Figure 1** (Figure 3.5 of Ammerman and Cavalli-Sforza 1984 [13]) that we worked on at Stanford University and then presented as a paper with the title "Simulation study of the Bandkeramik settlement patterns" at the Symposium on the Application of Computer Simulation to Archaeology, which was given at the annual meeting of the Society of American Archaeology (San Francisco, May 1973 [14]; for more on it, see Ammerman 2022 [3]). The second line of investigation involved the creation at Stanford of "Synthetic maps of human gene frequencies in Europe" published in *Science* (see Menozzi, Piazza and Cavalli-Sforza 1978) [15] such maps would then play a role in our 1984 book. In the third case, we returned to the wave of advance model (see Fisher 1937) [8] and its subsequent formulation in two dimensions by Skellam (1951, 1973) [14,16] and consider the model in greater depth in "The wave of advance model for the diffusion of early farming in Europe" (see Ammerman and Cavalli-Sforza

1979) [17], which was published in *Transformations: Mathematical Approaches to Culture Change*, a book edited by Renfrew and Cooke). The fourth study involved the archaeological fieldwork that I directed in Calabria, the region in the toe of Italy, in the years between 1974 and 1980. At Acconia on the west coast, we first did several seasons of survey work that brought to light many Neolithic settlements in the area for the first time (see Ammerman 1985, The Acconia Survey: Neolithic Settlement and the Obsidian Trade) [18]. In 1979, we then went on to do a magnetometer survey in combination with extensive coring and a series of excavations at the settlement called Piana di Curinga (see Ammerman, Shaffer and Hartman 1988: A Neolithic household at Piana di Curinga, Italy) [19], which documented 48 wattle and daub houses dating to the 6^{th} millennium BC, see **Figure 2** (Figure 2 in Ammerman 2020 [1]). In short, the fieldwork at Acconia yielded direct evidence for local population growth there at the time of the Neolithic transition.

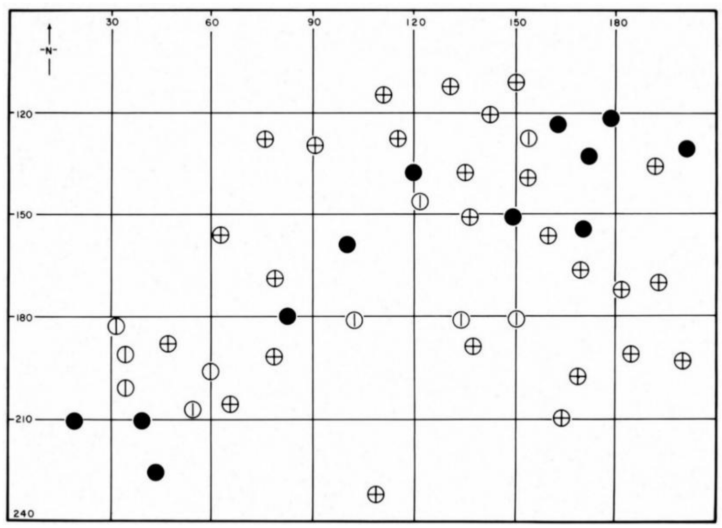

Figure 2 The spatial distribution of the 48 wattle-and-daub houses of Stentinello age at the settlement of Piana di Curinga at Acconia. Circles with a cross indicate those cases (26) where a structure was first identified as an anomaly by the magnetometer survey and then confirmed by a hand boring. Solid circles represent those cases (12) where a house was tested by excavation following its identification by the magnetometer and borings. Circles with a vertical line comprise those cases (10) where a structure was identified by means of hand borings alone (based on the recovery of fired daub). The grid system is in metres (see Ammerman 2020) [1].

3. The Synthesis in 1984

The 1984 Synthesis was presented in *The Neolithic Transition and the Genetics of Populations in Europe* (see Ammerman and Cavalli-Sforza 1984) [13] published by Princeton University Press in that year. The book gives a comprehensive account of the various lines of research on the subject that we had done by this time. The aim was to make the archaeology accessible to those in the fields of genetics and the biological sciences in wider sense and the genetics to be within the reach of those in the fields of archaeology and anthropology. It took a fair number of years to strike the right balance. In the book, we draw a clear distinction between demic diffusion, our working hypothesis and the wave of advance model, the scientific tool that we used to explore the research question. We now measure the rate again: this time using 106 dated sites and the isochrone method of analysis, which avoided the issue of arbitrarily selecting an archaeological site where the spread of early farming began in the Near East. It gave essentially the same result as the study published in 1971 and showed the regional variations in a graphic form. We presented at greater length the logistic form of local population growth and explained how it arose from sedentism in reducing the interval between births as well as the contribution of domestic cereals to the health and survival of infants and young children. One of the results highlighted in the book is an evaluation of the wave of advance, see **Figure 3** (Figure 5.9 in Ammerman and Cavalli-Sforza 1984 [13]) based on a series of curves indicating the rate of advance under various combinations of the rate of local population growth at the frontier and the rate of local migratory activity, yielding rates of advance in the range from 0.5 km to 2.5 km per year. All the values of these two variables (population growth and local mobility) are feasible ones and produce rates of spread that fit with what is observed on the ground in Europe. In addition, we took up the question of the forms of interaction that can take place between a population of first farmers and one of late hunter-gatherers. They include acculturation, warfare, disease and mutualism. The seventh and last chapter turns to simulation studies. Without going into details here, they constitute a means of delving into the processes involved in the Neolithic transition.

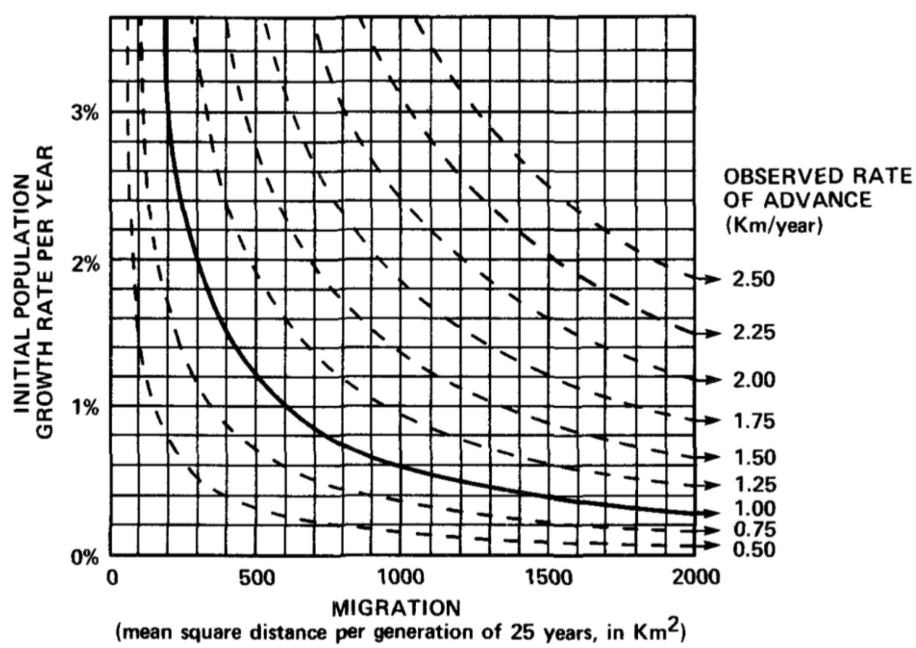

Figure 3 An elaboration of the wave of advance model. The curves indicate the rate of advance that will occur under the various combinations of values of *M* (rate of migratory activity) and α (rates of population growth). The heavier curve represents the value that in combination would produce a rate of advance of 1 kilometer per year (Figure 5.9 in Ammerman and Cavalli-Sforza 1984 [13]).

During the years between 1980 and 1995, we also had the chance to write several other publications of related interest. Returning to the fieldwork at Acconia, one documented the survey there (see Ammerman 1985) [18] and another dealt with the many early houses documented at the settlement known as Piana di Curinga (Ammerman, Shaffer and Hartman 1988) [19] as mentioned before. In the case of Cavalli-Sforza (1986) [20], he published a book called *African Pygmies*, which recounts his first-hand experience of visiting some of the last bands of hunters and gatherers in the African continent and studying their gene frequencies. Then in a book of major importance, Luca and two of his colleagues published *The History and Geography of Human Genes* (see Cavalli-Sforza, Menozzi and Piazza 1994, and Menozzi and Piazza, 2024) [21,22]. It now became the benchmark volume for those working in the field of human population genetics. By this time on the archaeological front, I had published a comment in the journal *Antiquity* on the unsound nature of an article claiming that Luca and I had put forward the wave of advance hypothesis – mixing up the model and the hypothesis ("On the Neolithic transition in Europe: a comment on Zvelebil and Zvelebil 1989," (see Ammerman 1989) [23]). Even at this time, some archaeologists still did not really understand the difference between a working hypothesis and a model in the scientific literature. The comment then goes on to place in historical context the paradigm of indigenism in fashion among archaeologists at the time. A last comment worth adding here is that the genetics of modern populations was still being used as a proxy for the genes of first farmers some 300 generation ago; even as late as 1995, those working in the laboratory still had difficulty extracting sufficient DNA from the bones of first farmers. Soon this would begin to change.

4. The Widening Harvest

The next main stopping place in our journey is the Wenner Gren Workshop entitled *The Neolithic Transition in Europe: Looking Back, Looking Forward*. Held in Venice in October of 1998, there were 21 participants from many different countries at the meeting that honored Luca at the time of the 25th anniversary of the publication of the wave of advance model. However, it unfortunately took several long years to edit all the chapters in the book, whose short title is *The Widening Harvest* (see Ammerman and Biagi 2003) [11]. On the positive side, the chapters in the book provide a wide coverage of the situation in most of the regions of the Europe and Southwest Asia. One of the purposes of a Wenner Gren Workshop is to bring together scholars from different backgrounds and nations so that they can discuss with one another where a given field of study in Anthropology is heading. Indeed, this is what happened at the meeting. For instance, beyond the official program of the meeting, Guilaine proposed to me that he had interesting things to say about his new project at Shillourokambos on the island of Cyprus. Thus, at the last minute, we arranged for him to speak one evening about his new excavation there. In addition, out of the conference arose my collaboration with Zilhão (more on this below).

As mentioned before, "Radiocarbon evidence for maritime pioneer colonization at the origins of farming in the west Mediterranean Europe" (see Zilhao 2001) [10] happened to come out first in the *Proceedings of the National Academy of Sciences USA.*

The paper that he gave at the Workshop, "*The Neolithic transition in Portugal and the role of demic diffusion in the spread of agriculture across West Mediterranean Europe*" (see Zilhão 2003) [24] would finally make its appearance two years later. But this is not the place to review the other contributions of interest to *The Widening Harvest*. Had I not listened to the added talk that Guilaine gave at the Wenner Gren Workshop, it would never have crossed my mind to go out to Cyprus and look for the missing pre-Neolithic sites on the island. In short, I first went out to Cyprus in 2003 and then worked there for the next ten years on the question of early voyaging. Our first report was published in the *RDAC*, the journal of the Department of Antiquities, Cyprus: "Two new early sites on Cyprusa" (see Ammerman et al. 2006) [25]. The plan is to return to the question of voyaging in the last section. In the years following the Workshop, advances of major interest were made on several fronts. As introduced briefly before, one of them was the article called "Time-delay theory of the Neolithic transition in Europe" (see Fort and Mendez 1999) [9]. It now gave Fisher's model a new and more realistic spin, when it came to the relocation of early Neolithic households and settlements. Even in theory, first farmers were no longer ceaselessly moving around on the landscape. On a different front, there was a major gain when it came to measuring the average rate of the spread of early farming in Europe: "Tracing the origin and spread of agriculture in Europe" (see Pinhasi, Fort and Ammerman 2005) [7]. Now the analysis was based on a total of 753 sites with radiocarbon dates, and the results obtained turned out to be much the same as we found before in 1971 and 1984.

5. The Analysis of Ancient DNA in the Bones of First Farmers

For many years, the argument for the demic hypothesis of the Neolithic transition in Europe had been based on a proxy: the genetics of modern populations living in various regions of Europe. When I wrote "*The Neolithic transition in Europe at 50 Years*", there had been major advances over a broad front in the study of old DNA extracted from the bones of first farmers. In section 4 of Ammerman (2020) [1], I selected eight case studies from various geographic contexts and wrote a few words about each one to illustrate the gains made recently. Again, this is not the place to repeat what is already in print. For our present purposes, the focus will be on two of them as well as the wider background on the early history of this field of investigation. For instance, what is available today is a good overview of the steps leading from the first discovery of ancient DNA in old bones of animals and human beings to how it is now used in the study of their genetics (see Barbujani 2024: 79-83) [26]. In his recent book, *L'Alba della Storia*, Barbujani provides a comprehensive framework for reading the case studies that are included in section 4. For the reader who wishes to know more about early attempts to use DNA to test the demic hypothesis, see Barbujani, Bertorelle and Chikhi 1998, Chikhi et al. 1998, Chikhi et al. 2002, Cavalli-Sforza 2003 [27-30]. Recall that even in the 1990s, it was often difficult to extract enough DNA from ancient samples, such as the bone of a first farmer to obtain a good result.

We now turn briefly to the first of the eight case studies presented in section 4 of Ammerman (2020) [1]. Written by Haak and co-workers, it is entitled "*Ancient DNA from the first European farmers in 7500-year-old Neolithic sites.*" It was a muchawaited paper when it appeared in the pages of *Scienc*e in 2005. But the article had a major flaw on the archaeological (and genetic) side. This is why it is labeled “a false start” in section 4. The problem from the archaeological point of view involves the ages attributed to some of the burials in the analysis; which do not always go back to the time of first farming in central Europe. This is why we wrote a critical comment, which the editors at *Science* accepted for publication (see Ammerman, Pinhasi and Banffy 2006) [25]. Here it is worth adding that we made no attempt to comment on the article’s genetics. In short, the archaeology itself was already bad enough. And as it turned out, the genetic analyses too did have their own limitations, as the editors of this journal recently explained to me (for their reasons, without going into the details here, see Gamba et al. 2012 [31], or Rasteiro and Chikhi 2013) [32]). In a few words, they mistakenly considered that haplogroup ages could serve as proxies for the age of populations (see Barbujani, Bertorelle and Chikhi 1998, Chikhi et al. 2002, or Cavalli-Sforza 2003 [27,29,30]) and concluded incorrectly that aDNA favoured the cultural diffusion hypothesis.

Five years later, Haak and his co-workers reached the opposite conclusion, and tried to bring the two sides together in “*Ancient DNA from European early Neolithic farmers reveal their Near Eastern affinities*”, which came out in *PLoS Biology*. In their new study they concluded that aDNA favoured the demic diffusion hypothesis, as had been concluded by Cavalli-Sforza, Barbujani, Chikhi and others on the basis of the analysis of modern DNA and population genetics modelling. This is the second case study given in section 4, where Haak et al. (2010) [33] is now labelled “*The real thing.*” At the same time, on the broad front of the so-called great DNA hunt of the first farmers (see Powledge and Rose 1996) [34], let us not forget to mention the work by Bramanti and co-authors (2009) [35]. Once again we cannot ignore the limitations of the population genetics (see Rasteiro and Chikhi 2013 [32] for a critical analysis). In a few words, the morale of the story is that, in interdisciplinary research of this kind, one has to get both the archaeology and the population genetics right. And this may be difficult to do at times. As an archaeologist interested here in remembering the work Cavalli-Sforza and I did, I will not spend more time on such issues.

The fifth case study is entitled: “*Genome-wide patterns of selection in 230 Eurasians*” (Mathieson et al. 2015) [36]. Published in *Nature*, it was produced by the research group at Harvard led by David Reich, which took advantage of its state-of-the-art sequencing equipment and software and of the recent discovery that the Petrous bone was the most promising bone for aDNA studies because it was richer in DNA than other bones, as had been recently shown by Ron Pinhasi’s group (more on this below.). The label that I gave to it is “*The Breakthrough*”, since, in one study, whole genomes for a total of 230 individuals were published for the first time. In addition, it included samples from western Anatolia for the first time: that is, evidence of special relevance for the demic hypothesis. The weakness of the article was its claim for making an advance in terms of natural selection. In fact, most of the examples of natural selection that are taken up in the discussion do not move beyond what Luca had been writing about for years.

On the whole, the eight studies in section 4 do give new direct support for the demic hypothesis. The notable exception is, of course, the first case study, which misleadingly claimed to favour the cultural hypothesis. As mentioned before, its problem has to do with both chronology and population genetics. Some of the bones of the LBK farmers used in the analysis come from later times in the Neolithic period and not the early Neolithic (that is, not 7500 years ago, as in its title). When this was pointed out to the editors at *Science*, they realized that there was a major flaw in the argument and encouraged us to write a comment to correct the situation.

6. The Discovery of the Petrous Bone

As mentioned before, one of the great challenges that those in the field of genetics had to face for years was the modest amounts of old DNA in the bones of the first farmers. In retrospect, one was analyzing the wrong bones in the human body. To change things, it would take a person who had worked for years on human bones as a physical anthropologist. The advance came when Ron Pinhasi at Dublin put forward the idea that the best bone to work with is its densest one, the petrous bone in the ear (see Pinhasi et al. 2015) [37]. Studies of this bone and, in particular the cochlea portion, documented that it consistently yields many more times ancient DNA than any other bone in the human body. With this new knowledge in hand, it now became much easier and more productive to work on the genomes of first farmers in various regions of Europe. This was soon illustrated by the Harvard group (Mathieson et al. 2015) [36]. In their case study, there are also samples from the western part of Anatolia for the first time, and, as mentioned before, their study now yielded genome-wide results for a large number of individuals. To put it another way, what the article offers is good direct genetic evidence that early farming began in the Near East and then spread over Europe without contributions from local hunter-gatherers in other regions of Europe. This was important to confirm the inference that had been made by Cavalli-Sforza and I in the 1970s, and later by population geneticists working on modern DNA (see references above).

No attempt will be made here to comment on the other studies of ancient DNA included in section 4. Instead, it is perhaps worth saying a few brief words about two recent publications that focus on the Mesolithic side of the story. The first one deals with burials at the site of Grotta dell'Uzzo in southern Italy: "*Genomic and dietary transition during the Mesolithic and Early Neolithic in Sicily*" (see Yu et al. 2022) [38]. The second study presents the results of the analysis of Mesolithic burials at the sites of Hoedic and Téviec in southern Brittany: "*Genomic ancestry and social dynamics of the last hunter-gatherers of Atlantic France*" (see Simões et al. 2024) [39]. Again, the genes are mostly those of Mesolithic age with little or no evidence for mixing with first farmers. In both cases, the late hunter-gatherers seem to be content to keep their distance from first farmers. More studies of the ancient DNA in late hunters and gatherers who lived elsewhere in Europe are called for to explore this matter further.

7. Discussion

We return now to the question of voyaging and the Neolithic transition in the lands on the north side of the Mediterranean Sea. What is happening on the south side is, of course, less well known today. As a starting point, this takes us back to the two studies by Zilhão cited before and the start of my fieldwork on the island of Cyprus in 2003. In the latter case, it was soon possible to find on coastal formations of aeolianite all around the island, ten new candidates for early sites dating to the time before the Neolithic period. The implication is that hunter gatherers who lived in the Levant and Anatolia were making voyages there in the time before early farming reached the island of Cyprus. It was in this context that I was asked to review the situation in the eastern Mediterranean at the conference on The Global Origins and Development of Seafaring held at Cambridge University in 2007. The title of this paper is "*The first Argonauts: towards the Study of the earliest Seafaring in the Mediterranean*" (see Ammerman 2010) [40]. In its first section, evidence for obsidian from natural volcanic sources on islands in the Aegean and Tyrrhenian Seas is used to document voyaging to early Neolithic sites in the Mediterranean (see **Figure 4**) In the case of Cyprus, the island itself has no source of obsidian, and the artifacts in this material recovered there — at a PPNB site such as Shellourokambos or a PPNA site such as Klimonas — come from sources in eastern Anatolia, meaning that they too arrived by boat. And almost all the early Neolithic sites on the coasts of Greece and Italy do have artifacts in obsidian as well. On the other hand, this is not the case for early Neolithic sites in the Iberian Peninsula, where obsidian is not recovered. Furthermore, while obsidian tools are found at Mesolithic sites on the Greek mainland and Crete, they are not present at Mesolithic sites on the Italian mainland. The implication is that the circulation of obsidian in the west has less time depth than it does in the east. On the other hand, there is a marked difference between the average rate of spread of early farming in the east Mediterranean and that in the west. In short, such contrasts led me to write "The paradox of early voyaging in the Mediterranean and the slowness of the Neolithic transition between Cyprus and Italy" (see Ammerman 2011) [41]. In the case of Cyprus, there is also an innovation in our fieldwork that should be mentioned here. On the seabed in front of the early site of Aspros on land, we conducted an underwater survey that led to the first recovery of lithics in such a context, which go back to around 12,000 years ago; "Cyprus: the submerged final Palaeolithic at Aspros Dive Site C" (see Ammerman 2019) [42]. In a nutshell, voyaging comes before early farming in the case of Cyprus.

To make a long story short, given the various projects concerned with early voyaging in the Mediterranean world, it was time to organize another Wenner Gren Workshop. Now it would address the question of early voyaging. Held at Reggio Calabria in October of 2012, its proceedings are called *Island Archaeology and the Origins of Seafaring in the Eastern* Mediterranean (see Ammerman and Davis 2013-2014) [43], which came out in two volumes of the journal *Eurasian Prehistory*.

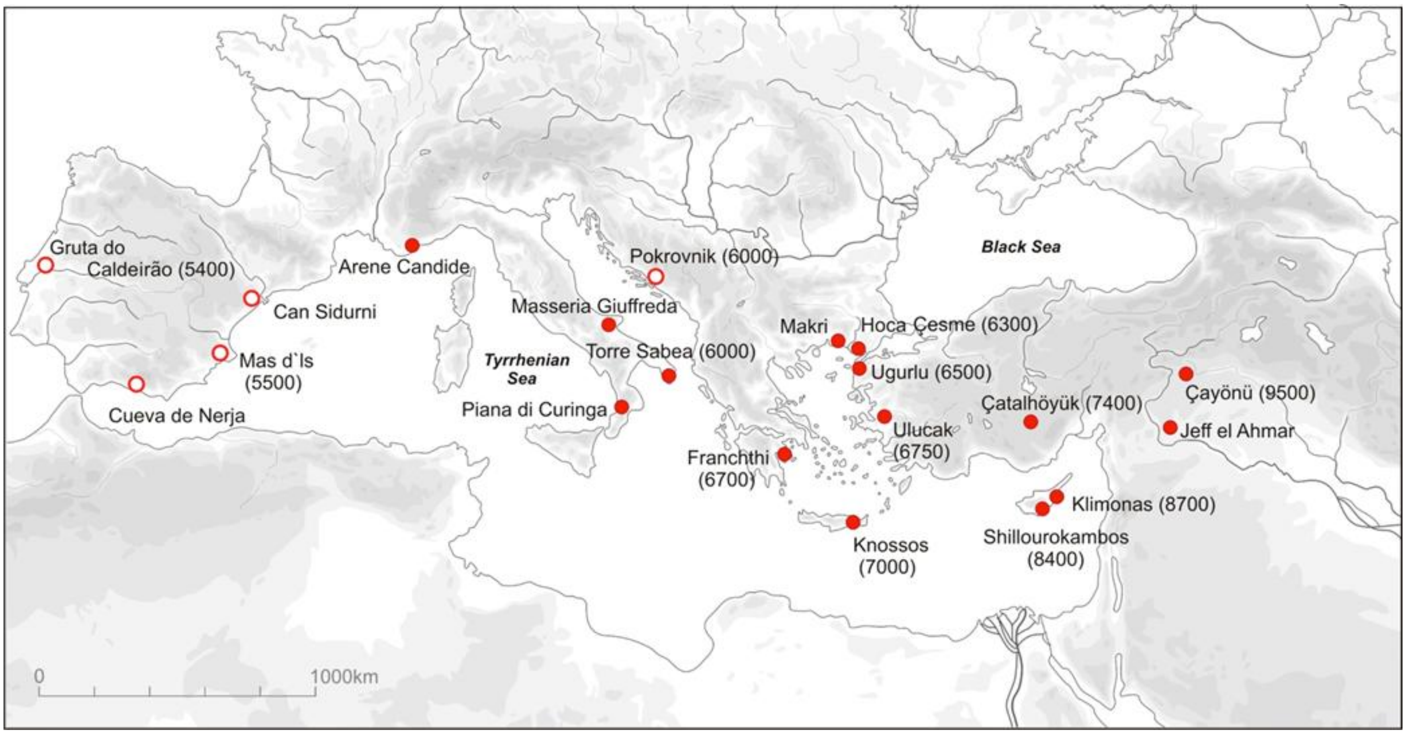

Figure 4 Map of the Mediterranean showing the location of a selection of early Neolithic sites. Obsidian is present at those with red dots (Figure 1 in Ammerman 2014 [44]).

Again, Zilhão was one of the participants at the Workshop, and over the due course of time, this would lead to our collaboration in writing our paper for the *PNAS*. In late October of 2013, I made a trip to Barcelona where I first met with Fort at his office and later in the same day with Zilhão. Somehow, they had never met before even though they shared an interest in the Neolithic transition and lived in the same region of Spain. The next day all three of us had dinner together, and Fort and Zilhão agreed to share their data. We met in Barcelona again for a few days in 2014 and then again in 2015, and finally for a few more days in 2016, when we worked on the final draft of "Modeling the role of voyaging in the coastal spread of the Early Neolithic in the West Mediterranean" (see Isern, Zilhão, Fort and Ammerman 2017) [5]. The archaeological record in the West Mediterranean now yielded an even faster rate of spread than previously. Indeed, such a rapid rate was at odds with the classical overland model. The purpose of the article was thus to develop a new quantitative model to explain the notably fast spread of early farming in the far west. A computational model was put forward that identified the key elements and mechanisms in the question and estimated the values that yield outcomes that fit the observations. The results (**Figure 5**) show that long-distance voyaging is required to fit the observed pattern (Figure 3 in Isern et al. 2017 [5]). In retrospect, we had just the right team to explain the exceptionally fast pace of first farming along the coasts of the Iberian Peninsula.

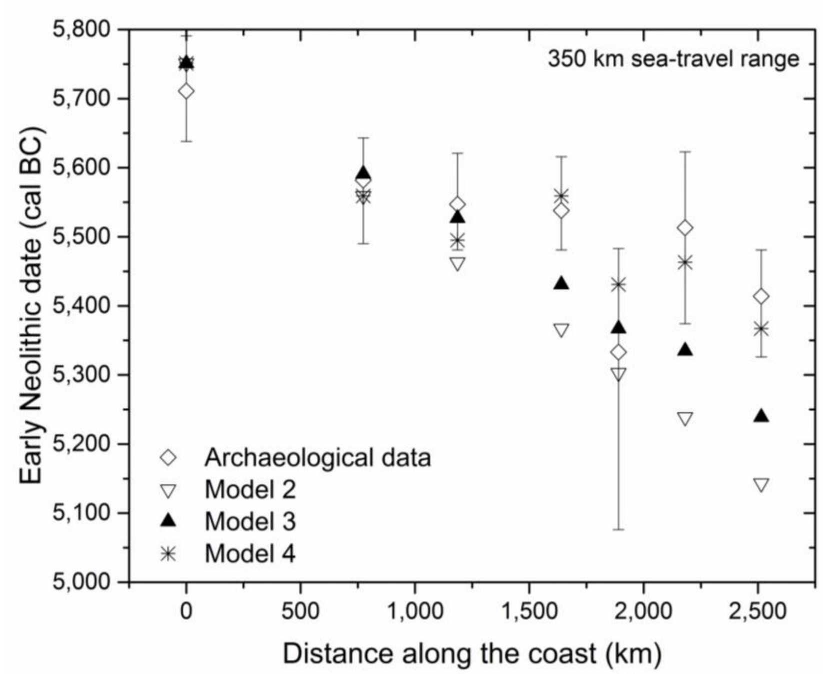

Figure 5 Early Neolithic dates plotted against distance along the coast from Arene Candide in Liguria (for its location see Figure 3), which is displayed for the archaeological evidence and three simulation models. Model 4, which takes a leapfrog approach to site relocation, yields the best fit with lower voyaging ranges (Figure 3 in Isern et al. 2017 [5]).

In some ways, much the same now holds when it comes to how we now think about the matter of space on the landscape. Clearly, what first farmers were trying to achieve did not involve random and continuous movement in space, as Fisher's model assumes. The best places for first farming were not just the same over the landscape as a whole. The conditions for first farming were good in some places and less favorable in others. This insight is considered at some length in my most recent publication on the Neolithic transition (see Ammerman 2022) [3]. It arises from returning to the settlement patterns in two areas of Europe where I have done fieldwork at one time or another. The first is the Aldenhovner Platte in Germany, where whole areas of the landscape were excavated by archaeologists prior to the use of the land for mining brown coal. The second is Acconia in southern Italy where repeated, intensive survey work was carried out on the landscape over five years. In a nutshell, the settlement patterns of first farmers commonly turn out to be selective in character, and they often take up only a small proportion of the space in a region. There are two leading factors that enter the picture when it comes to cultivation and the location of new settlement. The first is a fertile soil with a light texture, making it easy to cultivate the land with the technology available in Neolithic times. The second factor concerns placing a new house or settlement close to a good source of fresh water such as a nearby stream. In other words, the loess soils at Aldenhoven and the paleo-dunes with their light, well-developed soils at Acconia were just what was called for in the respective places. Moreover, the stream called the Merzbach on the Aldenhovener Platte (**Figure 1**) and the four short streams at Acconia made them both excellent places for first farming. The implication is that, on the ground, the wave of advance did not move on a broad front over the landscape as a whole. Instead, it took place on a narrower and more selective front chosen by the first farmers themselves. To put it another way, the spread of early farming in both places ran through an ecology corridor—a habitat that took up only a modest amount of space in the territory. In effect, what was involved in these two cases was a niche-based process to use the language of ecology.

In closing, by measuring the rate of spread and putting forward the wave of advance model based on local population growth and the relocation of the households of the first farmers on the landscape, Cavalli-Sforza and I pioneered the move from the so-called Neolithic revolution (a misguided metaphor for a major change in human history that unfolded over a long span of years) to the Neolithic transition (a slower and more processual approach to change). Our contribution was just one among many others by scholars who are interested in the shift from hunting and gathering based on the consumption of natural resources in a mobile style of life to food production with its focus on the production of domesticated plants and animals in the context of sedentism. In this article I have attempted to give due credit to three scholars who made major contributions to the study of the Neolithic transition in Europe; they are Joaquim Fort, Ron Pinhasi and João Zilhão. In terms of the big picture, the spread of early farming was mound-based in the east. In the West Mediterranean, the advance was spurred by voyaging with its much faster rate in coastal areas and dispersed patterns of settlement. In retrospect, time-delay, which is now incorporated in the process (slowing down the advance), and niche-oriented patterns of advance in the west (speeding up the process) compensated for one another, and thus the wave of advance model made sense as a good first approximation in the 1970s and 1980s. Of course, we did not appreciate the compensation at the time. Science continues to move forward by steps of approximation. Today we are in a better position than ever before, and as one would expect, studying the genomes of first farmers in the years to come will lead to learning more about the social processes that were in operation behind the spread of first farming in Europe.

References

1. Ammerman AJ. The Neolithic transition in Europe at 50 years: Working draft. Festschrift prepared for the 45th anniversary of Ryszard Grygiel and Peter Bogucki's scientific cooperation. 2020.
2. Ammerman AJ. Returning to the rate of spread of early farming in Europe: comment on the article by Manen et al.(2019) in Radiocarbon. Radiocarbon. 2021;63(3):741-749. DOI
3. Ammerman AJ. The transition to early farming in Europe. In: Bergen S, Pardo-Gordo S. editors. Simulating Transitions to Agriculture in Prehistory. Springer; 2022. p. 225-253. DOI
4. Ammerman AJ. The Neolithic transition in Europe at 50 years. In: Grygiel M, Obst P, editors. Walking among ancient Trees. Pękowice near Krakow, Poland: Profil-Archeo; 2023. p. 149-168.
5. Isern N, Zilhão J, Fort J, Ammerman AJ. Modeling the role of voyaging in the coastal spread of the Early Neolithic in the West Mediterranean. Proc Natl Acad Sci U S A. 2017;114(5):897-902. DOI
6. Ammerman AJ, Cavalli-Sforza LL. Measuring the rate of spread of early farming in Europe. Man. 1971;6(4):674-688. DOI
7. Pinhasi R, Fort J, Ammerman AJ. Tracing the origin and spread of agriculture in Europe. PLoS Biol. 2005;3(12):e410. DOI

8. Fisher RA. The wave of advance of advantageous genes. Ann Eugen. 1937;7(4):355-369. DOI
9. Fort J, Méndez V. Time-delayed theory of the Neolithic transition in Europe. Phys Rev Lett. 1999;82(4):867. DOI
10. Zilhão J. Radiocarbon evidence for maritime pioneer colonization at the origins of farming in west Mediterranean Europe. Proc Natl Acad Sci U S A. 2001;98(24):14180-14185. DOI
11. Ammerman AJ, Biagi P, editors. The widening harvest. The Neolithic transition in Europe: looking back, looking forward. Boston: Archaeological Institute of America; 2003.
12. Hodson RH, Kendall DG, Tautu P, editors. Mathematics in the Archaeological and Historical Sciences. Edinburgh: Edinburgh University Press. 1971.
13. Ammerman AJ, Cavalli-Sforza LL. The Neolithic transition and the genetics of populations in Europe. Princeton: Princeton University Press; 1984.
14. Skellam J. The formulation and interpretation of mathematical models of diffusionary processes in biology. In: Barrlett M, Hiorns R, editors. The Mathematical Theory of the Dynamics of Biological Populations. London: Academic Press. 1973. p. 63-85.
15. Menozzi P, Piazza A, Cavalli-Sforza L. Synthetic Maps of Human Gene Frequencies in Europeans: These maps indicate that early farmers of the Near East spread to all of Europe in the Neolithic. Science. 1978;201(4358):786-792. DOI
16. Skellam JG. Random dispersal in theoretical populations. Biometrika. 1951;38(1/2):196-218. DOI
17. Ammerman A, Cavalli-Sforza L. The Wave of Advance model for the diffusion of early farming in Europe. In: Renfrew C, Cooke K, editors. The Explanation of Cultural Change. New York: Academic Press; 1979. p. 275-294.
18. Ammerman AJ. The Acconia survey: Neolithic settlement and the obsidian trade. London, UK: Institute of Archaeology; 1985.
19. Ammerman AJ, Shaffer GD, Hartmann N. A Neolithic household at Piana di Curinga, Italy. J Field Archaeol. 1988;15(2):121-140. DOI
20. Cavalli-Sforza LL. African pygmies. Orlando: Academic Press. 1986.
21. Cavalli-Sforza LL, Menozzi P, Piazza A. The history and geography of human genes. Princeton: Princeton university press; 1994.
22. Menozzi P, Piazza A. The 30th anniversary of "The History and Geography of Human Genes". Hum Popul Genet Genom. 2024;4(4):0011. DOI
23. Ammerman AJ. On the Neolithic transition in Europe: a comment on Zvelebil & Zvelebil (1988). Antiquity. 1989;63(238):162-165. DOI
24. Zilhao J. The Neolithic transition in Portugal and the role of demic diffusion in the spread of agriculture across West Mediterranean Europe. In: Ammerman AJ, Biaggi P, editors. The Widening Harvest. Boston: Archaeological Institute of America; 2023. p. 207-223.
25. Ammerman AJ, Pinhasi R, Bánffy E. Comment on" Ancient DNA from the first European farmers in 7500-year-old Neolithic sites". Science. 2006;312(5782):1875-1875. DOI
26. Barbujani G. L'Alba della Storia. Bari-Rome: Editori Laterza; 2024.
27. Barbujani G, Bertorelle G, Chikhi L. Evidence for Paleolithic and Neolithic gene flow in Europe. Am J Hum Genet. 1998;62(2):488-491. DOI
28. Chikhi L, Destro-Bisol G, Bertorelle G, Pascali V, Barbujani G. Clines of nuclear DNA markers suggest a largely Neolithic ancestry of the European gene pool. Proc Natl Acad Sci U S A. 1998;95(15):9053-9058. DOI
29. Chikhi L, Nichols RA, Barbujani G, Beaumont MA. Y genetic data support the Neolithic demic diffusion model. Proc Natl Acad Sci U S A. 2002;99(17):11008-11013. DOI
30. Cavalli-Sforza LL. Returning to the Neolithic transition in Europe. In: Ammerman AJ, Biagi P, editors. The widening harvest. Boston: Archaeological Institute of America. 2003. p. 297-313.
31. Gamba C, Fernández E, Tirado M, Deguilloux MF, Pemonge MH, Utrilla P, et al. Ancient DNA from an Early Neolithic Iberian population supports a pioneer colonization by first farmers. Mol Ecol. 2012;21(1):45-56. DOI

32. Rasteiro R, Chikhi L. Female and male perspectives on the neolithic transition in Europe: clues from ancient and modern genetic data. PLoS One. 2013;8(4):e60944. DOI
33. Haak W, Balanovsky O, Sanchez JJ, Koshel S, Zaporozhchenko V, Adler CJ, et al. Ancient DNA from European early neolithic farmers reveals their near eastern affinities. PLoS Biol. 2010;8(11):e1000536. DOI
34. Powledge TM, Rose M. The great DNA hunt. Archaeology. 1996;49(5):36-43.
35. Bramanti B, Thomas MG, Haak W, Unterländer M, Jores P, Tambets K, et al. Genetic discontinuity between local hunter-gatherers and central Europe’s first farmers. Science. 2009;326(5949):137-140. DOI
36. Mathieson I, Lazaridis I, Rohland N, Mallick S, Patterson N, Roodenberg SA, et al. Genome-wide patterns of selection in 230 ancient Eurasians. Nature. 2015;528(7583):499-503. DOI
37. Pinhasi R, Fernandes D, Sirak K, Novak M, Connell S, Alpaslan-Roodenberg S, et al. Optimal ancient DNA yields from the inner ear part of the human petrous bone. PloS One. 2015;10(6):e0129102. DOI
38. Yu H, van de Loosdrecht MS, Mannino MA, Talamo S, Rohrlach AB, Childebayeva A, et al. Genomic and dietary discontinuities during the Mesolithic and Neolithic in Sicily. Iscience. 2022;25(5):104244. DOI
39. Simões LG, Peyroteo-Stjerna R, Marchand G, Bernhardsson C, Vialet A, Chetty D, et al. Genomic ancestry and social dynamics of the last hunter-gatherers of Atlantic France. Proc Natl Acad Sci U S A. 2024;121(10):e2310545121. DOI
40. Ammerman AJ. The first Argonauts: Towards the study of the earliest seafaring in the Mediterranean. In: Anderson A, Barrett JH, Boyle KV, editors. The Global Origins and Development of Seafaring. Cambridge: McDonald Institute Monographs; 2010. p. 81-92.
41. Ammerman AJ. The paradox of early voyaging in the Mediterranean and the slowness of the Neolithic transition between Cyprus and Italy. In: Vavouranakis G. editor. The seascape in Aegean prehistory. The Seascape in Aegean Prehistory. Athens: Monograph of the Danish Institute at Athens 14; 2011. p. 31-49.
42. Ammerman AJ. Cyprus: The Submerged Final Palaeolithic of Aspros Dive Site C. In: Bailey G, Galanidou N, Peeters H, Jöns H, Mennenga M, editors. The Archaeology of Europe’s Drowned Landscapes. Coastal Research Library. Springer, Cham. 2020; Vol 35. DOI
43. Ammerman AJ, Davis DW, editors. Island Archaeology and the Origins of Seafaring in the Eastern Mediterranean. Eurasian Prehistory; 2013-2014, Vols. 10-11.
44. Ammerman AJ. Setting our sites on the distant horizon. In: Ammerman AJ, Davis DW, editors. Island Archaeology and the Origins of Seafaring in the Eastern Mediterranean. Eurasian Prehistory; 2014. Vol. 11; pp. 203-236.