



Open Research Online

The Open University's repository of research publications and other research outputs

DNA and Etruscan identity

Book Section

How to cite:

Perkins, Phil (2017). DNA and Etruscan identity. In: Naso, Alessandro ed. Etruscology. Berlin: De Gruyter, pp. 109–118.

For guidance on citations see [FAQs](#).

© 2017 Walter de Gruyter GmbH

Version: Proof

Link(s) to article on publisher's website:

<https://www.degruyter.com/view/product/128551>

Copyright and Moral Rights for the articles on this site are retained by the individual authors and/or other copyright owners. For more information on Open Research Online's data [policy](#) on reuse of materials please consult the policies page.

oro.open.ac.uk

Philip Perkins

8 DNA and Etruscan identity

Abstract: From the time of Herodotus, who suggested that the Etruscans were immigrants to Italy, to the present day, the origin of the Etruscans has been debated. Since the mid-twentieth century a convincing academic consensus has been built that the Etruscans were an autochthonous people. The development of molecular archaeology, investigating ancient biological molecules, particularly DNA, has brought new evidence to the debate. This area is still developing and many of its findings are experimental or provisional.

Keywords: Etruscan origin; DNA; molecular archaeology

Introduction

From the time of Herodotus—who suggested that the Etruscans were immigrants to Italy—to the present day, the origin of the Etruscans has been debated.¹ Since the mid-twentieth century a convincing academic consensus has been built that the Etruscans were an autochthonous people. The development of molecular archaeology, investigating ancient biological molecules, particularly DNA, has brought new evidence to the debate.² This area is still developing and many of its findings are experimental or provisional.³

1 The search for Etruscan DNA

A fundamental feature of gene distribution in Europe is a gradient of variability from high diversity in the southwest of Asia toward lower diversity in the northwest of Europe.⁴ This gradient is thought to derive from the Neolithic colonization of Europe after the last Ice Age when much of Europe was depopulated.⁵ The variability in the mitochondrial DNA (mtDNA) in modern samples from southern Tuscany lies between

¹ See chapter 2 Ulf.

² MacIntosh Turfa 2006; Perkins 2009; Kron 2013.

³ Richards, Macaulay, Bandelt, et al. 1998; Jones 2001; 2006; Richards and Macaulay 2001; Hummel 2003; Jobling, Hurles, and Tyler-Smith 2004; Barbujani 2007; Graham 2007. For a general introduction to the science see Jobling, Hurles, and Tyler-Smith 2004 and for more detail Crawford 2007.

⁴ E.g. Belle, Landry, and Barbujani 2006; Rosser, Zerjaj, Hurles, et al. 2000; Simoni, Calafell, Pettener, et al. 2000.

⁵ Ammerman and Cavalli-Sforza 1984.

these extremes.⁶ Assuming some degree of continuity between the modern Tuscan and Etruscan population,⁷ this observation suggests that the Etruscan population was descended from the Neolithic population, which would be consistent with the hypothesis that the Etruscan language is a relic of pre-Indo-European times and with the current archaeological consensus of an autochthonous origin. Subsequent research has sought to identify genetic material distinct from this generalized Neolithic “background” that might be related to a distinct Etruscan ethnicity, whether autochthonous or immigrant. A further challenge for studies using contemporary genetic variability is that it is associated with contemporary linguistic and geographic variability and the distribution of recent social groups.⁸ This means that contemporary samples from Tuscany will have patterns of variability generated by their geographic, linguistic, and social origins and contacts, irrespective of any relationship to an ancient Etruscan ancestry.

Since about 2000, the study of population genetics has made significant advances in its methodology, particularly in the adoption of statistical techniques to interpret laboratory findings, the development of computer simulation techniques to model population histories, the extraction and analysis of ancient DNA, and the development of techniques that can analyze sections of the genome that are larger than the single molecules that were the focus of earlier studies.⁹

The first major investigation of the Etruscans analyzed eighty samples of bone from ten cemeteries in Etruria along with samples from Adria in the Po Valley and Capua in Campania.¹⁰ The investigation sought to answer two questions. (1) Were the Etruscans a biological population or just people who shared a culture but not ancestry? And (2) what is their relationship to modern populations and are they linked to other Eurasians?¹¹ The first question is interesting because it directly addresses a basic assumption: that the Etruscans were a people. This assumption is rarely questioned in Etruscology; after all, the Roman sources identify the Etruscans (the *nomen Etruscum*) as a group, even if they are then subdivided into the *duodecim populi Etruriae* (twelve peoples of Etruria).¹² The research group led by Vernesi found that the internal genetic diversity in the Etruscan DNA was low, comparable to that in modern European populations, and not distinct, meaning there is no clear Etruscan “genetic

6 Francalacci, Bertranpetit, Calafell, et al. 1996; Francalacci 1997.

7 Guimaraes et al. 2009 have found relationships between medieval and modern Tuscan DNA, but not Etruscan and modern. Ghirotto et al. 2013 have suggested continuity between ancient Etruscan DNA and modern Tuscan DNA from Volterra and the Casentino, but not with DNA from Murlo.

8 Piazza, Cappello, Olivetti, et al. 1988; Barbujani and Sokal 1991; Novembre et al. 2008.

9 Barbujani and Bertorrelle 2001; Excoffier 2004; Jobling, Hurles, and Tyler-Smith 2004; Bandelt 2005; Thomas, Gilbert, Bandelt, et al. 2005; Richards and Macaulay 2001.

10 Vernesi, Caramelli, Dupanloup, et al. 2004.

11 Vernesi, Caramelli, Dupanloup, et al. 2004, 695.

12 Torelli 1985; Colonna 2000; Perkins 2005, 110.

fingerprint” that could be detected. The research also suggested that the Etruscan samples had a shared set of ancestors,¹³ and this is consistent with the existence of the gentilicial system of family structure based on blood lines that is directly observable in Etruscan personal names and in the sharing of family chamber tombs over several generations that became widespread from the Late Orientalizing period onward. Genetic relationships between individuals from the same chamber tomb have also been demonstrated using mtDNA evidence at Tarquinia.¹⁴ At a more general level, the findings are consistent with Etruscan autochthony, since cultural and settlement continuity from the Late Bronze Age to the Etruscan period would generate a shared ancestry extending over at least ten generations.

2 Etruscans and modern DNA

The second question, posed by Vernesi and colleagues, of the relationship between the genetic diversity in the ancient DNA from Etruria and the genetic diversity observed in modern populations, aimed to investigate any genealogical or emigrational links between the Etruscans and other Eurasian populations. The results were not decisive: the samples were found to have less genetic resemblance to modern Tuscans than there is resemblance between randomly chosen modern European populations.¹⁵ Analyses of the shortest genetic difference between the (Etruscan) samples and modern populations found them closest to Tuscans, with Turks, other Mediterranean peoples, and the Cornish (from the southwest of England) following. Assessment of the mix of genetic material in the samples (admixture coefficient)¹⁶ suggested that Etruscans are more closely related to Turks and North Africans than to Basques and northeast Europeans, and that the samples were more likely to have components of Turkish or North African DNA than samples from Tuscans, southern Italians, or Sicilians. The conclusion drawn was that the findings support an autochthonous origin for the Etruscans, inasmuch as their DNA is similar to that of other Europeans, but without excluding some component of female-derived DNA originating in the eastern or southern Mediterranean. This study was subsequently criticized for technical and methodological reasons, including the origin of the samples in old, possibly contaminated museum collections;¹⁷ however, this need not invalidate tentative conclusions

¹³ Vernesi, Caramelli, Dupanloup, et al. 2004, 701.

¹⁴ Cappellini, Biella, Chiarelli, et al. 2004; Cappellini, Chiarelli, Sineo, et al. 2004.

¹⁵ Vernesi, Caramelli, Dupanloup, et al. 2004, 699.

¹⁶ Dupanloup and Bertorelle 2001.

¹⁷ Bandelt 2004; Malyarchuk and Rogozin 2004; Bandelt 2005; Thomas, Gilbert, Bandelt, et al. 2005.

despite the hazards involved in being certain that the DNA identified is authentically ancient.¹⁸

The tentative observation that Tuscans have the shortest genetic distance from the Etruscan ancient DNA (aDNA) has been further investigated by attempts to simulate population histories that could have led to the degree of relatedness between Etruscans and Tuscans that was observed by Vernesi's group.¹⁹ This work concluded that the Tuscans are largely descended from non-Etruscan ancestors.²⁰ Projecting the simulations backward in time suggests that the genetic lines of the Etruscan samples emerged in the early Neolithic ca. 5500–4000 BCE (coalescence), a hypothesis consistent with an unbroken sequence of cultural development.²¹

Contrary to these studies, principal component analysis comparing 322 samples of modern Tuscan DNA with samples from other parts of western Eurasia found that Tuscan mtDNA has many affinities with European DNA but samples from Murlo had a higher proportion of haplogroups that are commonly found in the Near East.²² Eleven haplotypes in the Tuscan samples were not found in 10,589 samples from Europe, including Italy, but were found in samples from Near Eastern populations spread from the Levant through Jordan, Mesopotamia, Iran, and the Caucasus, with one in Turkey. The findings indicate post-Neolithic, genetic input from the Near East to the present-day population of Tuscany.²³

A subsequent, more detailed study of 258 samples from Tuscany has identified that approximately three percent of these contain typical Near Eastern haplogroups, significantly reducing the proportion estimated by Achilli and colleagues in 2007.²⁴ Other studies have also identified a link between modern Tuscan and Anatolian DNA but suggested that the two populations divided at least as far back as the Neolithic Period.²⁵

An alternative approach to identifying intrusive populations is to identify a restricted geographic distribution of a gene mutation and then attempt to chronologically reconstruct the history of the mutation of that gene to provide a date for the first occurrence of that mutation. In Tuscany, nine of fifty-three samples from Elba contained a distinct mutation (U7a2a subsequently renamed U7b1) of a haplotype most commonly found in southwest Asia, with a distribution centered in Iran.²⁶ The occurrence of this mutation has been tentatively dated to 750 BCE–950 CE, which could

18 Barbujani, Vemesi, Caramelli, et al. 2004

19 Belle, Ramakrishnan, Mountain, et al. 2006.

20 Belle, Ramakrishnan, Mountain, et al. 2006.

21 Pallottino 1984, 35–75; Malone 2003.

22 Achilli, Olivetti, Pala, et al. 2007, 762, fig. 1.3.

23 Achilli, Olivetti, Pala, et al. 2007, 766–67, fig. 5.

24 Cf. n. 22. Brisighelli, Capelli, Álvarez-Iglesias, et al. 2009.

25 Ghiretto et al. 2013; Tassi 2013.

26 Brisighelli, Capelli, Álvarez-Iglesias, et al. 2009.

indicate the arrival of a Near Eastern immigrant carrying the mutation in the Etruscan period. However, the date range is wide and many other historical scenarios could easily account for the presence of this material in Italy.

Yet more recent work, using genome-wide, rather than maternal mtDNA, has identified a component of near eastern DNA in Tuscan samples, estimating that the genetic material mixed into the pool between 600–1100 BCE. Once again, as the authors note, these are estimates and various historical circumstances may have led to the formation of the observed dataset. Likewise, from an archaeological point of view, eastern genetic material in Italy is not to be unexpected in that period, and does not do anything to prove migration from Anatolia to Etruria. One new element of the study is the identification [as](#) the Caucasus as the area with the most closely related DNA to Tuscany, as an ancestral location this would seem, on the face of it, to be historically unlikely.²⁷

3 Italian cattle DNA

A study of DNA from eleven rare breeds of Italian cattle identified Near Eastern haplotypes in Tuscan breeds,²⁸ and this led to a hypothesis that the cattle arrived in Tuscany with Etruscan settlers in the Late Bronze Age. Earlier studies of cattle DNA also detected genetic variation in European cattle that can be associated with southwest Asia, where *Bos taurus* was originally domesticated. Those studies also identify the highest levels of alleles associated with *Bos indicus* (zebu) in Italian cattle and relatively high levels of them in Greek cattle, and these are said to derive from cultural associations between Anatolia, Greece, and Italy over the past three millennia.²⁹

A more comprehensive study concluded that the cattle originating in the Neolithic in the Near East also have mtDNA deriving from North African cattle and wild aurochs; it presents a circum-Mediterranean distribution of cattle DNA illustrating that the African (T1) and Near Eastern (T and T2) haplotypes are found around most of the northern shores of the Mediterranean, making the Tuscan cattle less of a special case that could be associated with a hypothetical migration of (Etruscan) people from the Near East.³⁰

²⁷ Pardo-Seco, Gómez-Carballa, Amigo, et al. 2014.

²⁸ Pellecchia, Negrini, Colli, et al. 2007.

²⁹ Cymbron, Freeman, Malheiro, et al. 2005.

³⁰ Beja-Pereira, Caramelli, Lalueza-Fox, et al. 2006.

4 Conclusions

Given the Neolithic colonization of Europe, it is to be expected that Tuscan, or indeed Etruscan, DNA should contain haplotypes characteristic of southwest Asia. The Tuscans or Etruscans occupy a position on the clines of various distributions of haplotypes, just like any other European population. There have not yet been enough studies to reliably distinguish a Tuscan combination of haplotypes as distinct from other combinations in Italy, even if it is now possible to separate northern Italian samples from Bergamo from Tuscan samples.³¹ Even if the arrival of southwest Asian haplotypes could be dated to ca. 2,800 years ago, this would not confirm that the Etruscans were immigrants, because we already know that people moved around the first-millennium Mediterranean, either as immigrants or as groups of Greek or Phoenician colonists. Traditional archaeological techniques find it challenging to convincingly identify intrusive alien individuals, but ethnic diversity is indicated by the presence of foreigners, particularly Sardinians, in cemeteries in Etruria from the tenth–ninth centuries onward,³² and there is plentiful evidence for cultural and economic exchange in the subsequent Orientalizing period³³ that has led to the suggestion of Near Easterners in the elite of Etruria³⁴ and provides a plausible context for genetic exchange to occur. Mythistorical accounts, new artistic styles or uses of materials, and personal names occasionally suggest the movements of people³⁵ and also occasionally suggest a non-Etruscan origin of individuals, who are usually assumed to be males. The mtDNA evidence indicates there was also immigration of childbearing females across the Mediterranean, possibly in the Etruscan period.

None of the DNA studies to date conclusively prove that Etruscans were an intrusive population in Italy that originated in the Eastern Mediterranean or Anatolia. Likewise, none conclusively prove that Tuscans are descended from Etruscans. On balance, there are indications that the evidence of DNA can support the theory that Etruscan people are autochthonous in central Italy. The absence of decisive results derives from the fundamental fact that archaeological ethnicities do not neatly map onto patterns in genetic diversity. Studies of modern genetic variation mapped with socio-cultural categories can demonstrate correlation between the two,³⁶ but the time-depth of the archaeological perspective creates complex layering in genetic diversity as population dynamics change, populations relocate and intermingle over

³¹ Li, Absher, Tang, et al. 2008, fig 2a.

³² Camporeale 1997, 48–49; Bartoloni 1988, 48–49.

³³ Cristofani 1996; Giangiulio 1996, 518–25.

³⁴ Magness 2001. Novembre et al. 2008.

³⁵ Pallottino 1971, 83–84; Ampolo 1976–77; Ridgway 1992; Colonna 1989, 21; Cristofani 1996; Winter 2009.

³⁶ Novembre et al. 2008.

time.³⁷ The genetic diversity of the ancient people we identify as Etruscans, will have been a complex mix of genetic material deriving from western European, south west Asia and neighboring areas. Unraveling that mix, and relating it to the socio-cultural development of archaeological societies is an exciting challenge for both archaeogeneticists and archaeologists.

References

- Achilli, A., A. Olivieri, M. Pala, E. Metspalu, S. Fornarino, V. Battaglia, M. Accetturo, I. Kutuev, E. Khusnutdinova, E. Pennarun, N. Cerutti, C. Di Gaetano, F. Crobu, D. Palli, G. Matullo, A. S. Santachiara-Benerecetti, L. Cavalli-Sforza, O. Semino, R. Villems, H.-J. Bandelt, A. Piazza, and A. Torroni. 2007. "Mitochondrial DNA Variations of Modern Tuscans Supports the Near Eastern Origin of Etruscans." *American Journal of Human Genetics* 80: 759–68.
- Ammerman, A. J., and L. L. Cavalli-Sforza. 1984. *The Neolithic Transition and the Genetics of Populations in Europe*. Princeton: Princeton University Press.
- Ampolo, C. 1976–77. "Demarato. Osservazioni sulla mobilità sociale arcaica." *DialArch* 9–10: 333–45.
- Badro, D.A., B. Douaihy, M. Haber, S.C. Youhanna, A. Salloum, M. Ghassibe-Sabbagh, B. Johnsrud, G. Khazen, E. Matisoo-Smith, D. F. Soria-Hernanz, R. Spencer Wells, C. Tyler-Smith, D. E. Platt, P. A. Zalloua. 2013. "Y-Chromosome and mtDNA Genetics Reveal Significant Contrasts in Affinities of Modern Middle Eastern Populations with European and African Populations." *PLoS ONE* 8(1): e54616.
- Bandelt, H.-J. 2004. "Etruscan Artifacts." *American Journal of Human Genetics* 75: 919–20.
- . 2005. "Mosaics of Ancient Mitochondrial DNA: Positive Indications of Nonauthenticity." *European Journal of Human Genetics* 13: 1106–12.
- Barbujani, G. 2007. "DNA and Etruscan Origins: G. Barbujani's response to J. Turfa." *Etruscan News* 8:4.
- Barbujani, G., and G. Bertorelle. 2001. "Genetics and the Population History of Europe." *Proceedings of the National Academy of Sciences of the United States of America* 98(1):22–25.
- Barbujani, G., and R. Sokal. 1991. "Genetic Population Structure of Italy, II: Physical and Cultural Barriers to Gene Flow." *American Journal of Human Genetics* 48:398–411.
- Barbujani, G., C. Vernesi, D. Caramelli, L. Castrì, C. Lalueza-Fox, and G. Bertorelle. 2004. "Etruscan Artifacts: Much Ado about Nothing." *American Journal of Human Genetics* 75:923–27.
- Bartoloni, G. 1989. "Marriage, Sale and Gift. A proposito di alcuni corredi femminili dalle necropoli popoloniesi della prima età del ferro." In *Le donne in Etruria*, edited by A. Rallo, 35–58. Rome: L'Erma di Bretschneider.
- Beja-Pereira, A., D. Caramelli, C. Lalueza-Fox, C. Vernesi, N. Ferrand, A. Casoli, F.Goyache, L. J. Royo, S. Conti, M. Lari, A. Martini, L. Ouragh, A. Magid, A. Atash, A. Zsolnai, P. Boscato, C. Triantaphyllidis, K. Ploumi, L. Sineo, F. Mallegni, P. Taberlet, G. Erhardt, L. Sampietro, J. Bertranpetit, G. Barbujani, G. Luikart, and G. Bertorelle. 2006. "The Origin of European Cattle: Evidence from Modern and Ancient DNA." *Proceedings of the National Academy of Sciences of the United States of America* 103(21):8113–18.

³⁷ Badro et al. et al. 2013; Haber et al. 2013; Pardo-Seco et al. 2014.

- Belle, E. M. S., P.-A. Landry, and G. Barbujani. 2006. "Origins and Evolution of the European Genome: Evidence from Multiple Microsatellite Loci." *Proceedings of the Royal Society B* 273:1595–1602.
- Belle, E. M. S., U. Ramakrishnan, J. L. Mountain, and G. Barbujani. 2006. "Serial Coalescent Simulations Suggest a Weak Genealogical Relationship between Etruscans and Modern Tuscans." *Proceedings of the National Academy of Sciences of the United States of America* 103(21): 8012–17.
- Brisighelli, F., C. Capelli, V. Álvarez-Iglesias, V. Onofri, G. Paoli, S. Tofanelli, Á. Carracedo, V. L. Pascali, and A. Salas. 2009. "The Etruscan Timeline. A Recent Anatolian Connection." *European Journal of Human Genetics* 17: 693–96.
- Camporeale, G. 1997. "On Etruscan Origins, Again." *Etruscan Studies* 4: 45–51.
- Cappellini, E., M. C. Biella, B. Chiarelli, and D. Caramelli 2004. "Lo studio del DNA antico: Il caso della tb. 5859 della necropoli dei Monterozzi di Tarquinia." *StEtr* 69: 263–75.
- Cappellini, E., B. Chiarelli, L. Sineo, A. Casoli, A. Di Gioia, C. Vernesi, M. C. Biella, and D. Caramelli. 2004. "Biomolecular Study of the Human Remains from Tomb 5859 in the Etruscan Necropolis of Monterozzi." *Journal of Archaeological Science* 31: 603–12.
- Colonna, G. 1989. "Gli Etruschi e l' 'invenzione' della pittura." In *Pittura etrusca al museo di Villa Giulia*, edited by M. A. Rizzo, 19–26. Rome: De Luca Edizioni d'Arte.
- . 2000. "The Original Features of the Etruscan Peoples." In *The Etruscans*, edited by M. Torelli, 25–41. London: Thames & Hudson.
- Crawford, M. H., ed. 2007. *Anthropological Genetics. Theory, Methods and Applications*. Cambridge: Cambridge University Press.
- Cristofani, M. 1996. *Etruschi e altre genti nell'Italia preromana. Mobilità in età arcaica*. Archeologica 120. Rome: Giorgio Bretschneider.
- Cymbron, T., A. R. Freeman, M. I. Malheiro, J.-D. Vigne, and D. G. Bradley. 2005. "Microsatellite Diversity Suggests Different Histories for Mediterranean and Northern European Cattle Populations." *Proceedings of the Royal Society B* 272: 1837–43.
- Dupanloup, I., and G. Bertorelle. 2001. "Inferring Admixture Proportions from Molecular Data: Extension to any Number of Parental Populations." *Molecular Biology and Evolution* 18(4): 672–75.
- Excoffier, L. 2004. "Patterns of DNA Sequence Diversity and Genetic Structure after a Range Expansion: Lessons from the Infinite-Island Model." *Molecular Ecology* 13: 853–64.
- Franclacci, P. 1997. "Mitochondrial DNA variability in Tuscany." *Etruscan Studies* 4: 103–19.
- Franclacci, P., J. Bertranpetit, F. Calafell, and P. A. Underhill. 1996. "Sequence Diversity of the Control Region of Mitochondrial DNA in Tuscany and Its Implications for the Peopling of Europe." *American Journal of Physical Anthropology* 100: 443–60.
- Ghirotto, S., Tassi, F., Fumagalli, E., Colonna, V., Sandionigi, A., Lari, M., Vai, S., Petiti, E., Corti, G., Rizzi, E., De Bellis, G., Caramelli, D., and Barbujani, G. 2013. "Origins and Evolution of the Etruscans' mtDNA." *PLoS ONE* 8(2): e55519.
- Gianguilio, M. 1996. "Avventurieri, mercanti, coloni, mercenari. Mobilità umana e circolazione di risorse nel Mediterraneo arcaico." In *I Greci. Storia cultura arte società*, part 2. *Una storia greca, 1 Formazione*, edited by S. Settis, 497–525. Turin: Einaudi.
- Graham, E. A. M. 2007. "DNA Reviews: Ancient DNA." *Forensic Science, Medicine, and Pathology* 3: 221–25.
- Guimaraes, S., S. Ghirotto, A. Benazzo, L. Milani, M. Lari, E. Pilli, E. Pecchioli, F. Mallegni, B. Lippi, F. Bertoldi, S. Gelichi, A. Casoli, E. M. S. Belle, D. Caramelli, and G. Barbujani. 2009. "Genealogical Discontinuities among Etruscan, Medieval, and Contemporary Tuscans." *Molecular Biology and Evolution* 26(9): 2157–66.

- Haber, M., D. Gauguier, S. Youhanna, N. Patterson, P. Moorjani, L. R. Botigué, D. E. Platt, E. Matisoo-Smith, D. F. Soria-Hernanz, R. Spencer Wells, J. Bertranpetit, C. Tyler-Smith, D. Comas, P. A. Zalloua. 2013. "Genome-Wide Diversity in the Levant Reveals Recent Structuring by Culture." *PLoS Genetics* 9(2): e1003316. doi:10.1371/journal.pgen.1003316.
- Hummel, S., ed. 2003. *DNA Typing: Methods, Strategies and Applications*. Berlin: Springer.
- Jobling, M., M. Hurles, and C. Tyler-Smith. 2004. *Human Evolutionary Genetics: Origins, Peoples and Disease*. New York: Garland Science.
- Jones, M. 2001. *The Molecule Hunt. Archaeology and the Hunt for Ancient DNA*. London: Allen Lane.
- . 2006. "Archeology and the Genetic Revolution." In *A Companion to Archaeology*, edited by J. Bintliff, 39–51. Oxford: Blackwell.
- Kron, G. 2013. "Fleshing out the demography of Etruria." In *The Etruscan World*, edited by J. Macintosh Turfa, 56–75. London-New York: Routledge.
- Li, J. Z., D. M. Absher, H. Tang, A. M. Southwick, A. M. Casto, S. Ramachandran, H. M. Cann, G. S. Barsh, M. Feldman, L. L. Cavalli-Sforza, and R. M. Myers. 2008. "Worldwide Human Relationships Inferred from Genome-wide Patterns of Variation." *Science* 319:1100–1104.
- MacIntosh Turfa, J. 2006. "Staring Down Herodotus: Mitochondrial DNA Studies and Claims about Etruscan Origins." *Etruscan News* 7: 4–5.
- Magness, J. 2001. "A Near Eastern Ethnic Element Among the Etruscan Elite?" *Etruscan Studies* 8: 79–117.
- Malone, C. 2003. "The Italian Neolithic. A Synthesis of Research." *Journal of World history* 17: 235–312.
- Malyarchuk, B. A., and I. B. Rogozin. 2004. "On the Etruscan Mitochondrial DNA Contribution to Modern Humans." *American Journal of Human Genetics* 75: 920–23.
- Novembre, J., T. Johnson, K. Bryc, Z. Kutalik, A. R. Boyko, A. Auton, A. Indap, K. S. King, S. Bergmann, M. R. Nelson, M. Stephens, and C. D. Bustamante. 2008. "Genes Mirror Geography within Europe." *Nature* 456: 98–101.
- Pallottino, M. 1971. *Civiltà artistica etrusco-italica*. Florence: Sansoni.
- . 1984. *Storia della prima Italia*. Milan: Rusconi.
- Pardo-Seco J, A. Gómez-Carballa, J. Amigo, F. Martín-Torres, and A. Salas. 2014. "A Genome-Wide Study of Modern-Day Tuscans: Revisiting Herodotus's Theory on the Origin of the Etruscans." *PLoS ONE* 9(9): e105920.
- Pellecchia, M., R. Negrini, L. Colli, M. Patrini, E. Milanese, A. Achilli, G. Bertorelle, L. Cavalli-Sforza, A. Piazza, A. Torroni, and P. Ajmone-Marsan. 2007. "The Mystery of Etruscan Origins: Novel Clues from *Bos taurus* Mitochondrial DNA." *Proceedings of the Royal Society B* 274:1175–79.
- Perkins, P. 2005. "Who Lived in the Etruscan Albegna Valley?" In *Papers in Italian Archaeology VI*, edited by P. Attema, A. Nijboer, and A. Zifferero. BAR Supp. 1452, 1:109–17. Oxford: Archaeopress.
- . 2009. "DNA and Etruscan Identity." In *Etruscan by Definition*, edited by P. Perkins and J. Swaddling, 95–111. London: British Museum Press.
- Piazza, A., N. Cappello, E. Olivetti, and S. Rendine. 1988. "A Genetic History of Italy." *Annals of Human Genetics* 52: 203–13.
- Richards, M. B., and V. A. Macaulay. 2001. "The Mitochondrial Gene Tree Comes of Age." *American Journal of Human Genetics* 68:1315–20.
- Richards, M. B., V. A. Macaulay, H.-J. Bandelt, and B. C. Sykes 1998. "Phylogeography of Mitochondrial DNA in Western Europe." *Annals of Human Genetics* 62:241–60.
- Ridgway, D. R. 1992. "Demaratus and His Predecessors." In *Greece between East and West, 10th–8th Centuries BC*, edited by G. Kopcke and I. Tokumaru, 85–92. Mainz: Philipp von Zabern.
- Rosser, Z. H., T. Zerjal, M. E. Hurles, M. Adojaan, D. Alavantic, A. Amorim, W. Amos, M. Armenteros, E. Arroyo, G. Barbujani, G. Beckman, L. Beckman, J. Bertranpetit, E. Bosch, D. G. Bradley,

- G. Brede, G. Cooper, H. B. S. M. Côrte- Real, P. de Knijff, R. Decorte, Y. E. Dubrova, O. Evgrafov, A. Gilissen, A. Glisic, M. Gölge, E. W. Hill, A. Jeziorowska, L. Kalaydjieva, M. Kayser, T. Kivisild, S. A. Kravchenko, A. Krumina, S. Kučinskias, J. Lavinha, L. A. Livshits, P. Malaspina, S. Maria, K. McElreavey, T. A. Meitinger, A.-V. Mikelsaar, R. J. Mitchell, K. Nafa, J. Nicholson, S. Nørby, A. Pandya, J. Parik, P. C. Patsalis, L. Pereira, B. Peterlin, G. Pielberg, M. J. Prata, C. Previderé, L. Roewer, S. Rootsi, D. C. Rubinsztein, J. Saillard, F. R. Santos, G. Stefanescu, B. C. Sykes, A. Tolun, R. Villems, C. Tyler-Smith, and M. A. Jobling. 2000. "Chromosomal Diversity in Europe Is Clinal and Influenced Primarily by Geography, rather than by Language." *American Journal of Human Genetics* 67: 1526–43.
- Simoni, L., F. Calafell, D. Pettener, J. Bertranpetit, and G. Barbujani. 2000. "Geographic Patterns of mtDNA Diversity in Europe." *American Journal of Human Genetics* 66: 262–78.
- Tassi, F., S. Ghirotto, D. Caramelli, and G. Barbujani. 2013. "Genetic Evidence Does Not Support an Etruscan Origin in Anatolia." *American Journal of Physical Anthropology* 152: 11–18.
- Thomas, M., P. Gilbert, H.-J. Bandelt, M. Hofreiter, and I. Barnes. 2005. "Assessing Ancient DNA Studies." *Trends in Ecology and Evolution* 20(10): 541–44.
- Torelli, M. 1985. "I duodecim populi Etruria." *AnnMuseoFaina* 2: 37–53.
- Vernesi, C., D. Caramelli, I. Dupanloup, G. Bertorelle, M. Lari, E. Cappellini, J. Moggi-Cecchi, B. Chiarelli, L. Castri, A. Casoli, F. Mallegni, C. Lalueza-Fox, and G. Barbujani. 2004. "The Etruscans: A Population-Genetic Study." *American Journal of Human Genetics* 74: 694–704.
- Winter, N. A. 2009. "Solving the Riddle of the Sphinx on the Roof." In *Etruscan by Definition*, edited by P. Perkins and J. Swaddling. British Museum Research Publications 173, 69–72. London: British Museum Press.