Population Structure and Frankish Ethnogenesis (AD 400-900)

by

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ABSTRACT

The transition from Late Antiquity to Early Medieval Europe (ca. AD 400-900) is often characterized as a period of ethnogenesis for a number of peoples, such as the Franks. Arising during protracted contact with the Roman Empire, the Franks would eventually form an enduring kingdom in Western Europe. However, there is little consensus about the processes by which they formed an ethnic group. This study takes a fresh look at the question of Frankish ethnogenesis by employing a number of theoretical and methodological subdisciplines, including population genetics and ethnogenetic theory. The goals of this work were 1) to validate the continued use of biological data in questions of historical and archaeological significance; and 2) to elucidate how Frankish population structure changed over time.

Toward this end, measurements from the human dentition and crania were subjected to rigorous analytical techniques and interpreted within a theoretical framework of ethnogenetic life cycles. Results validate existing interpretations of intra-regional biological continuity over time. However, they also reveal that 1) there are clear biological and geographical differences between communities, and 2) there are hints of diachronic shifts, whereby some communities became more similar to each other over time. These conclusions complement current ethnohistoric work arguing for the increasing struggle of the Frankish kingdom to unify itself when confronted by strong regionally-based politics.

This work is dedicated to my family, friends, colleagues, and mentors.

"Joy shared is twice the joy. Sorrow shared is half the sorrow."

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CHAPTER 1

INTRODUCTION

1.0.0 INTRODUCTION

Ethnicity has been an increasingly popular field of inquiry in archaeology and bioarchaeology. An aspect of social identity popularized by Frederik Barth (1969) and scholars of the Manchester School (e.g., Gluckman, 1958; Cohen, 1978), ethnicity has been viewed as a valuable analytical concept that diverged from more static and essentialist notions of people in the past (e.g., tribes). More specifically, ethnic identity "results from identification with a broader group in opposition to others on the basis of perceived cultural differentiation and/or common decent" (Jones, 1997: xiii). It can change in saliency during the life course and forms a dynamic relationship with other forms of social identity, such as gender and age. On a supra-individual scale, differences in ethnic identities of groups often manifest in a variety of passive and active ways; some as subtle as minor stylistic variations in material culture, others as group proscriptions that impact mate choice (and hence, biological relationships).

Compared to other social scientists, archaeologists have come late to the study of ethnicity. Indeed, some of the earliest *theoretically informed* studies of ethnicity in archaeological contexts developed in the 1980s and 1990s (for a review, see Emberling, 1997). Although the use of material remains to address the creation, maintenance, and transformations of ethnic groups is controversial, numerous studies have successfully done so (for examples, see Emberling, 1997; Jones, 1997; Voss, 2008).

Arguably, it is less common to find such explorations incorporating biological data in a theoretically informed manner—one that is not deterministic, reductionist, typological, or purely synchronic (for example, Stojanowski, 2010). In fact, many scholars both in America and Europe view the use of biological data for biodistance analyses to be a "reversion" to earlier, racist and typological mindsets (Armelagos and Van Gerven, 2003: 53). However, these arguments ignore recent advances in the development of model-bound quantitative genetic analyses (Stojanowski and Buikstra, 2004: 430) and the application of a biosocial framework for understanding ethnicity in the past (Stojanowski, 2005a,b, 2009, 2010). Newer approaches avoid the simplistic use of phenetic similarity, propose testable evolutionary models, do not focus on taxonomies, and take an explicitly diachronic approach. These approaches are also biosocial in nature and avoid asking descriptive questions of how biology and culture interact. Rather, they redefine the salient questions by asking how processes of microevolution, like gene flow, impact aspects of identity. Yet, some scholars—many of them in non-anthropological disciplines—misunderstand or perpetuate the idea that biological data cannot be used in a meaningful way to inform on social processes, such as ethnogenesis. The case of Frankish ethnogenesis is a perfect example of this troubling tendency.

The collapse of the Roman Empire, the impact of "barbarian" peoples, and the rise of post-Roman successor states in the early Middle Ages (c. AD 450-1000) transformed the ethnic, socio-political, and religious characteristics of Europe (Geary, 1988). By the end of the first millennium AD, a number of diverse peoples would coalesce into ethnic groups and become the approximate predecessors of the proto-European nation-states (e.g., the Franks/France) (Geary, 2002; Gillett, 2002c). The most

enduring of these groups was the Franks, and the development of their kingdom has been well documented.

Yet, the coalescence of Frankish identity was not an obligatory or predetermined process, thereby providing scholars with the opportunity to assess the social and biological factors significant in the development of group identities in pre-modern, non-colonial contexts like Late Antique and Early Medieval Europe. Furthermore, a study of Frankish ethnogenesis sheds light on a key transitional period in history—one that separated the Classical or Antique World from the Early Modern one most familiar to people today.

Consequently, this study has two main objectives. **The first, and most general, goal is to emphasize the continued utility of biological data to important social questions for the study of the Late Antiquity and the Early Middle Ages in Europe, and indeed for any time period or region of interest. Secondly and more specifically, I seek to clarify the relationship(s) between population structure and Frankish ethnogenesis during the first millennium AD.** Toward this end, I collected phenotypic data (e.g., human cranial and dental measurements) from a variety of sites dated to the Late Roman and Early Medieval Periods (c.a. AD 200-900). Using principles from quantitative genetics, population genetics, and biodistance, I analyzed these data and interpreted them within a theoretically informed framework on ethnogenesis (i.e., ethnogenetic lifecycles).

Most historians and archaeologists agree that, by the end of the Early Middle Ages, a Frankish identity coalesced under the Carolingian dynasty of the Frankish Kingdom (c. AD 700-900) (McKitterick, 1983; Wood, 1993; Reimutz, 2008; Broome,

2014). However, there is a striking lack of consensus on this ethnogenetic process. Some view it as a result of a migration in the 4th century AD by an extant ethnic group (i.e., Wenskus, 1961; Hummer, 1998); others view it as a result of migration of a multi-ethnic confederation that also began in the 4th century AD (i.e., Pohl, 1998). Still others dispute the existence of large numbers of migrating people at all (i.e., Geary, 1988; Goffart, 2006), while others debate the effect of migrating groups (if they even existed) on indigenous Gallo-Romans (Goffart, 2006). Finally, there are scholars who argue that ethnicity played no (or only a small) role during this transformational time period and that other mechanisms are better suited for explaining the observed changes in social identities (Gillett, 2006). How important was gene flow to changes in group identity over time? Was the Early Medieval period primarily characterized by population continuity, as is commonly believed? If so, how might this have impacted the development of group identity?

In this work, I suggest that the answer to some of these lingering debates related to Frankish ethnogenesis is to employ modern bioarchaeological methods, one of which is a theoretically driven biodistance approach. More specifically, I employ a model of ethnogenetic lifecycles (Hickerson, 1996) to assess any changes in biological variation over time. Specifically, I suggest that Frankish ethnogenesis may be better understood as passing through different stages of formation (*ibid*). These are 1) separation; 2) liminality; and 3) reintegration; this model is fully explored in Chapter 6. While each of these stages is employed to generate generalized expectations for changes in population structure, they may also be used to explore changes and intersectionality in other datasets,

such as archaeological and ethnohistorical[1]. In this manner, I aim to avoid a simple correlation of biological and social data.

The problem of Frankish ethnogenesis is a thread in a larger tapestry of inquiry surrounding the transition from Late Antiquity to Early Medieval Europe. But it is not some idle question limited to a few specialists. Not only do the Early Middle Ages (c. AD 450-1000) form a bridge between the Classical world and pre-modern Europe, but they also provide an exceptional situation for assessing the inter-relationships between a wide variety of social and biological processes, how they change over time, and what impact (if any) these processes have on each other. Arguably, few other time periods and geographic regions are as rich in historical texts, archaeological materials, and biological remains[2].

In this introductory chapter, I provide a summary of the debate concerning Frankish ethnogenesis. First, I elaborate on the theoretical foundations of the so-called "ethnogenetic paradigm" that originated from studies on German culture. Furthermore, I describe the theoretical "turning points" in the discussion commonly accepted by Early Medieval scholars, before finally outlining the most pertinent critiques. Then, I expound on the potential benefits of a bioarchaeological approach to this topic of Frankish ethnogenesis. Finally, a brief outline of subsequent chapters is provided.

[1] The full exploitation of this particular model of ethnogenesis is beyond the immediate scope of this project. However, it has been done successfully by scholars, such as Stojanowski (2010).

[2] Halsall (2010: 84) eloquently sums up this potentiality: "The greater the written record, the *greater* the potential of material culture to complement—*and to question*—that record, to provide further insights into social and ideological structure." Perry's (2007) exploration of the divergences between bioarchaeological and textual data for the Classic Period of the Near East is a good illustration of this potentiality.

1.1.0 DEBATED ETHNOGENESIS

1.1.1 Germanic Altertumskunde

In contrast to the more recent popularity of the topic amongst (bio)archaeologists in the Americas, ethnogenesis has been discussed for decades by philologists and historians, including during Late Antiquity and the Early Middle Ages. However, research on such issues originates primarily from early work that focused on the *Germani* and Germanic antiquity (*Germanische Altertum*). As traditionally understood, the *Germani* were any of those speakers of three interrelated ancient language branches that stemmed from the Indo-European language tree (Murdoch and Read, 2004). The Romans also applied the name generally to those living outside their Empire on the left bank of the Rhine River—a literary topos clearly evident in Tacitus's *Germania* (1840 [AD 83])[3].

As early as the Renaissance, there was a "conscious nationalism in which the *Germani* rose to become a unique source of popular Germanic thought and culminated in the formula that Germanic equals German (Beck, 2004: 25; see also Gillett, 2002a). In other words, the "Germans" were considered by certain early scholars, such as Grimm (1848), to be the most German of the Germans (*ibid*: 26). Further research that sought to locate the original homeland (the *Urheimat*) of the *Germani* only served to reinforce the presumed importance of Germanic antiquity to understanding group interactions during Late Antiquity and the Early Middle Ages (for examples, see Hoops, 1911; Kossinna, 1911).

The importance of studying Germanic antiquity (*Germanische Altertumskunde*) should not be underestimated, as it arguably has influenced all subsequent discussions concerning ethnicity and ethnogenesis for this time period (Gillett, 2006). Indeed, from

[3] How classical writers viewed themselves and others is itself subject to a large debate. See Wells (1999).

the late 19th through early 20th century, *Germanische Altertumskunde* contributed to a form of nationalist archaeology, history, and philology best exemplified by research under the Third Reich. Scholars emphasized the antiquity and continuity of the nation-state, wherein groups 1) could be defined by language, biology, and other objective cultural traits (James, 2014), 2) had engaged in a collective movement/migration that exerted an increasing pressure on Roman boundaries (Goffart, 2006: 7), and 3) had existed for centuries within a geographic space that often coincided with national boundaries (Heather, 2008: 18). As a fundamental form of human organization, these groups were culturally homogeneous, bound together by strong ties of group identity, and could, along with commonalities in language, be used to define narrative accounts of the Migration Age[4] of Western Europe (*ibid*: 18-19). In other words, to understand the transition from Late Antiquity to the Early Middle Ages, it was believed that one had to understand the continuity over time of discrete, migrating groups of people that gave rise to early modern nation states.

1.1.2 Reinhard Wenskus and the "Ethnogenetic Paradigm"

Following the emergence of new ideas on German constitutional history[5] (i.e., lordship theory) and other scholarship that claimed the supremacy of "Germanic" political thinking (see Murray, 2002: 54-58), Reinhard Wenskus (1961) wrote his famous

[4] The Migration Age or *Völkerwanderung* is traditionally understood as overlapping parts of Late Antiquity and the Early Middle Ages (c. AD 350-700). The term used in this document best coincides with Goffart's (2006: 14) primary definition: "In the mid-fourth century, various peoples were parked, perhaps enduringly, on the Roman frontier… Two centuries later, these foreigners had moved to new positions in a process of conquest, settlement, and kingdom foundation… Movement in these cases began near the imperial border and ended, after relatively limited displacements, in settlement somewhere within the former frontiers of the Empire or (in quite a few cases) in annihilation."

[5] Murray (2002: 52-53) also argues that Wenskus was influenced by the earlier work of Hector Munro Chadwick (1907).

treatise on “Stammesbildung und Verfassung”. The forefather of the ethnogenetic paradigm in Late Antique and Early Medieval studies (Gillett, 2006: 244, but see Murray, 2002), Wenskus argued for the existence of great “discontinuities in the history of Germanic-speaking groups in the Roman and early medieval periods” (Heather, 2008: 26). Thus, in contrast to earlier work that emphasized cultural continuity of named, migrating, coherent groups during the Migration Period, Wenskus’s re-reading of ethnohistoric sources showed how simple it was “to find individual Germanic groups being exterminated, such as the Ampsivarii or Bructeri, and entirely new ones being created, such as the Batavi who splintered away from the Chatti” (Heather, 2008: 26).

Amidst the evidence for such discontinuity and changing group identities, Wenskus then sought to understand those instances in which continuity may have still occurred. For example, “the term ‘Goth’ turns up in the literary evidence from the first to the seventh centuries. Burgundians, likewise, show up in different places over much the same kind of period… Whatever they were, these labels were substantial enough to play major historical roles: some of the groups involved being able to field armed forces which were large and coherent enough to survive sustained conflict with a still-powerful Roman state, before emerging as the founding bodies of its early medieval successors” (Heather, 2008: 27; see also Wolfram, 1990: 19-35). If, as Wenskus and others have argued, some groups show evidence for continuity over time as based on the punctuated (re)appearance of specific names, then an explanation for this diachronic continuity is required. In other words, “why was there any continuity in the names of Germanic groups at all, and how did group identities work among those entities who carved out successor states to the Roman Empire” (Heather, 2008: 35)?

To answer this question, Wenskus proposed that an ethnic group was "defined, not by language, culture, or law, but by *political* allegiance and distinctive pattern of political thinking… Only recognition of the subjective, self-conscious perceptions of ethnicity, and the political processes that lay behind them, reveal the true character of ethnic groups and the forces of early European history" (Murray, 2002: 45). Although Wenskus believed that a "people" or *gens* was primarily a group formed by political allegiances, he also argued that their members perceived themselves as a community sharing a similar ideological perspective (Murray, 2002: 46). The process by which individuals and different ethnic groups came to this shared consciousness was due to the presence of kings and their followers. These aristocratic elites functioned as bearers of shared tradition and ethnic consciousness – a kind of 'nucleus/core of tradition' or *Traditionskern*. These individuals possessed "connections to the near and distant past [which] gave a focus to multicultural recruits and encouraged them to associate and identify themselves with the ancient tradition promoted by the leading families" (Goffart, 2002: 21). In other words, "*Traditionskern* theory posits the replication of a group identity through the subscription by members to a mythic narrative of the group's past (the 'core of tradition'), focused on the divine descent of its rulers" (Gillett, 2002a: 3). The hallmarks of any of these traditions were "genealogy and origin legends, archaic sacral institutions, surrounding kingships, and above all, the name of the *gens*" (Murray, 2002: 46). Indeed, group names were perceived as an "embodiment of living, historically dynamic traditions" (*ibid*: 47), such that the lines and arrows depicted on modern historical atlases for the Migration Age reflect the movements of these named *Traditionskernen* (Goffart, 2006: 116).

More recently, scholars from the 'Vienna School' like Herwig Wolfram and Walter Pohl expanded on Wenskus's work (Wolfram, 1990; Pohl, 1998a,b; Pohl and Beaupré, 2005). Wolfram not only introduced Wenskus's work to a broader academic audience, he also elaborated on the nature of a self-conscious elite whose survival "imparted some sense of community to the various followers who attached themselves to its train at different points. Those followers could be many and varied, and were subject to substantial changes in composition over time" (Heather, 2008: 28-29). These elites could also deliberately adopt certain traditions depending on the situation (e.g., instrumental ethnicity). Pohl elaborates on this latter point by noting that "identities had be flexible and largely virtual to accommodate all whose loyalty Frankish or Visigothic kings wanted to encourage" (1998b: 63). Thus, identity could be constructed and consciously adopted by individuals who use a specific identity for self-advancement, as well as by leaders who embrace assertions of a broader group identity to build larger population groupings, like those that became successor states to the Roman Empire (Pohl, 1998a, 1998b).

Today, an ethnogenetic model is one of the most accepted and integrated "paradigms" for understanding the shift from the Roman Empire to Western European kingdoms (Gillett, 2006: 243; see also Bowlus, 2002). Other models cited as factors helping to shape the post-imperial world include 1) the influence of the Christian Church (i.e., Catholic administrative structure), and 2) the Roman Empire and its complex socio-political organization (Gillett, 2006: 242). Regardless, the discussion hinges primarily on the impact of the 'barbarians' of Europe: their migrations, their relationships to each other, and their interactions with existing Gallo-Roman populations. In other words,

ethnicity is viewed as the primary "social and political force in Late Antiquity and the Middle Ages" (*ibid*: 242). In summary, the most commonly accepted paradigm for understanding the transition from Late Antiquity to Medieval Europe stipulated that the "particular dynamics of ethnic identity-formation pre-dated the hegemony of Roman imperialism and Hellenistic culture; they served as the dominant ideological bond for social cohesion in proto-historical European culture. Muted by Roman domination, these ethnic dynamics revived in the course of the late antique/early medieval period, when they surmounted classical political ideologies, becoming the basis for the formation and maintenance of both 'peoples' and 'states' in early Europe" (*ibid*: 243).

1.1.3 Criticism

This emphasis on ethnicity and ethnogenesis is not without criticism, however. Followers of the 'Toronto School' (i.e., Bowlus, 2002; Gillett, 2002a,b, 2006; Murray, 2002) in particular, are increasingly vocal. For example, Gillett (2006: 244) argues that, although ethnogenesis is fairly well defined within anthropology, scholars of Late Antiquity and the Early Middle Ages are less precise in their usage of the term. Instead, these studies often conflate the phenomenon and process of ethnic group formation with the theoretical models of the processes involved in ethnogenesis. As Gillett suggests, the form of ethnogenetic models employed by these scholars actually developed in parallel to those of the social sciences and have "foundations that antedate the development of current anthropological thought by some generations" (i.e., *Germanische Altertumskunde*) (*ibid*: 245; see also Gillett, 2002a: 6-7).

Additional critiques include 1) the reflexive use of "ethnogenesis" without actually engaging the theoretical literature on the topic or providing clear definitions (Bowlus, 2002: 242; Gillett, 2006: 243; Goffart, 2006: 1-12); 2) the over-emphasis on ethnic self-identification to the exclusion of other possible explanatory models (Bowlus, 2002: 243-244; Gillett, 2002a: 17; Gillett, 2006: 247); 3) the black-box reliance on the continuation of 'traditions' and memory (Goffart, 2002: 22); 4) an over-emphasis on the role of elites; 5) the ubiquity and individuality of migration in the past (*ibid*: 31; see also Reynolds, 1998; Goffart, 2006); and 5) the lack of an historiographical and literary awareness (Gillett, 2006: 247; see also Goffart, 1988, 2002; Reynolds, 1998; Bowlus, 2002; Murray, 2002;).

Much of the criticism derives from this final point, and is discussed at length by scholars of the "Toronto School". Gillett (2006), for example, argues that too much of the ethnogenetic model applied to Late Antiquity and the Early Middle Ages is based on philological rather than historical arguments. This tendency is especially problematic since early group formation and tradition-making is claimed to have occurred as early as the Iron Age, prior to the written records of the Greco-Roman period (for example, see Pohl and Beaupré, 2005). Yet, Germanic linguistic sources, such as group names or the rare case of literary texts, are not necessarily "fossilized" remains of ancient concepts (Gillett, 2006: 248). For example, a study of royal titulature in Early Medieval Europe yields little compelling evidence for the early adoption of ethnically politicized discourse (Gillett, 2002b). Similarly, the reading of ancient and medieval texts through a narrative lens of ethnicity ignores or minimizes the impact of the authors' biases, history, and literary goals. In other words, these written sources should be analyzed as texts, "using

traditional means of textual analysis (e.g. genre criticism, source criticism, historical contextualisation) and current theoretical approaches to literary analysis (e.g. narratology)" (Gillett, 2006: 249, 251).

Further criticism, albeit less overt, revolves around the issue of migration. A growing number of scholars contend that tales of migrating Germanic or barbarian tribes (e.g., *Volkerwanderung*) told by Late Roman authors and attributed by more modern historians as a cause (if not *the* cause) of the fall of the Roman Empire, cannot be factually supported, whether based on archaeology or ethnohistoric texts (Goffart, 2006; see also Wells, 1999; James, 2014). Despite what appears to be "overwhelming evidence illustrating a different course of events before and during late antiquity," migrations of barbarians (often "Germanic" ones) are still treated as a determining factor in the "collapse" of the Roman Empire (Goffart, 2006: 21).

Yet, as Goffart argues, the "core Migration Age starts near A.D. 370 from a position of rest and equilibrium" during which people living north of the Roman frontiers "had been settled there for as many as four centuries, others for less but all for long enough to consider themselves well rooted. There were long past the point of having "come" from somewhere and were definitely not "going" anywhere" (*ibid*: 21). The most dramatic examples often cited for migration during the first millennium A.D. are highly specific (e.g., the Goths), and may have stemmed from the relationship of prestige goods to local indigenous economies, changes in social status signaling, and the iterative process by which Romans and non-Romans were integrated in the Roman military (*ibid*: 112; see also Curta, 2005b).

1.2.0 BIOARCHAEOLOGICAL CONTRIBUTION

Given the obvious impasse presented by scholars of the Late Roman and Early Medieval periods, is ethnogenesis still a viable theoretical framework? Can anything be stated with confidence about people living during the first millennium and their possible forms of group-level identification and organization? I argue that a complementary approach to ethnohistoric data (i.e., texts) should continue to engage archaeological[6] and biological[7] data when possible—two sources of information which are seemingly downplayed or ignored by recent critics of the so-called ethnogenetic paradigm[8] (for example, see Goffart, 2006: 10-11). Furthermore, the incorporation and better understanding of anthropological theory on ethnicity and ethnogenesis could also benefit the discussion. While critics claim that historiographical problems and early romantic notions of Germanic culture bias traditional historical and philological approaches, the same may not be said of the rich theoretical genre pertaining to ethnicity and ethnogenesis that can be found in the modern social sciences, like anthropology[9].

[6] Archaeological inquiry has fared comparatively better among critics and scholars of Late Antiquity and the Early Middle Ages than biological. For a thorough and well-articulated summary of how archaeology in particular can contribute to studies of the transformation of the Roman world, see Halsall (2007).

[7] Biological data can include molecular approaches (e.g., aDNA), biogeochemical approaches (e.g., strontium isotope ratios), and skeletal approaches (e.g., craniometrics).

[8] Halsall (2010: 41) suggests that a lack of engagement in archaeological data by historians may stem from three traditional uses of archaeology by historians. These uses are 1) illustrative, 2) justificatory, and 3) 'filling in the gaps'.

[9] This does not imply that ethnicity and ethnogenesis as topics of inquiry are not subject to debate by anthropologists, nor colored by 19th century ideas. On the contrary, the dynamic and constant discussion on these subjects suggests active attempts to generate applicable theories rather than merely consuming established concepts. Nor, as Halsall (2010: 157) alarmingly claims, does the reference to anthropological theory entail running the risk of "becoming subject to another sort of tyranny, that of anthropological fieldwork of uncertain relevance to the early Middle Ages".

More specifically, I argue that the inclusion in particular of biological data within a bioarchaeological framework presents a timely and productive approach to answering some of the lasting questions relevant to this period, of which Frankish ethnogenesis is only one. Interestingly, a common lament by historians and archaeologists of Late Antiquity and the Early Medieval Period is a lack of mutual respect and understanding of their respective disciplines by each other[10] (for examples, see Austin, 1990; Moreland, 2001, 2006; Halsall, 2003, 2010). Attempts to bridge these disciplinary divides have led to some of the most productive and thought-provoking work currently available to students of Late Antiquity and the Early Middle Ages (Geary, 1988; Wells, 1999; Halsall, 2003, 2010; Effros, 2002, 2003; Wickham, 2005; Heather, 2008).

In contrast, few(er) attempts are being made to re-engage biological data in a similar manner, especially biological data within a theoretically informed framework like bioarchaeology[11]. This dearth of active engagement is understandable, though regrettable, and a discussion concerning the uses and abuses of biological data within physical anthropology can be found in Chapter 4. However, there should be a similar lament by Late Antique and Medieval scholars for the common mischaracterization of a rich field of inquiry—bioarchaeology—that has blossomed over recent years (Blakey and Rankin-Hill, 2004; Stojanowski and Buikstra, 2005; Stojanowski, 2005b, 2010; Buikstra and Beck, 2006; Sofaer, 2006Perry, 2007; Klaus, 2008; Knudson and Stojanowski, 2008; Peck, 2009; Knüsel, 2010; Larsen, 2010; Agarwal and Glencross, 2011; Buzon, 2011).

[10] As Halsall (2010: 65) points out, "it still appears to be *de rigueur* for young (and even not-so-young) archaeologists to open with a polemic against the tyranny of documentary history".

[11] For example, Halsall (2010) often disparages the use of skeletal morphology in studies of Late Antiquity and Early Medieval Europe. His dispute is correctly aimed against the use of racist typologies. However, his wholesale approach at disagreement has the (unintended?) consequences of disregarding what biological data can truly contribute and of dismissing newer approaches, such as biodistance.

Bioarchaeology not only unites the biological and social sciences, it does so by providing a link between evolutionary and social theory. Quite simply, it is the biology of the human body understood within its archaeological, historical, and social contexts (Buikstra, 1977). The human skeleton is both changeable and fixed, subject to intentional modification, yet also static and serving as a "passenger" to individual behavior and choices (i.e., Blom, 2005; Sofaer, 2006). Recent research on embodiment and social identity exemplifies this complex interaction, illustrating how social meaning and personal expression is manifested and incorporated into the body and skeleton (e.g., Fowler, 2004; Joyce, 2005).

Bioarchaeology thus stands poised at the nexus of these facets of social interaction and the medium of the human body/skeleton. Increasingly, a bioarchaeological approach facilitates inferences about many aspects of the social realm (not just those focusing on the elites), as well as the study of broadly applicable research questions, such as social identity (see Buikstra and Beck, 2006; Knudson and Stojanowski, 2008; Agarwal and Glencross, 2011). Indeed, identity, whether at the individual, community, or group level, is just one example of a research question with broad appeal in today's world (e.g., Knudson and Stojanowski, 2008; Buikstra and Scott, 2009). Furthermore, a bioarchaeological approach allows "inferences that are transformational, and not simply historical, in nature" (Knudson and Stojanowski, 2008: 399). In other words, it facilitates the study of biological and social processes and how they change over time.

Thus, the bioarchaeological approach used in this study complements existing methodological and theoretical approaches, such as historical and archaeological. I also

argue that it complements molecular approaches, while also holding some distinct advantages. These advantages include the use of non-destructive analyses[12], such as biodistance methods, and the incorporation of larger and more representative datasets. The time depth afforded by archaeological skeletal assemblages also permits, in some cases, the repeated sampling of a group(s) over time (Knudson and Stojanowski, 2008: 414).

In addition to the bioarchaeological approach already advocated, I combine it with a focus on biodistance and population genetics. By thoughtfully avoiding typological methods (i.e., morphological descriptions) for exploring biological variation in the past, this research seeks a more "nuanced processual approach to biosocial evolution" – one that emphasizes a social perspective (*ibid*: 414). The combination of biodistance within a bioarchaeological framework ultimately facilitates a powerful exploration of how biological variation changes through time and how these changes may relate to internal or external social stimuli (*ibid*: 414). Thus, used jointly with archaeological and historical methods, the approach employed in this study is well suited for exploring the questions of population structure and Frankish ethnogenesis.

1.3.0 ORGANIZATION

In Chapter 2, I summarize the theoretical background on ethnicity and ethnogenesis. Knowledge of existing anthropological theories and models is a relevant step in evaluating the question of Frankish ethnogenesis. Subsequently in Chapter 3, I present the historical and archaeological background related to the Franks, their confederation, and the Gallo-Roman populations that inhabited Gaul. This survey spans

[12] Methods involving biogeochemistry and aDNA are an exception to this statement.

from c. AD 400 – 1000 and reviews key aspects of society, including economy, politics, and religion. Similarly, in Chapter 4, I summarize the main studies that use biological data and that relate to population structure. These include studies of skeletal morphology and anthropological genetics. Although the goal of this chapter is to present a survey of what has been published using skeletal morphology, it is also intended to reveal the limits of existing biological approaches. Therefore, I outline the methods and theories underlying biodistance and population genetics in Chapter 5 and show how biodistance can be used to infer aspects of social identity. To further illustrate the biosocial approach used in this study, I present examples from recent work on ethnogenesis that incorporate skeletal morphology. Finally, Chapter 6 outlines the ethnogenetic model used in this study and summarizes generalized research expectations for population structure.

Chapter 7 presents the primary skeletal collections used in this study. Specifically, odontometric data are collected from 11 sites dated to Late Antiquity and/or the Early Middle Ages. Available information from each site is presented, general characteristics of the cemeteries are described, and important interpretations drawn by the original field archaeologists and physical anthropologists are summarized. An additional 20 sites are included for the secondary skeletal collections composing the craniometrics portion of this study. Next, in Chapter 8, I introduce the methods of data collection for both the odontometric and craniometric data. Special attention is given to discussing the principals of dental development and morphology, as odontometric data are especially well suited for biodistance studies. Observational and measurement protocols for both odontometric and craniometric data are also outlined. All data were subject to extensive statistical analysis, including statistical treatments to minimize error. Therefore, all steps taken for

pre-analysis data treatment are outlined, and the resulting variables used in subsequent analyses are listed. Likewise, the mathematical formulation of the Relationship Matrix (R-matrix), the population parameters being estimated by the R-matrix, its analysis using the Relethford-Blangero model, and the different demographic models used for each analysis of the R-matrix are presented in detail.

Chapters 9 through 12 provide results for each portion of the analyses using the odontometric and craniometric data. Because both a synchronic and diachronic assessment of population structure is potentially informative, each data type is subject to a synchronic and diachronic analysis. Similarly, each analysis is evaluated using specific demographic scenarios that account for the possible impact of different parameters important in population genetics. Thus, each chapter introduces the data that are used and the demographic scenario being assessed before finally presenting the results of the R-matrix analysis. These results are then interpreted and discussed in Chapter 13.

CHAPTER 2

ETHNICITY AND ETHNOGENESIS

2.0.0 INTRODUCTION

In this chapter, I outline the historical and theoretical background relating to ethnicity and ethnogenesis and provide definitions of key terms. Primordialist and instrumental approaches to ethnicity are discussed, and critiques of both are provided. Although primordialist and instrumental approaches are the most well cited theoretical perspectives on ethnicity, integrated approaches also exist. Consequently, I also outline some of the most common integrated approaches (i.e., practice theory). Finally, theoretical approaches to ethnogenesis are described, terms defined, and examples provided.

2.1.0 THEORETICAL APPROACHES TO ETHNICITY

2.1.1 A Brief History of Thought

Modern approaches to ethnicity largely originated from an ethnographic concern with categorizing groups of people (i.e., tribe, race) (Huxley and Haddon, 1935; Naroll, 1964; Moerman, 1965; Naroll, 1968; Moerman, 1968). This etic or objectivist practice defined much of the work by anthropologists and ethnologists in the nineteenth century (Prichard, 1813; Tylor, 1873) who sought to classify human diversity. Although this period of scholarship often resulted in the conflation of race with language and with culture (Barth, 1969: 13), the development of social and cultural anthropology in the

early twentieth century eventually led to the concept of plurality of cultures within particular historical contexts, as well as the separation of the theoretical concepts of race and culture (e.g., Boas, 1905). This progression promoted the idea that the job of the cultural anthropologist was to "delineate cultural patterns and, beyond that, to compare and classify types of patterns" (Singer, 1968: 530; for archaeological applications, see Kossinna, 1911; Childe, 1929, 1933). Consequently, and despite the theoretical critique that occurred during the early twentieth century, there was a continuing concern for group homogeneity and boundedness that contributed to the idea that cultural practices and beliefs were uniform throughout a society or culture. This notion of discrete cultures with homogenous traits was shared by both cultural anthropologists (i.e., Radcliffe-Brown, 1952; Clifford, 1988) and archaeologists (i.e., Binford, 1962).

However, with the eventual critique of terminology like "culture" and "tribe" (see Leach, 1964; Moerman, 1965), as well as the development of post-colonial scholarship (Colson, 1968; Fried, 1968) and of modern sociology (Glazer and Moynihan, 1975; Gordon, 1975), there was a shift to considering the "role of ethnic phenomena in the organization of social groups and social relations" (Jones, 1997: 52-53), as well as the processes by which ethnic groups were constructed (Barth, 1969) and how they defined themselves (e.g., emic or subjectivist perspectives) (Moerman, 1965, 1968).

In fact, Barth's (1969) seminal work reshaped how many anthropologists and archaeologists approached the concept of ethnicity. While his primary focus was to investigate the social dimensions of how and why ethnic boundaries were maintained (*ibid*: 9-11), Barth argued that subjective definitions of ethnic categorizations (i.e., self-definition) should form the basis for ethnic identification. Moreover, he suggested that

these categorical ascriptions became an “ethnic ascription when it classifies a person in terms of his basic, most general identity” (*ibid*: 13-14).

Although the popularization of subjective definitions of ethnicity was a primary outcome of Barth’s work, he also provided one of the first theoretical explanations for the formation of ethnic groups. Specifically, he argued that boundaries functioned as structuring ‘agents’, ones in which the dichotomization of “us” and “them” occurred during the processes of social interaction (see also Turner, 1920). Ethnicity was thus seen as a result of a power differential between groups of people and reflected the most general or widest scaled identity (Barth, 1969: 27). In this perspective, ethnic group identification expressed a shift by individuals “to multicultural, multiethnic interactive contexts” in which the ethnic group is “marked by some degree of cultural and social commonality. Thus, membership criteria by members and nonmembers may or may not be the same, and the creation and maintenance of the ethnic boundary within which members play according to similar and continuing rules” was believed to be a major aspect of the phenomenon of ethnic groups (Cohen, 1978: 386). Barth’s work led to a greater emphasis on considering the subjective, emic identification of ethnic groups (i.e., Cohen, 1978; de Vos, 1975; de Vos and Romanucci-Ross, 1975; Eriksen, 1993), and resulted in a lasting “conceptualization of ethnic groups as self-defining systems, [with] an emphasis on the fluid and situational nature of both group boundaries and individual identification” (Jones, 1997: 64).

2.1.2 Definitions

Ethnicity, ethnic identity, and ethnic group are three interrelated concepts with a complex history operating on multiple scales. For the purposes of this manuscript, I employ adapted definitions derived from Jones (1997). Consequently, *ethnic identity* is a social identity that is individualized and self-conceptualized, "results from identification with a broader group in opposition to others on the basis of perceived cultural differentiation and/or common descent", and can change in saliency during the life course (*ibid*: xiii). Due to its generative, rather than passive nature, it might be better to conceive of it as a process, one of *ethnic identification* (Voss, 2008: 14). An *ethnic group* is any group or community of people "who distinguish themselves and/or are distinguished by others with whom they interact on the basis of their perceptions of cultural differentiation and/or common descent." I understand ethnic groups to be comprised of individuals and institutions, with the latter comprised of individual agents. Finally, *ethnicity* is "all those social and psychological phenomena associated with culturally constructed group identity" and emphasizes the "ways in which social and cultural processes intersect with one another in the identification of, and interaction between, ethnic groups."

An understanding of ethnicity and the construction of ethnic group differences derive from two main theoretical approaches: primordialist and instrumentalist perspectives. Both of these approaches can also be evaluated in terms of how interactionist or isolationist they are in particular contexts (see Royce, 1982; Hu, 2013), and both provide a foundation for exploring the formation of ethnic groups.

2.1.3 Primordialist Perspective

Proponents of this approach emphasize an essential and ineffable quality to ethnicity shared between individuals in ethnic groups. These qualities of ethnicity are "involuntary and possess a coerciveness which transcends the alliances and relationships engendered by particular situational interests and social circumstances" (Jones, 1997: 65; see also Shils, 1957; Geertz, 1963; Isaacs, 1974). Understood in this sense, ethnicity is something ascribed upon birth – via 'blood', language, religion, or culture (Jones, 1997) – that serves "psychological motives such as the need for acceptance and belonging" and functions to bond individuals together (Knudson and Stojanowski, 2008: 412-413; Maslow, 1954; Isaacs, 1974; Keyes, 1976; Connor, 1978; de Vos, 1975). It is the primordial bond of a basic group identity that underlies all other characteristics ascribed at birth, such as name, group history and origin, nationality, religion, or language (Isaacs, 1974; Keyes, 1976). Being primarily ascriptive, then, ethnic cultural traits function collectively to define group membership (Dormon, 1980: 25). Thus, "the qualities which operated to define an ethnic group and distinguish its members [are] essentially primordial in nature, and for that reason more or less fixed and permanent, changing but little over time" (Dorman, 1980: 25).

The formation of ethnic groups can be understood to arise in "changing social contexts [that disrupt] conventional ways of understanding and acting in the world" and that cause people to seek refuge in pre-existing (i.e., primordial), communal sentiments and identities (Bentley, 1987: 26). In other words, ethnic group formation is a response to some kind of emotional need (Geertz, 1963: 119-128; see also de Vos, 1975; Isaacs, 1974; Keyes, 1976), may exist even without any kind of political or economic threat, and

are more value-oriented than politically- or economically-oriented. In fact, primordialists point to "the persistence of ethnic sentiment in the absence of rational benefits," sometimes over long spans of time, as evidence of an essential aspect of ethnicity (Knudson and Stojanowski, 2008: 413; see also Bromley, 1974; de Vos, 1975; Epstein, 1978; Keyes, 1981; McKay, 1982).

2.1.4. Instrumentalist Perspective

Instrumentalist approaches stem from a general shift in the social sciences toward a "concern with the role of ethnicity in the mediation of social relations and the negotiation of access to resources, primarily economic and political resources" (Jones, 1997: 72). Instrumentalists assert that ethnic groups are the result of interaction, whether geographic or social, with others and which oftentimes occur along boundaries (Barth, 1969). These boundaries function like structuring 'agents': "Cultural differences are thus ascribed; then they come to mark the boundaries, which in turn structure and order the interaction of groups, which interaction then allows for the persistence of the groups in the larger social system" (Dorman, 1980: 26). Individuals use various strategies based on a particular identity role or niche (*sensu* Barth) to advance their personal economic or political interests in these interaction zones.

Ethnic groups themselves are viewed as collectively organized interest groups who systematize the social behavior of their members by the use of shared cultural practices and beliefs (Cohen, 1969, 1974). Thus, ethnic groups function situationally in order to maximize economic or political potential (Dorman, 1980: 27). As long as a

shared benefit exists, ethnic affinity will be maintained. In other words, ethnic groups form due to humans acting in a rational and goal-oriented manner.

To illustrate, Cohen (1978) proposed that ethnicity is a "set of descent-based cultural identifiers used to assign persons to [ethnic] groupings that expand and contract in inverse relation to the scale of inclusiveness and exclusiveness of the membership [in the group]" (*ibid*: 387). In other words, the number of descent-based cultural identifiers used to assign individuals to an ethnic group will decrease as membership in that ethnic group becomes more exclusive. In addition to this concept of nested dichotomization of inclusiveness and exclusiveness, Cohen believed that ethnicity is always situational and cannot exist apart from its relations with other ethnic groups. He described types of ethnic interrelations based on their nature, the degree of contact between them, and the relative amount of power that is involved (*ibid*: 389). He cautioned, though, that ethnic relations are not only based on power differentials and that group equity in terms of power will not necessarily imply the lack of ethnic differences. Likewise, he believed that ethnicity and stratification can vary independently, and that migration is a common source of "occupational specialization in which ethnicity and occupational stratification enhance one another with the lower status ethnic groups restricted to lower regarded and poorly paid economic positions" (*ibid*: 393).

Ethnicity, then, is often the consequence of power differentials between groups of people. Identification with an ethnic group expresses a shift by individuals to interactive contexts that are multicultural and multiethnic. There is still a degree of cultural and social commonality within these interactive contexts that serve to create and maintain

ethnic boundaries. However, the "membership criteria by members and nonmembers may or may not be the same" (*ibid*: 386).

2.1.5 Critiques

Together the primordial and instrumental approaches to ethnicity have encouraged the study and exploration of ethnic groups and the construction and displays of ethnicity in social relations. However, both of these approaches suffer from conceptual weaknesses, including how ethnic identity is actually constructed and how people actually "recognize the commonalities (of interest or sentiment) underlying claims to common identity" (Bentley, 1987: 26).

Primordialist

By relying on deep, indefinable attachments as an explanation for ethnicity, proponents of the primordial perspective leave unexplained the "purported psychological and/or biological bases" to these attachments (Jones, 1997: 72). Ethnic identity becomes a romanticized and mystical process, with foundations in an atavistic and universal aspect of human nature (de Vos, 1975; Connor, 1978; Kellas, 1991). Shaded by obscurity, then, the primordialist perspective lacks an explanatory concept for the "dynamic and fluid nature of ethnicity" in various contexts (Jones, 1997: 72). Consequently, this approach de-contextualizes ethnicity, stripping it of any social or historical grounding, and suggests that ethnicity is a "determining and immutable dimension of an individual's self-identity" that does not change over time (*ibid*: 69).

Instrumentalist

Proponents of the instrumental perspective give economic and political relationships a primacy in the formation of ethnicity, reduce human behavior to efforts at maximizing self-interest, assume all human behavior is rational, downplay or ignore the role of cultural and psychological dimensions in the formation and transformation of ethnicity, and disregard the "dynamics of power in both intra-group and inter-group relations" (*ibid*: 77-79). Following Barth, this perspective tends to over-emphasize individual identity formation and the role of boundaries without sufficiently addressing the importance of institutions and culture in ethnic identity formation and maintenance (Buchignani, 1982: 6). Likewise, the importance of other social identities and phenomena, and the distinction between ethnic groups and other collective-interest groups, remain underappreciated (Hechter, 1986: 19). Finally, these approaches fail to explain fully the micro-processes of identity formation, why they were meaningful, why they were activated or how they could change (e.g., Bentley, 1987), and the importance of identification of others' ethnicity (e.g., Buchignani, 1982).

2.1.6 Integrated Approaches

There is a large corpus of literature exploring how individuals and institutions embody, learn, reify, transform, and impose ethnic identification and ethnicity. These are often based on theories of social iteration, such as Gidden's (1984) structuration theory and Butler's (1990) performance theory. One of the best examples of an integrated approach to ethnic identity construction is Bentley's (1987) application of Bourdieu's (1977) practice theory. Specifically, practice theory explains why people may be

disposed to act in certain – and mostly unconscious – ways. This is accomplished via *habitus*, which is a "set of generative schemes that produce practices and representations that are regular without reference to overt rules and that are goal directed without conscious selection of goals or mastery of methods of achieving them" (Bentley, 1987: 28). These schemes or dispositions are acquired through life as individuals encounter objective conditions (e.g., sexual division of labor), embody them, imbue them with meaning, and reproduce them. According to Bentley, patterns of conflict and disagreement are a result of differences in habitus, while patterns of coordinated or collective action result from similarities in habitus. Although an infinite variety of behaviors can result from habitus, they would only be "understood" by those who shared in them. Consequently, a sense of ethnic unity results from "commonality of experience and of the preconscious habitus it generates" (*ibid*: 33). According to Bentley, this explains why many ethnic groups employ "idioms of kinship and descent for expressing ethnic affinities" (*ibid*: 33). Furthermore, since various social contexts evoke different aspects of habitus, individuals could possess many different identities depending on the context (*ibid*: 35). Thus, instrumentalist and primordialist models largely overlook the intervening variable of habitus, how habitus becomes inculcated in members of a group, and how the experience of shared habitus becomes symbolized in a group.

According to Bentley, another benefit of the ethnicity as habitus perspective resides in the explanation for collective action, domination, and leadership. Specifically, a conscious exploitation by the elite is not necessary in order to explain internal organization and coordinated action within ethnic groups (*ibid*: 41). This perspective permits the possibility of organized ethnic groups in the absence of interest competition

and stems from the observation that the "symbolism of ethnicity will carry the same sense of authenticity and moral compulsion for ethnic leaders as for their followers. This symbolism will carry moral force so long as the coordination of habitus holds, that is, so long as leaders and followers operate within a coherent field of domination" (*ibid*: 43).

Bentley's observation does not assert that individuals will avoid manipulating ethnic symbolism for their own advantage. Rather, it eschews the assumption that *all* ethnic mobilization is for a strategic advantage. In addition, change, whether political or economic, can quickly disrupt regimes of domination and "alter structures of objective interest within a population" (*ibid*: 43). As people adjust to new circumstances, ethnic mobilization leads to new lifeways or reemphasis upon existing lifeways. With this perspective, ethnic mobilization can represent 1) an attempt to reify or renew group self-conceptualization or extant forms of domination, or 2) a modification in understandings of personal identity (*ibid*: 45). Finally, Bentley argues that the success of individual leaders depends upon the personal identity myths that best conformed to changing notions of habitus, practice, and experience (*ibid*: 47).

Although Bentley's approach attempts to explain *how* ethnic identity and consciousness occurred, many scholars believe that it is flawed (e.g., Yelvington, 1991; Eriksen, 1992; Jones, 1997). Critics assert that the emphasis on ethnicity as habitus cannot explain "which kinds of practices engender ethnic identification and those that attenuate identification because everything is put down to the mysterious workings of the habitus" (Yelvington, 1991: 161). Some practices may relate to class, regionalism, occupation, or community, rather than "ethnicity." In addition, the effect of ethnic others is absent from Bentley's approach. "[I]f an individual's or a group's habitus does not

wholly determine ethnic identity, then this suggests that some of the answers are "external" and have to do with the practices of 'ethnic others'" (Yelvington, 1991: 163).

Yelvington stresses the importance of contrast and interaction with others, as well as the power relations involved in these relationships. He then suggests that ethnicity can be characterized by referring to a dynamic intergroup process, such as Durkheim's "social representations." Ethnicity is a social identity – one that is "socially constructed with reference to class, gender, and other variables" (*ibid*: 167). This approach is also advocated by third-wave feminists from the 1990s and 2000s (Stockett and Geller, 2006: 11) and contemporary scholars of social identity theory (e.g., Meskell, 2001; Díaz-Andreu, 2005; Insoll, 2007; Voss, 2008; Knudson and Stojanowski, 2009).

2.2.0 THEORETICAL APPROACHES TO ETHNOGENESIS

2.2.1 Definitions

Ethnogenesis is the process by which new ethnic groups materialize (Sturtevant, 1971). It is diachronic in nature and socio-historically contingent. In contrast, the study of ethnic origins typically presupposes a normative and homogenous view of ethnic groups and assumes that an "origin" can be identified in time and space. The definition of ethnogenesis is elaborated by Kohl (1998) who uses the term *ethnomorphosis* to suggest all historical processes of ethnicity, including genesis, maintenance, and dissolution. Although the term ethnogenesis bears the unintended impression that ethnic groups have well-defined origins (*sensu* Childe, 1933; Kossinna, 1911), it is commonly used in recent bioarchaeology research to encompass the same processes as ethnomorphosis.

Consequently, I employ the term ethnogenesis to facilitate continued dialogue within the discipline.

2.2.2 Ethnogenetic Processes

As made clear by historic and modern ethnographic analyses, ethnogenesis results from a process, or combination of processes (for examples, see Singer, 1968, Sturtevant, 1971; Albers, 1996). It is diachronic in nature and is part of an ongoing transformation of social identity or identities (Voss, 2008). It can include group fission and fusion, cultural accommodation and adaptation, group power differentials, warfare, migration, and/or combinations of any of these (Sturtevant, 1971; Sharrock 1974; McGuire, 1982; Ferguson and Whitehead, 1992; Albers, 1996; Hickerson, 1996; Hill, 1996; Voss, 2005, 2008; Bell, 2005; Stojanowski, 2010;). Indeed, it can be argued, that there is "no single, uniform process of ethnogenesis" (Roosens, 1989: 149). Rather, each case must be reconstructed on an individual basis. Furthermore, it should be noted that historically- and culturally-contingent factors that play an initial part in an ethnogenetic process are not necessarily the same factors used in maintaining ethnic boundaries.

Despite what appears to be an impossible task, ethnogenesis and its effects can still be viewed through some basic conceptual lenses, described briefly below. These models only provide a framework by which to assess patterns and changes in social, material, and biological markers (*sensu* Stojanowski, 2010; Voss, 2008). They in no way reflect the totality of ways in which group identity is manifested, maintained, or transformed. Indeed, it is only by emphasizing the socio-historical contexts of identity negotiation, that ethnogenesis can be better understood and explored.

Fission-Fusion

The concept of ethnogenesis by fissioning is based on the principal of a sub-group breaking off from a parent group. It has been emphasized by a number of scholars studying Native American and New World groups (Sturtevant, 1971; Brumfiel, 1994; Hill, 1996; Stojanowski, 2010). Although these works represent a number of different cultures and peoples, they all share a common thread whereby an original group splits or fissions to produce a different ethnic group. This is often the result of political factionalism or economic maneuvering (see Brumfiel, 1994; Bandy, 2001; Levy, 2008), but the influence of shared cultures and histories can also be a factor (Ortman, 2010; Stojanowski, 2010).

Newly differentiated groups may become spatially separated or geographically isolated from each other, leading over time to greater group distinctions, which become reinforced through iterative daily practices (Sturtevant, 1971; Ortman, 2010; Stojanowski, 2010; Hu, 2013). However, spatial separation is not a necessary requirement, since continued interaction can also function to fortify emerging differences. Regardless, new ethnonyms (i.e., Levy, 2008), ritual and cultural practices (i.e., Bawden, 2005; Bawden and Reycraft, 2009; Ortman, 2010), and even political structures can form.

Institutionalized Inequalities and Colonialism

Ethnogenesis can also occur as a result of institutionalized hierarchies. A ruling or dominant class or caste uses the categorization of sub-groups within the hierarchy to legitimize unequal access to power and resources. As Hu (2013) points out, these

categorizations can often lead to enduring ethnic identifications since these etic classifications are often tied to a political and legal framework that serve as a straightforward point of reference. Some of the best examples of this form of institutionalized inequality stem from colonial and imperial powers.

However, these inequalities frequently result in an active or passive struggle by sub-ordinate groups within the hierarchy. This theory of ethnogenesis is often described as "ethnogenesis as resistance", and is a narrative used to describe the ethnogenesis of African American, French Canadian, and Caribbean ethnic identities (Matthews et al., 2002; Wilkie and Farnsworth, 2005; Mann, 2008). For example, Matthews and colleagues (2008) suggest that the continued production of ceramic styles used by African Americans was a conscious and active form of resistance against the institutionalized slavery typical of the time period. This resistance can also be used to supersede previous divisions among groups, such as old ethnic or religious differences.

Frontiers

Frontiers also function as fundamental influences in the formation of ethnic groups. Indeed, frontier zones have been objects of study for decades, as researchers note the fluid and dynamic contexts they afford to many different aspects of social relations (Turner; 1920; Kopytoff, 1987; Willems, 1989; Comaroff and Comaroff, 1991; Chappell, 1993; Lightfoot and Martinez, 1995; Alconini, 2004; Rice and Rice, 2005). Curta's (2001, 2005b) work on the Roman frontiers in central Europe shows how non-Roman populations coped with and co-opted relations with the neighboring Empire, often resulting in the social mobilization of groups and eventual ethnogenesis. Likewise,

Brather (2005) argued that the creation of a frontier culture in northwestern Europe during the first to fifth centuries AD led to increasing political and social prominence of Germanic chiefs, to new forms of syncretic Romano-German material culture, and to the disruption of existing mechanisms of ethnic group coalescence.

2.2.3 Ethnogenetic Life-Cycles

As the above discussion on ethnogenetic processes made clear, there are a number of ways by which scholars can understand the formation and transformation of ethnic group identity/-ies over time. Another of these approaches, and the one taken in this study, is Nancy Hickerson's (1996) "life-cycle transitions". She describes three phases (separation, liminal, reintegration) in the creation and maintenance of ethnic groups (Hickerson, 1996: 70). In the initial phase of separation, existing group loyalties of the separated persons or group are no longer influenced by the parent group (*ibid*: 70). Hickerson describes the liminal phase as the withering away of any surviving social and/or economic ties and the initiating or strengthening of alternative connections. Finally, reintegration occurs when a "new identity is consolidated, affirmed through ritual and the adoption of a validating mythology" (*ibid*: 70).

Hickerson's model implicitly views ethnogenesis as transformative in nature and complements/embraces other integrated approaches without limiting the manner(s) by which ethnogenesis occurs. In other words, the concepts of time and change are explicitly included, and any number of factors (i.e., institutionalized inequalities, group fission) may play important roles in the ethnogenetic process. This type of approach clearly rejects static concepts of group identity (primordialist), while also avoiding simplistic

notions of manipulative or naïve self-interest in ethnic group formation (instrumentalist). It also accommodates the possibility that the historically- and culturally-contingent factors that play initial roles in the ethnogenetic process may be different from those used to maintain or reify ethnic group boundaries. Using a life-cycle model, however, does not make it an imperative or evolutionary framework, as ethnic groups are not required to go through these stages. Rather, they represent the degrees by which groups may (re)incorporate and dissolve over time, scaling up and down the spectrum of ethnogenesis depending on the situation (Stojanowski, 2010: 43-44).

In addition to providing an interpretive framework for ethnogenesis in the past, Hickerson's approach is useful for generating research expectations. Thus, for this particular study, these ethnogenetic life-cycle phases provide a means for exploring possible changes in phenotypic variation and their intersectionality with ethnogenetic processes. These topics and more will be explored in Chapter 5. Likewise, research expectations will be generated and outlined in Chapter 6.

2.3.0 SUMMARY

This chapter provided definitions and summaries of the current anthropological models for ethnicity and ethnic identity, including primordialist and instrumentalist approaches. On the one hand, primordialist approaches emphasize the essential and inexpressible quality of shared ethnicity between individuals that is ascribed upon birth. On the other hand, instrumentalist approaches emphasize the situational and often strategic nature of ethnicity whose qualities are often ascribed in the course of social interactions. Critiques of both of these approaches were presented in this chapter,

followed by recent suggestions for more integrated methods, such as Bentley's (1987) application of Bourdieu's (1977) practice theory, and Yelvington's (1991) emphasis on dynamic intergroup processes. Finally, the concept of ethnogenesis was introduced. As the process by which new ethnic groups materialize (Sturtevant, 1971), ethnogenesis is diachronic in nature and often forms part of an ongoing transformation of other social identities (Voss, 2008). This operational definition of ethnogenesis was then combined with different models by which various scholars have assessed it. Finally, a discussion of the theoretical approach taken in this study was outlined (e.g., ethnogenetic life-cycles).

CHAPTER 3

HISTORICAL AND ARCHAEOLOGICAL BACKGROUND

3.0.0 INTRODUCTION

This chapter provides a brief summary of the historical and archaeological contexts for the development of Frankish identity. First, I discuss dating standards and outline the temporal framework employed in this study, proceeding from circa the 3rd century AD and extending to the 10th century[13]. Spanning at least five centuries, the historical background for the transition from Late Antiquity through the Early Middle Ages is understandably broad and can form the basis of large encyclopedias of knowledge. Consequently, attempts were made to synthesize the most widely accepted interpretations advocated by recent historians. Archaeological data were also incorporated to provide additional support from the perspective of material culture and of settlement patterns[14].

3.1.0 DATING CONVENTIONS

Chronologies and terminologies for the Gallo-Roman and Early Middle Ages vary between historians and archaeologists and reflect a long tradition of being defined nationally. So, while German archaeologists define the Early Middle Ages from about

[13] The decision to begin with the 3rd century AD in no way implies that this century witnessed or exclusively acted as the origin of the social and biological processes discussed in this work.

[14] The structuring of the chapter is not meant to imply that the included archaeological data are exhaustive in nature. Nor are they intended to suggest that archaeological and ethnohistorical data are in complete agreement or that alternative interpretations are nonexistent.

AD 450 to 700, German historians define the period from AD 476-1024 (Graham-Campbell, 2007: 17). Regardless, most scholars define the Early Middle Ages from the 5th-10th centuries AD, and these are the primary dates employed in this manuscript. Likewise, conventional dating of the Gallo-Roman Period is from approximately the first century AD through the 4th century. References to the Early and Late Gallo-Roman Period coincide with the 1st-2nd centuries AD and 3rd-4th centuries AD respectively. Finally, the Frankish Period (c. AD 450-900) is considered a larger categorization that includes both the Merovingian (c. AD 450-750) and Carolingian (c. AD 750-900) Periods.

3.2.0 THE SETTING

3.2.1 Third through Fourth Centuries

During the 3rd-4th centuries AD, the Mediterranean region remained the economic, political, and cultural nexus of the Roman Empire. According to some scholars (Wells, 1999), dual processes of "Romanization" of the frontiers and "barbarization" of the Italian peninsula had already been well established by the 3rd century AD. Additionally, barbarian elites from the inner and outer peripheries of the Roman Empire had selectively adopted various aspects of Roman[15] ways and material culture and integrated them within their own cultural traditions (e.g., Wells, 1999; Brather, 2005; Heather, 2010).

This period also witnessed the economic and population growth of the Roman provinces and a concomitant rise in regionalism—an increasing number of powerful

[15] Most authors on the topic of ethnicity in Early Medieval Europe use the term "barbarian" to refer to the various, but unspecified, non-Roman *gentes* (i.e., peoples) living at this time. Thus, for the sake of expediency and clarity of discussion, the term "Roman" and "barbarian" will be adopted within this text.

provincials emerged within the imperial system. Multiple emperors rose and fell, their fates often rooted in military leadership. A dependence on military backing led to an increase in demand for troops and barbarian recruitment (Elton, 1996: 92-94). By the 4th century, barbarian recruitment by emperors (usually after barbarian military defeat, see *ibid*: 129, 135) typically resulted in a thorough assimilation of barbarian troops into regular Roman military units, unlike the wholesale hiring of barbarian groups as *federates*[16] that occurred later during the 5th century[17] (*ibid*: 92, 137; see also Heather, 1997).

Archaeologically, scholars have shown that there is a greater frequency of defensive walls built around cities, along with an increase in defenses along key communication routes. By the 4th century, there is a decrease in the range and volume of long-distance exchange, replaced by an increase in regional and local supply networks used to furnish the armies and settlements in northwestern Gaul and along the Rhine frontier (Hodges, 1982: 29-30; see also Hedeager, 1978; Greene, 1991; van Ossel and Ouzoulias, 2000). At the same time, scholars have pointed to archaeological evidence that reveals a decline in population size, especially in urban contexts (Burns and Eadie, 2001: xiii). Roman elites shifted their foci from an urban public display of status to a life of rural luxury situated in Roman *villas—villas* that often increased in number and elaborateness in many of the provinces (Randsborg, 1991: 102-114; for example, see Jouffroy, 1986). Finally, cemeteries were predominantly located outside city walls, away from the communities of the living (e.g., Cologne). According to many historians (i.e.,

[16] *Federates* (or *foederati*) were groups of barbarians formally allied to the Roman government. In exchange for subsidies – usually in the form of land or tax receipts – *foederati* would provide warriors or armed units in the defense of Roman interests (Goffart, 1980: 34).

[17] See pages 25-26 for a discussion on the impact and use of *foederati* during the 5th century AD.

Wood, 1993) these processes reflected the ongoing contraction of the Roman state from the provinces to the Mediterranean core—a contraction which facilitated the expansion in power of the provincial elites and the replacement of imperial trade goods and networks with local and regional ones.

Although the majority of religion was still regionally specific, the Christian Church gradually began to replace the old structures of civic life that once revolved primarily around Roman markets and politics. Via granting official status, land endowments, and fiscal privileges beginning in AD 313-314, the Emperor Constantine effectively moved Christianity to a position of supremacy amongst the complex religious movements of the day[18] (Momigliano, 1963; Brown, 1996). In addition, the Christian Church's hierarchy became increasingly integrated into the official infrastructure of the state, beginning in the Mediterranean core and spreading outward. It has been argued that this process allowed episcopal power to cohere and become an important influence in local/provincial administration as well as in the Mediterranean core (Innes, 2007: 45). Since bishops were so thoroughly integrated into state administration, the Church administration began to mirror the state (*ibid*: 45). Importantly, the Church also functioned as a spiritual community that offered membership to everyone, while at the same time rejecting regional (i.e., heretical) forms of Christianity and pagan cults (Momigliano, 1963; Brown, 1996).

In the provinces and along the frontiers, ethnohistorical records and archaeological excavations have been used to suggest that indigenous barbarian social and political organization was complex and largely sedentary (Pohl, 2000; Hamerow,

[18] A number of other religious movements also occurred at this time, including different versions of neo-Platonism and a variety of mystery cults (Brown, 1996).

2002). Rulers were likely independent and locally based (Pohl, 2000; Innes, 2007). Settlements were often scattered and small-scale; elite sites, such as Feddersen Wierde, were still small in comparison to Late Roman frontier settlements (Hamerow, 2002: 77-79; see also Parker, 1965). The basic unit of barbarian society is believed to have been the farmer household, with many coming together to form settlement communities (Hamerow, 2002: 52-53). Housing, especially in northern Europe, typically consisted of longhouses made of wood (i.e., Feddersen Wierde, Vorbasse) (Hamerow, 2002: 15), and evidence of enclosed complexes within settlements has been interpreted by some archaeologists as an indication of a property-based society (Haarnagel, 1979: 49-70; Hamerow, 2002: 78-79; but see Steuer, 1982 for an alternate interpretation).

Agricultural and non-agriculture production, such as metalworking, increased in the Roman frontier zones. This, along with trade in Roman goods, led to greater development of the barbarian economy, but one that was unequally shared within and between groups along the frontiers (Heather, 2010: 14). Historians and archaeologists believe that barbarian society became more stratified between the 3rd and 5th centuries, historians and archaeologists, with wealth and power being more limited (*ibid*: 43-64; see also van Es, 1967; Hamerow, 2002). Evidence for this interpretation stems from 1) the development of clearer internal hierarchies within agrarian settlements (van Es, 1967); 2) the emergence of richly accoutered barbarian burials (i.e., *Fürstengraber* or 'princely burials') or of monumentalized graves, like at Odry (Heather, 2010: 56; see also Brather, 2005); and 3) the emergence of new, high-status sites associated with warrior elites (i.e., new political dominance) (Haarnagel, 1979: 92-96; Heather, 2010: 56-57). The Alemannic hill-top settlement of Runder Berg is an example of a 3rd-4th century elite

residence (Christlein and Natter, 1978). Other scholars, however, suggest that barbarian society was not simply divided between royal retinues and freemen (Heather, 2010: 70). Several classes of people, including freedmen and slaves, were often components of barbarian societies and should be considered when addressing questions of barbarian identity, social structure, and migration.

Both the frontier zones and the Roman army itself provided a vital source of integration for Roman and barbarian alike. Rather than an area of demarcation, both Miller (1994) and Heather (2010) have argued that the Roman frontier zones were regions of interaction (see also Wells, 1999; Curta, 2005a). Archaeologically, the volume of Roman goods decreased over distance in the frontier regions (Hedeager, 1978). It is believed that in areas where Roman goods were more scarce elites could control access and redistribution of these items, allowing them to serve as symbols of power (Heather, 2010: 74-81; see also Curta, 2005b; Brather, 2005). These frontier interactions tended to create a "homogenous cultural zone that straddled the political boundary" and became more heterogeneous over distance (Innes, 2007: 78; but see Wells, 1999). Likewise, the Roman army became a fusion of influences, witnessed in the adoption of "tribal" names and war cries (whether real or mock) by army units (Wenskus, 1961: 60).

Historians have pointed to the continuing internal crises within the Roman Empire In the latter portion of the 4th century, which encouraged the rise of recurrent usurpers in the Western Roman Empire and increased tensions between the Eastern and Western Roman portions of the Empire (Innes, 2007: 82). This shift in political focus by the Roman imperial administration to the region of Mediterranean Rome, rather than the provinces, further encouraged a power vacuum in the provinces. This process provoked

intervention in Roman politics by barbarians and induced the backing of usurpers by barbarian and Gallo-Roman elites (*ibid*: 85).

3.3.0 THE EARLY FRANKISH KINGDOM

3.3.1 Fifth through Seventh Centuries

During the 5th century, the settlement of barbarian war bands (i.e., federates) within the empire replaced the old frontier system (e.g., Goffart, 1980; Heather, 1997, 2010). Although not a new phenomenon, the scale and implications of this change were profound. Previously, barbarians were integrated via the medium of the Roman army. In the 5th century, however, they were settled as armies with dependents, sometimes granted land, and often granted the right to a share of tax receipts (Goffart, 1980: 102, 123-126, 154, 205). The Visigoths, for example, were settled in Aquitaine by a treaty in AD 418 with the Roman leader, Constantius (Wolfram, 1988: 161-162; Heather, 1991: 219-220). Likewise, the Burgundians were given the region of Sapaudia in ca. AD 436 by the patrician Aetius (Escher, 2006: 66).

Barbarian settlement served to ensure a steady supply of federate forces to provincial elites and Roman generals alike (Wood, 1993: 13). According to some scholars, these exchanges were typically peaceful and worked to integrate indigenous Gallo-Romans with barbarian groups via schemes of tax allotments rather than complete cooption of private land (*ibid*: 10-11, see also Goffart, 1980). However, others argue that such a conclusion overlooks much of the historical record documenting mass migrations and their often violent impact on Roman provinces (Heather, 2010: 333-342).

There were changing patterns of military recruitment, too, as powerful landowners and usurpers of the Western Roman empire, like Constantine III, developed their own personal armies (Innes, 2007: 104). Outside the eastern borders of the empire, the nomadic Huns had accumulated control, creating a system whereby barbarian elites (e.g., Goths, Suebi, Alans, Gepids) were either subjected to Hunnic rule or fled into exile in Roman service (Thompson, 1996: 79-84, 88, 184; but see Goffart, 2006). Archaeologically, scholars assert that there is little evidence that Hunnic conquest disrupted basic agrarian subsistence, although ethnohistoric documents commonly attest to pillaging and extortion (Thompson, 1996: 182). Eventually this nomadic empire collapsed in AD 454 after the death of Attila, but its rise and fall are argued to reflect the broader processes ongoing in the Roman Empire – the gradual dissociation of the provinces from the Mediterranean core and a "slow and steady unraveling of the authority of the imperial court" (Innes, 2007: 111; see also Wickham, 1984).

By the 470s, the interests of provincial elites in Gaul and Hispania were no longer those of Roman politics—a reflection of the trend toward provincialism, the growing number of barbarian settlements, and the increase in power of barbarian elites., Historians point out that aristocrats often sought local power by combining secular and spiritual leadership in the form of episcopal office, rather than gaining influence through the politics of Rome (Mathisen, 1989). Others, like the Gallo-Romans in southern France and Hispania, quickly accommodated barbarian rule (Wolfram, 1988: 199-200; Wood, 1993: 19; see also Kulikowski, 2005).

Despite the gradual contraction of active Roman power and politics in Western Europe, barbarian kings often relied upon the Roman political and administrative system

in order to develop new forms of political control and legitimacy (Innes, 2007: 124). For example, the Visigothic king Euric may have used Roman lawyers for his compilation of laws in the mid-400s (Wolfram, 1988: 194-195), while the Burgundians also issued the *Liber Constitutionum* in AD 517, which utilized a pre-existing Roman legal system. A number of scholars argue, however, that some barbarian kings, like the Franks in northern Gaul, did not leave existing systems of administration in place (Heather, 2010: 305-332). Heather cites legal evidence for a restructuring of Gallo-Roman society into one that incorporated three social classes possessing different rights and duties: 1) the free; 2) the freedmen; and 3) the slaves (*ibid*: 311).

Of all the post-Roman federations to materialize in Western Europe in the 5th century AD, one of the most influential and long-lasting was the Frankish (Wood, 1993; see Figure 1). Appearing in northern Gaul during the 4th century, the Franks arose in the midst of protracted contact and relations across the Rhine frontier (*ibid*: 35-38; see also Geary, 1988; Todd, 2004). Yet, the first ethnohistoric references to the *Franci* actually date as early as the mid-3rd century, when various 'tribal units' of a warrior-like confederacy were recorded as plundering the Rhine frontier (Aurelius Victor, *Liber* 33.3) and seizing a town in Spain (Eutropius, *Brevarium* 9.7, 9.8.2). However, this historical tracing implies a degree of continuity (cultural and/or biological) that likely did not occur and that may stem from modern re-readings of ethnohistoric documents.

Although there is much debate concerning the scope of Frankish self-perception (Hummer, 1998; see also Wood, 1993), Frankish generals were extensively incorporated into the Roman army, often bringing Frankish war bands with them, as in the case of Childeric I. Consequently, some historians, claim that the "'Francisation' of the frontier

provinces may have simply been a recognition of the close ties that had developed across the frontier, and the military power of the Franks in a period of scant Roman resources" (Innes, 2007: 269; see also Wood, 1993: 38-49).

Childeric's son, Clovis, conquered the region of northern Gaul in AD 486 and is considered the founder of the Merovingian kingdom (Wood, 1993: 49). He is also attributed with the "conversion" of the Franks to Christianity, although this conversion was probably "part of the process of political settlement and the consolidation of the regime" (Innes, 2007: 272; see also Wood, 1993: 43-48). In other words, Christianity likely did not affect the majority of the Franks at this time period (Wood, 1993: 48), and the nature of its spread throughout Europe has long been a subject of discussion (see Paxton, 1996; Armstrong and Wood, 2000).

Regardless, it is argued that the conquest of Gaul by Clovis shifted the focus of many Gallo-Roman elites from local politics to the Frankish king and his military backing, a trend that lasted until the mid-6th century. Thus, archaeologists have pointed to a change in burial practices that may reflect this political shift. During the late 5th and early 6th, indigenous Gallo-Romans and Franks started engaging in lavish burial displays, usually incorporating or expressing martial power (e.g., Gammertingen and Krefeld-Gellep) (Christlein and Natter, 1978; James, 1989). Although grave goods were included in burials prior to this time period, there were comparatively fewer of them, and some scholars (Heather, 2010: 305) describe the increase as an "explosion" in richly furnished burials. These more recent inhumations are often centered on a single burial or the closely situated burial of one or two individuals that are presumed to be related (i.e., "founder burials"). Consequently, the development of such ostentatious displays in

conjunction with the presence of "founder burials" during the turn of the 6th century AD is distinctive and has been suggested as a way to advertise the social status of the deceased and/or families of the deceased, *sensu* Lewis Binford (Effros, 2002: 48, 55; see also Heather, 2010: 305).

Clovis's eventual consolidation of most former Roman territories was likely due to a number of factors, including religion and the presence of existing Roman infrastructure. For example, Innes (2007) and Wood (1993) argue that the political integration and eventual cooperation of indigenous Gallo-Roman aristocracy with the Frankish elites was aided by religious rhetoric and identification (Innes, 2007: 273; see also Wallace-Hadrill, 1983). Clovis's "total avoidance of [Arian Christianity][19] is held to have made him more acceptable to the catholic Gallo-Romans, than were the other kings of his generation, and to have helped ensure that the Franks were more successful than either the Burgundians or the Visigoths" (Wood, 1993: 44). In comparison, the Visigoths continued their religious identification with Arian Christianity, which has been argued to be a source of tension with the indigenous Hispanic populations until its abandonment in favor of Catholicism in AD 589 (Wickham, 2005: 37-41; see also Kulikowski, 2005).

Roman infrastructure may also have aided the unification of Gaul. Political and economic administration, especially in southern Gaul, continued on the level of the city and its environs (i.e., the *civitas*), and on the diocese (Wood, 1993: 71; see also James, 1989). This situation both prevented extensive Frankish restructuring due to the existence of more powerful Gallo-Roman elites, and it encouraged co-opting the pre-existing

[19] Arianism was deemed a heretical form of Christianity, primarily because it denied the divinity of Christ.

infrastructure. As a result, both the diocese and the *civitas* probably formed much of the basis of the Merovingian taxation system (Wood, 1993: 62).

Such structural stability and commonality in religion aided in the gradual reunification of Gaul under the Merovingians and emphasized the roles played by bishops and *comes*[20], both of whom often gained their positions due to the influence of the king (Wood, 1993: 60, 78; see also Goffart, 1980: 213-231). Archaeologically, this continuity may be seen in the uninterrupted, but new, use of public spaces from the 5th through 6th centuries in urban contexts (Loseby, 1998: 256-263). For example, in Cologne the old Roman *praetorium* was used for local elite residences and some elites were buried beneath the cathedral as a sign of privilege (Werner, 1964: 201-216).

In areas possessing less Roman infrastructure, such as north and northeastern Gaul, administration on a local level is believed to have depended on larger regional units called *duces* (Lewis, 1976: 381-410). The *villa* sites so typical of late Gallo-Roman landlords and elites in northern Gaul were typically restructured by incoming Franks by the late 5th century (Innes, 2007: 283; Heather, 2010: 305). In these distant regions, continuous practice of Roman administration was often severed, even if Roman heritage in the form of cities and forts continued to be used (Innes, 2007: 282; see also Heather, 2010: 305).

Excavations in northern Gaul reveal mostly rural settlements made of wood (e.g., Mondeville) and housing using a sunken-floored technique (i.e., *grübenhausen*), which, according to most scholars, represent a non-Roman type of construction (Lorren, 1989; Hamerow, 2002; but see van Ossel, 1995). This technique consisted of buildings

[20] *Comes* (pl. *comites*) were typically the senior official in the *civitas* and had duties that included the enforcement of justice, hearing of lawsuits, and even military leadership (Murry, 1986: 787-805).

hollowed out of the earth with usually four corner posts or two gable posts (Hamerow, 2002: 31). Economically, rural settlements in both northern and southern Gaul appeared to rely on agro-pastoralism, which, according to scholars, would have minimized the need for routine exchange of utilitarian items. In fact, both ceramic production and metalwork appear to have occurred on local levels within rural communities (*ibid*: 172; Innes, 2007: 449).

Over time, differences between northern and southern Frankish Gaul are suggested to have led to increasing regional polarization, the rise of regional identities (i.e., Neustrian vs. Austrasian), and a political organization that emphasized discrete regional units (but see Wood, 1993: 146-149). Neustria, Austrasia, and Burgundy became the main *Teilreichen* (or segment kingdoms) of Merovingia (Figure 1). Aquitaine, another large region of Western Europe, was annexed in AD 507 and was considered a peripheral principality to an administration centered in Neustria. This trend in annexation and regionalization also served as a model by which surrounding principalities, such as Gascony, Brittany, and Frisia, were acquired and organized (*ibid*: 159-180). From the mid-6th through 7th centuries, power slowly shifted into the hands of local elites, such as *comes* and bishops, rather than resting exclusively with a central hierarchy under the Merovingian kings (*ibid*: 149, 152). Likewise, the *civitates* no longer functioned in the critical role of taxation and displays of power. Rather, land ownership became the most vital source of wealth and power (Innes, 2007: 292).

Similar trends also existed in Visigothic Spain and Lombardic Italy. In Spain, ambitious provincial elites sporadically warred against rivals in their bid to become part of the royal succession (Wickham, 2005: 37-41). Unlike Frankish Gaul, however, it is

argued that "the circulation of the royal office [in Visigothic Spain] kept aristocracies engaged with regnal politics, and enabled the creation of a palace-centred polity in which the social and military power of regional aristocracies was politically articulated through the royal court at Toledo" (Innes, 2007: 228). In Lombardic Italy, the kingdom was divided into three regions, which were equally divided over time (Wickham, 2005: 35). This fragmentation into a series of sometimes isolated microregional economies and societies likely encouraged the eventual conquest of the Lombard Kingdom by the Franks.

As evidence of this change in power-base from Frankish royalty to regional elites, archaeologists have pointed to burials and rural settlements that exhibit an increasingly differentiated social hierarchy. For example, more spatially discrete burials, the creation of above-ground markers, such as wooden huts (Dannenheimer, 1966), the construction or re-exploitation of barrows, and the increasing use of burial within the confines of a church are all interpreted as strategies to emphasize social stratification (James, 1989; Fehring, 1991). Archaeologists have also noted the construction of large halls by elites to mark themselves as different from their neighbors (e.g., Laucheim) (Stork, 1991; Innes, 2007) and the construction of monastic houses on elite rural estates (Le Jan, 2001: 253).

These practices reflected the changing role of cities and the rise in power of privileged churches and local elites in Frankish Gaul. The change in mortuary practices is also argued to reflect a shift in the relationships between the living and the dead. Previously the provisioning of the dead was performed by family members of the deceased and emphasized the daily needs of the deceased in the afterlife (Effros, 2002: 139-140). In the 6th and 7th centuries, the Christian Church came to be seen as the ritual

intermediary for the deceased. It emphasized the spiritual needs of the deceased, which some have interpreted as accounting for the widespread decrease in grave goods by the end of this period (e.g., Young, 1977; but see Paxton, 1990; Effros, 2003).

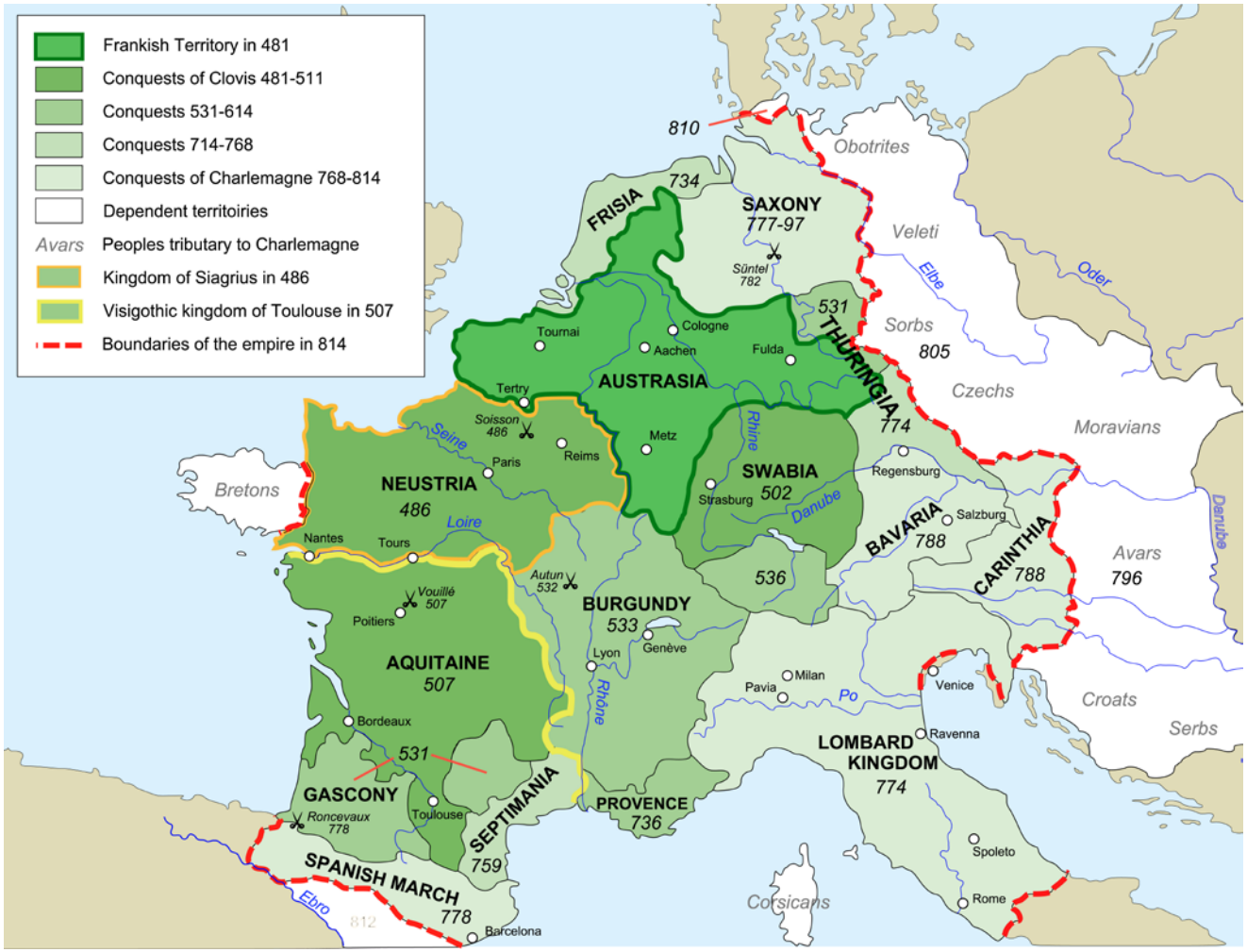

Figure 1. Map of the Frankish Empire (AD 481 – 814) (by Sémhur [FAL or CC BY-SA 3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons).

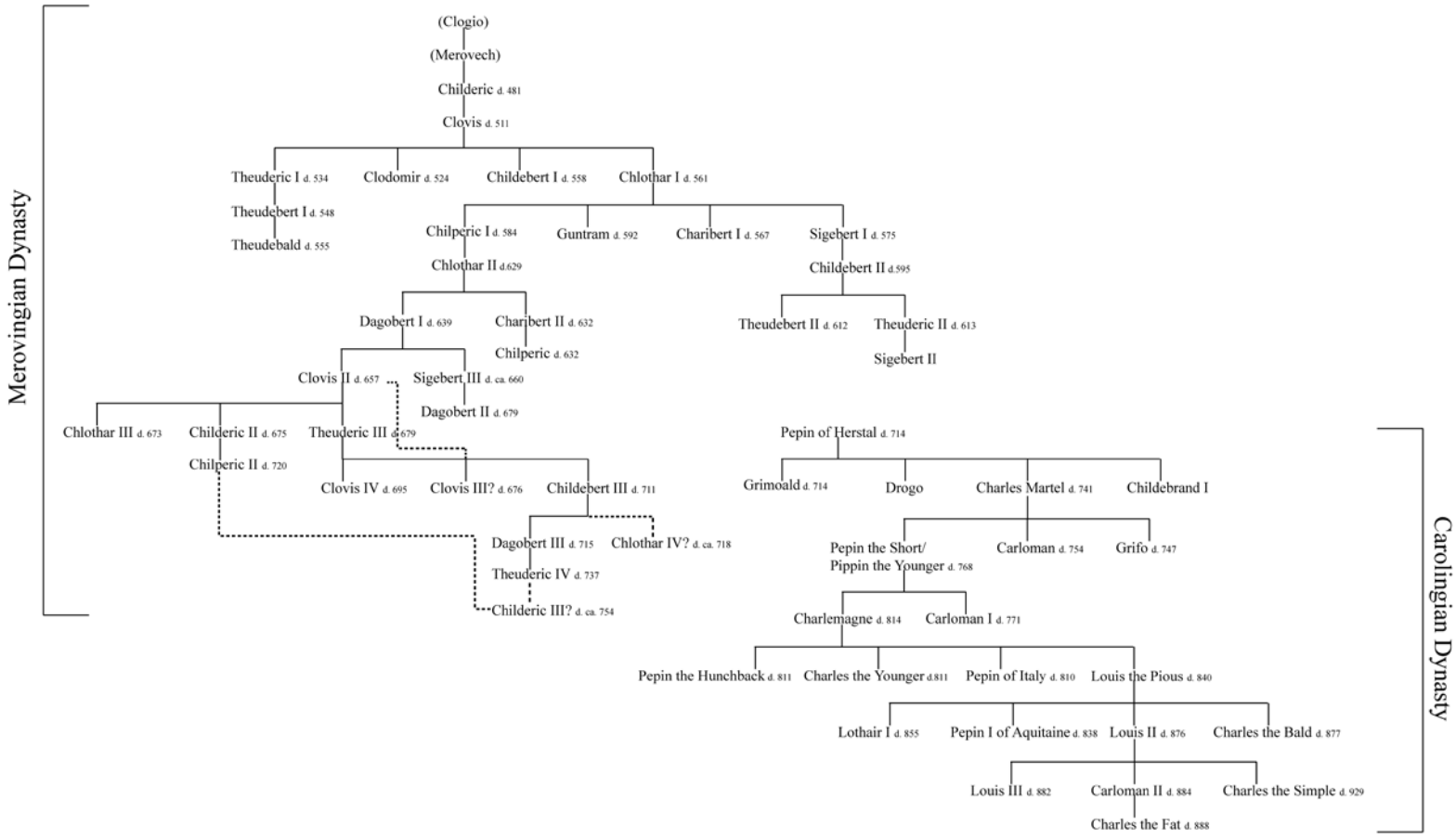

Figure 2. Genealogy of the Frankish Dynasties.

3.4.0 THE LATER FRANKISH KINGDOM

3.4.1 Eighth through Tenth Centuries

Historians, such as Wood (1993) and Geary (1998) maintain that the decline of the Merovingian dynasty was ultimately the result of internal politics centered on Neustria and Austrasia (Wood, 1993: 255-292). Political crises eventually lead to the integration of these two segment kingdoms and to an increased importance placed on the office of mayor of the palace[21] (*ibid*: 259). In AD 751, the last Merovingian king was exiled to a monastery and the former mayor of the palace, Pippin III, was crowned king. Three years later, Pippin's reign was formally recognized by Pope Stephen, giving rise to the Carolingian dynasty.

Under the Carolingians, the Frankish realm nearly doubled in size due to yearly military actions (see Figure 1) (McKitterick, 1983: 41-72). Bachrach (2001) maintains that this emphasis on military campaigns reflected the increasing value of landed resources and the necessity of integrating a splintered and localized political organization. He points out that the central focus for many of the Carolingian kings was re-conquest, since much of the territory nominally under Merovingian control had become heavily regionalized and fractured, especially during the civil war of AD 714-719 (*ibid*: 226; see also McKitterick, 1983). In addition to regaining lost land and tax revenues, these campaigns are believed to have tied landed elites to the Carolingian monarchy and to have enriched the Frankish aristocracy (Reuter, 1985: 81, 85-87). For example, the peripheral principality of Aquitaine, which had drifted away from Merovingian control,

[21] The mayor of the palace (i.e., m*aior domus*), or 'greater man of the royal household', held administrative and legal functions within the court (Wood, 1993: 153).

was reconquered by Pippin from AD 759-769. Likewise, the Italian peninsula was wrested away from Lombard control in AD 774.

Under Charlemagne, who was the son of Pippin III, and his successors, the Carolingians pushed further east of the Rhine to conquer and, in some cases, convert the Frisians, Saxons, Thuringians, Bavarians and Avars. In these regions, Carolingian success is argued to have hinged on collaboration with Christian missionaries who used their liminal status to join old and new converts together within an institutionalized Church hierarchy (Innes, 2007: 398). Moreover, as military campaigns slowed, or ceased altogether, in the late 8th century AD, Carolingian rulers increasingly used assemblies and capitularies to integrate their kingdom (McKitterick, 1983: 77-103). The capitularies "aimed fundamentally at a programme of re-education, promulgating a new ethos in which landowning elites were encouraged to see their dominant role in terms of a hierarchy of office in which they were responsible to the king, as God's representative on earth, for the maintenance of 'peace, unity and concord among the Christian people'" (Innes, 2007: 436, see also McKitterick, 1983, 1994).

With the creation of the office of count and the increasing importance of royal officials known as *missi dominici*, a pronounced hierarchy also came into being during the 8th century (Airlie, 2005: 90-101). Rather than a regional aristocracy formed on the basis of provincial identities, an imperial aristocracy with land, kin, and clients was scattered across the Carolingian Empire. This imperial aristocracy became increasingly separate from non-elite, local landowners who likely maintained their own local identities. Thus, archaeologists point to a change in the structure of rural settlements in north and northeastern Europe. Previously, rural settlements and their fields and

cemeteries shifted within a region, based on the fertility of the soil and access to resources. By the 8th century, most had become fixed, with habitation clustering around focal points, such as churches and cemeteries (Hamerow, 2002: 104-106). At the same time, landed elites began to distance themselves from village society, building residences further out in the countryside, such as Pettegem (Innes, 2007: 446). These elite residences tended to be large structures with ditches and palisades, which are archaeologically indistinguishable from royal estate centers. Unlike the construction of large halls by elites in the 5th-7th centuries, these residences were increasingly dissociated from surrounding settlements.

Economically, production was more interregional than in Merovingian times (Hodges, 2001: 4). Cereal agriculture became more intensive and focused, with surpluses being generated or at least attempted. Craft production also became more specialized and was often organized by monastic houses and royal estates (Wickham, 2005; see also Hodges, 1982; Hamerow, 2002). Finally, long-distance trade exchange with the North Sea coast took place during the 8th century. The flourishing of trade towns (i.e., emporia) such as Dorestad, Quentovic, and Hamwic, suggest an ever-increasing trade and, in some cases, production of luxury goods, perhaps controlled by royal power (Hodges, 1982: 66-86). During the 9th and 10th centuries, economic production developed to a point where markets arose in the countryside, primarily focused around monastic and aristocratic centers (e.g., Haithabu) (Müller-Wille et al., 1988; Hamerow, 2002). Later, some of these centers would become the foundation for medieval towns. Eventually, Viking raiding during the mid- to late-9th century and the rise in new market centers led to the decline of emporia (Hodges, 1982: 65; see also Randsborg, 1980).

By the 9th century, Christianity had become a critical component within the kingdom, leading to a greater solidification of an episcopal hierarchy with the royal court at the apex (McKitterick, 1977; Paxton, 1990). Bishops were central figures in the organization of the Frankish Church and the boundary between layman and cleric was firmly established. Archaeologically, this solidification of Christianity as the predominant religion is seen in the mortuary program. Burial by *ad sanctos* became the preferred means by which elites expressed their social status, allowing them to associate their ancestors with saintly relics (Duvall, 1988). Community cemeteries were relocated into churchyards; other times, churches were built directly onto existing cemetery sites. These acts brought the ancestors into the community of the living, Christian community (Effros, 2002). However, these ancestors were made anonymized and merged into the general community of the Christian dead. "Above-ground markers of all kinds, barrows and the like, were banned, as burial was to take standard Christian form, and social status in the grave was now expressed through lavish patronage to fund commemorative Masses and prayer which purged sin, or for members of the elite through privileged burial, perhaps in a monastery" (Innes, 2007: 477; see also Paxton, 1990). In other words, death became Christianized, and mortuary rituals were increasingly regulated (Paxton, 1990: 126-127). With the breakdown in royal succession, concomitant regional polarization, and frontier raiding by Vikings, Slavs, and Muslims, the Carolingian dynasty essentially ended in AD 888 with the deposition of the last Carolingian, Charles the Fat, and the formal fission of the realm into independent kingdoms.

3.5.0 SUMMARY

As outlined in this chapter, a confederation of people—the Franks—emerged and/or were recorded during a period of waning Roman imperial influence. Regardless of the nature of their presence on the landscape and their involvement with the Roman Empire, this confederation was associated with an ethnonym—"Frank"— and with various cultural and social characteristics. Although historians and archaeologists may not be able to agree on the exact nature of Frankish identity, how it developed, or how it changed over time, it is indeed clear that a group calling itself the Franks existed and became a salient political force in Western Europe for half a millennium.

CHAPTER 4

BIOANTHROPOLOGIAL BACKGROUND

4.0.0 INTRODUCTION

In this chapter, I describe how biological data from human skeletal remains have been used by scholars of this time period. This background on the history of physical anthropology focuses on the French discipline in particular, although many aspects are shared by other physical anthropologists in Western Europe. Details are also presented on the use of skeletal morphology to examine differences between skeletal assemblages. These studies do not explicitly assess population structure, nor do they use model-bound approaches—two distinctions that are described more fully in Chapter 5. However, they do reveal 1) what kinds of research questions were/are important to physical anthropologists, and 2) what general conclusions have been drawn. Finally, I summarize the comparatively smaller amount of research by molecular anthropologists that relates to this time period. Both the skeletal morphological and molecular research possess limitations to which newer approaches, such as model-bound biodistance analyses can overcome.

4.1.0 PHYSICAL ANTHROPOLOGY

4.1.1 Physical Anthropology in French Scholarship

Physical anthropology in France has a lengthy history. Heavily influenced by the work of Paul Broca[22] (1875, 1879) and Henri Vallois (1943) in the late 19th and early-to-mid 20th centuries respectively, French physical anthropology and more specifically skeletal morphology has long focused on questions related to human evolution and the history of population movements. Best classified as typological, and at worst racist, much of this early work viewed the human cranium as a clear indicator of an individual's racial or ancestral origins. Thus, consistencies in cranial shape and form reflected in cranial indices (Broca, 1875) were treated as typological of particular races (Vallois, 1943). These cranial types (i.e., Nordic, Mediterranean, Danubian) were then used to distinguish individuals from other groups, usually with the goal to determine invasions and migrations in the past.

Relative "homogeneity" of a cemetery sample was a concept linked to these typological studies. For example, a cemetery sample was considered "homogeneous" when a single cranial type was present, but "heterogeneous" when two or more types were identified based on cranial indices (Crubézy, 2000: 11). Likewise, the persistence of the same type over time indicated *in situ* population change[23], while the appearance of a new type over time indicated population migration (*ibid*). The theoretical shift away from such typological work has its origins in abuses by Nazi researchers and the eugenics movement (Meyran, 2000). However, through a system of institutional hierarchies in

[22] Broca himself was influenced by the work of Blumenbach (1776) and Morton (1839).

[23] Most commonly referred to as "l'évolution sur place de la population". This phrase may be roughly coterminous with "genetic drift", though this phrase is never used by Frénch physical anthropology and has its origins in population genetics.

France, typological approaches were considered standard methodology for most French physical anthropologists until the mid-to-late 20th century (Bocquet-Appel, 1989: 33).

Though a lamentable part of physical anthropology, the consequences of the shift from typological skeletal morphology is still felt within France and throughout Western Europe more broadly (Bocquet-Appel, 1989; Blondiaux and Buchet, 1990; but see Roberts, 2006). French physical anthropology now focuses almost exclusively on topics such as paleodiet (i.e., caries) and paleopathology (Bonzom, 1976; Dastugue, 1978, 1982; Crubézy, 1988; Blondiaux, 1989; Kramar, 1990; Zammit, 1990; Dastugue and Gervais; 1992; Mafart, 1996; Pálfi, 1997); paleodemography (Bocquet-Appel and Masset, 1982; Blondiaux, 1986; Masset, 1973, 1990; Simon, 1990; Masset, 1994; Buchet and Séguy, 2003); and reconstructions of kinship (Alduc-Le Bagousse, 1980; Bocquet-Appel, 1985; Darlu and Bocquet-Appel, 1987; Crubézy, 1989; Vatteoni, 1989; Crubézy and Sellier, 1990), to the clear exclusion of population-level studies incorporating skeletal morphology. Thus, morphological anthropology has declined precipitously, leaving many French physical anthropologists to question whether it holds any value, either to the discipline of physical anthropology or to other disciplines, like history and archaeology (Blondiaux and Buchet, 1990). This contraction of physical anthropology has only been exacerbated by the clear isolation of many French physical anthropologists in relationship to their Anglophone colleagues. Research by Anglo-American physical anthropologists are not widely read nor cited. Moreover, French physical anthropologists do not frequently publish in Anglophone reviews and journals.

Some scholars (e.g., Blondiaux and Buchet, 1990) have argued for the continued place of morphological studies in archaeology and history. Yet, few French physical

anthropologists have taken up the call. Rather, an implicit taboo on such studies is perpetuated, as most physical anthropologists have now ceded to geneticists those questions related to population structure and "biological" transformations.

4.2.0 SKELETAL MORPHOLOGY

4.2.1 Skeletal Morphology of Early Medieval Populations in Western Europe

Despite the topically limited use of skeletal material for exploring the interaction of social practices and biological data, there is still a rich history of human skeletal study by European scholars. Indeed, skeletal morphological studies involving Early Medieval populations began even earlier than the 20th century. Cemeteries from many periods are commonly found and excavated, and those from Late Antiquity to the first millennium A.D. are no exception. In the earliest periods of excavation, however, human skeletal remains were not retained as often as material remains found in graves. However, with the increasing interest in "scientific" anthropology, skeletal material (especially crania) were progressively preserved and studied.

Historically, most skeletal morphological studies of Early Medieval populations deal with three main regions in France: 1) Normandy, 2) Burgundy, and 3) Île-de-France. This focus reflects 1) continuous occupation and infrastructure construction by the modern French government; 2) good preservation of skeletal and material remains; 3) historical emphasis and interest by archaeologists and historians; and 4) institutional foundations in the form of large universities or research centers capable of studying any excavated skeletal remains. The following sections discuss research themes and general trends in studying population structure and skeletal morphology for each region.

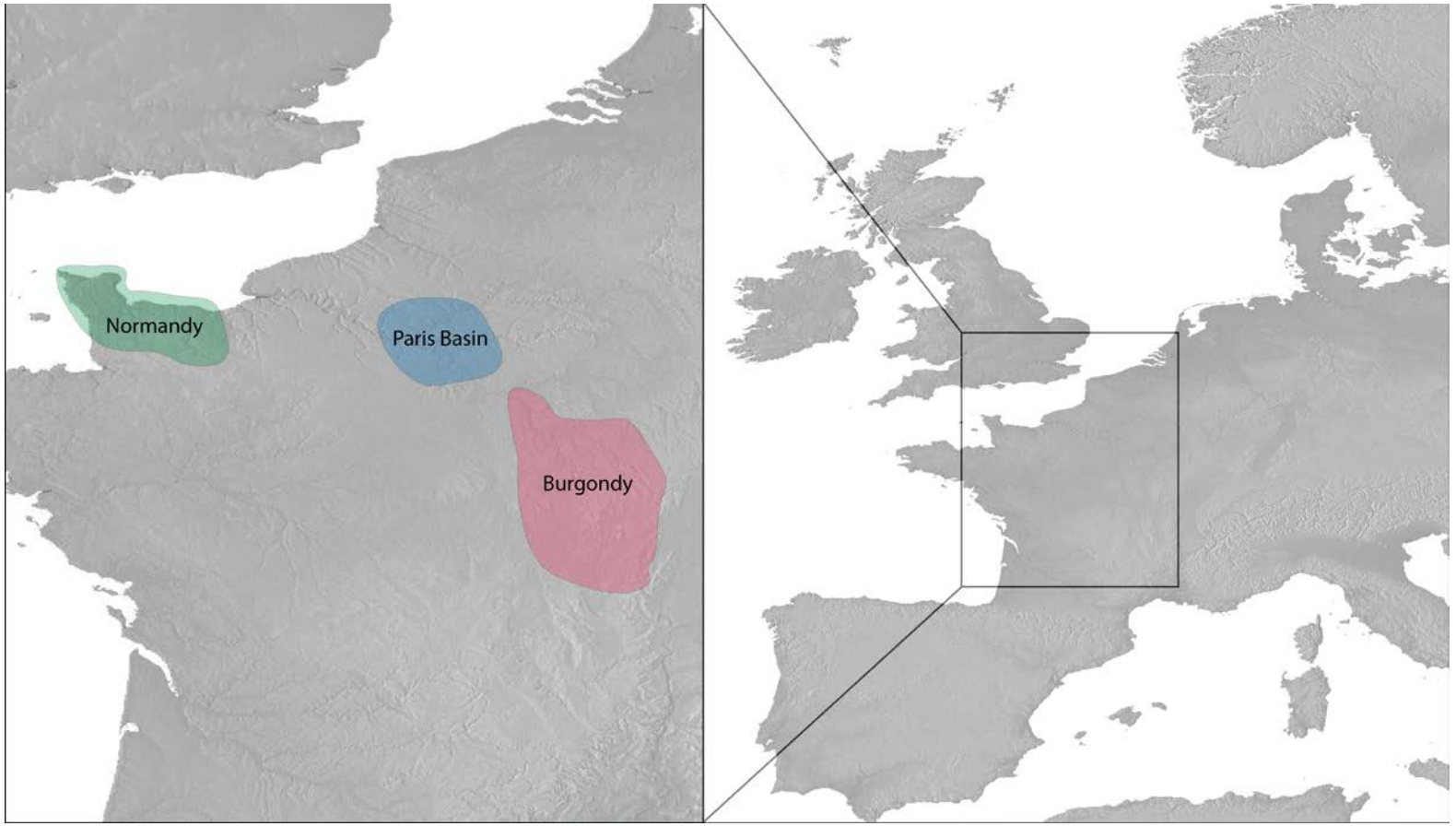

Figure 3. Map of the main regions studied in France.

4.2.2 Normandy

A large corpus of anthropological literature exists for this region of France. Roughly the north-central portion of the country, it includes most of the historical region of Neustria. Questions concerning the "peopling" of the region have been prevalent among physical anthropologists since the early 20th century. The area holds a number of Neolithic tumuli, such as Fontenay-le-Marmion, and human skeletal remains have been recovered (see Riquet, 1951; Dastugue et al., 1973, 1974; Dastugue, 1983). A number of Iron Age sites (e.g., Ifs, Soumont Saint-Quentin, and Baron-sur-Odon) with human skeletal remains have also been excavated (Dastugue and Torre, 1966; Varoqueaux, 1966; Dastugue, 1983). Focusing heavily on craniometrics, these studies typically conclude that gracile "Mediterranean types" who issued from the Danube region populated lower Normandy during the Neolithic period (Alduc-Le Bagousse, 1983: 170). Moreover, this "type" appeared to be homogeneous for centuries, exhibiting little evidence of exogenous influence (Dastugue, 1983:167).

While questions concerning human evolution and long-term migration are common for this particular region, the influence and impact of the historically attested "barbarian migrations" in Europe remain the most common topic of inquiry. Cranial morphological studies of sites spanning Late Antiquity and the Early Medieval period typically conclude that there was population continuity over time (Buchet, 1977, 1978; Alduc-Le Bagousse, 1980; Pilet, 1980; Alduc-Le Bagousse, 1983, 1985; Auboire, 1988; Pilet et al., 1990), with some authors inferring that Late Antique and Early Medieval populations were of autochthonous origins (Musset, 1963-1964; Dastugue and Torre, 1964, 1965; Alduc-Le Bagousse, 1980; Buchet and Torre, 1981; Alduc-Le Bagousse,

1983, 1985). In addition, most authors conclude that people in Normandy during the first millennium AD were morphologically homogenous, both within and between populations (Doranlo, 1921; Dastugue and Torre, 1971; Alduc-Le Bagousse, 1980, Buchet and Torre, 1981; Alduc-Le Bagousse, 1983; Pilet et al., 1990; Pilet, 1994; but see Auboire, 1988). Thus, any migration that may have occurred was insufficient to change the underlying biological substrate (Alduc-Le Bagousse, 1983:172). Furthermore, any observed morphological differences are attributed either to *in situ* population evolution (i.e., genetic drift; Dastugue and Torre, 1965; Alduc-Le Bagousse, 1985; Auboire, 1988), marriage patterns (i.e., assortative mating; Pilet et al., 1990), or sexual dimorphism (Pilet et al., 1990).

4.2.3 Burgundy

Burgundy includes the historical area of Sapaudia, which is the extreme portion of eastern France and the Swiss plateau. Due to its geographical and historical nexus between the Gallo-Romans and the Burgundian kingdom that arose in the area during the 4th century AD (Escher, 2005, 2006), it has long been of interest to physical anthropologists. Although eventually absorbed by the Frankish Carolingian dynasty in the late 8th century, the region is important since it is a well-documented case in which governmental authority and land were transferred and/or granted to a barbarian "people"—the Burgundians (*ibid*; but see Goffart, 2006). In fact, estimates for the number of people physically transferred into Sapaudia range from 5,000 to about 50,000, with smaller numbers most commonly supported (Escher, 2005: 68).

Unlike for Normandy, the skeletal morphology for the Burgundy region has overwhelmingly revolved around analyses of artificially modified crania found within Burgundian graves (Sauter, 1939, 1961; Simon, 1979; Gaillard de Semainville et al., 1978; Gaillard de Semainville, 1981; Simon, 1982; Buchet, 1988; Crubézy, 1990; Gaillard de Semainville, 1993; Castex et al., 1995; Gaillard de Semainville, 1995; Simon, 1995). These crania were proposed by some to be evidence of a racial "type"—specifically of the Huns—within the migrating Burgundians, or a result of cultural diffusion of the practice of cranial vault modification by the Burgundians themselves (however these people were defined). Thus, the presence of modified crania suggested something about the gene flow of Burgundians into the pre-existing Gallo-Roman population (but see Buchet, 1988; Crubézy, 1990). These studies were often supplemented with frequencies of other "Mongoloid" dental traits, such as dental enamel extensions and shovel-shaped incisors (Sauter and Moeschler, 1960; Sauter, 1961; Pétriquin et al., 1980; Gaillard de Semainville, 1981; Simon, 1982; Castex et al., 1995; Gaillard de Semainville, 1993)

Other studies of skeletal morphology focused on the use of cranial metrics to better understand the context of Late Antique and Early Medieval migration, the identification of physical "types", and the relative contributions of indigenous and exogenous peoples to the modern population of the region. These cranial morphological studies typically conclude that contemporaneous populations from the region share a similar suite of traits, with a few exceptions like at Sézégnin and Thoiry (Simon, 1982). These results are interpreted as representing the underlying population "type" of the indigenous Gallo-Romans at the period of Burgundian migration. Any differences are

consequently attributed to Burgundian gene flow. Regardless, most scholars argue that any migration or transfer of people to the region had little influence on the underlying biological substrate (*ibid*; but see Méry, 1968; Pétriquin et al., 1980).

4.2.4 Île-de-France / Paris Basin

Unlike Burgundy and Normandy, fewer modern studies of skeletal morphology have been broadly pursued for the Île-de-France, otherwise known as the Paris Basin. Regardless, the physical anthropology for the region shares many of the same research foci as those of Normandy and Burgundy: what was the underlying biological substrate in the region, and how did it change over time? Craniometric studies for Late Antique and Early Medieval sites are typically interpreted as showing no impact of barbarian migration on pre-existing biological variation (Auboire, 1982, 1988), thereby implying evidence of population continuity over time (Auboire, 1988). However, the authors often note greater morphologic homogeneity among females than males over time (Auboire, 1980) and an increasing frequency of brachycephalic individuals (Peyre, 1979, 1980; Auboire, 1982). The latter has been interpreted as indicating an increase of group endogamy (Auboire, 1982:72).

In contrast to studies of skeletal morphology performed for Normandy and Burgundy, the analyses for the Paris Basin are often multivariate in nature rather than typological (Menin, 1979; Peyre, 1979, 1980; Auboire, 1981, 1982, 1988). Finally, attempts to incorporate *concepts* of population structure (i.e., assortative mating, gene flow, genetic drift) are common (Auboire, 1980, 1981, 1982, 1988).

4.3.0 ANTHROPOLOGICAL GENETICS

Our understanding of prehistoric and historic European genetics derives primarily from modern genetic analyses. More specifically, the distribution of genetic markers in Europe is argued to reflect one or several expansive waves since the Late Upper Paleolithic (~40,000 ya) (Boyd and Silk, 1997), perhaps accompanied with admixture from population isolates in refugia (Torroni et al., 2001; Achilli et al., 2004). Additional influence on the distribution of modern European genetic markers likely follows the expansion north and northwestward by Neolithic agriculturalists from the Near East (Ammerman and Cavalli-Sforza, 1984; Chikhi et al., 2002; but see Novembre and Stephens, 2008). However, the relative contributions of Paleolithic and Neolithic populations to the European gene pool are still debated (but see Chikhi et al., 2002).

While the literature for prehistoric European genetics is quite rich, comparatively little has been done that assesses more recent historical events. This is perhaps due to the perceived homogeneity of modern and historic European populations, such that the use of molecular analyses to answer questions relevant to historians and archaeologists is diminished (i.e., Sokal, et al., 1989). Moreover, the particular genes or markers analyzed often have time-depths of tens of thousands of years, which are less useful for questions relevant to the more recent past, such as Early Medieval Europe (Roewer et al., 1996:1032). Other complicating factors stem from the complex patterns of genetic diversity that could arise due to a number of demographic and evolutionary factors, including genetic drift, migration, natural selection, and mutation (Jobling et al., 2004). European “archaeogenetics” focuses on questions with geographically defined scopes, such as the Anglo-Saxon and/or Viking “invasions” of Great Britain (Weale et al., 2002;

Capelli et al., 2003; Topf et al., 2006), the expansion and interaction of populations on the Iberian Peninsula (Corte-Real et al., 1996; Bosch et al., 2001; Dubut et al., 2004; Pereira et al., 2005; Peña et al., 2006; Adams et al., 2008; Ambrosio et al., 2010), and the settling of Iceland and other north Atlantic islands (Helgason et al., 2000, 2001; Mann, 2012).

Unfortunately, comparatively few studies address Frankish population structure[24]. However, recent work has shown that population history and structure for recent time periods can indeed be delineated (Zschocke and Hoffmann, 1999; Kayser et al., 2005; Varzari, 2006; Jakkula et al., 2008; Salmela et al., 2008; Nelis et al., 2009; Palo et al., 2009; Larmuseau et al., 2010; Rębała et al., 2013). These studies are compelling and show great promise for Late Antiquity and the Early Middle Ages as well. Those few studies that are relevant to Frankish population structure typically focus on three main markers[25]: Y-chromosomal single-nucleotide polymorphisms (Y-SNPs), Y-chromosomal short tandem repeat loci (Y-STRs), and mitochondrial DNA (mtDNA) (for a review on Y-chromosomal markers, see Novelletto, 2007). Y-SNPs are non-recombinant portions of the Y-chromosome, and are sensitive for investigating population movement and genetics (for modern forensic application, see Bøsting et al., 2014). However, they are slowly evolving, and so are better for studies of deeper time. For example, Lao and colleagues (2008) analyzed Y-SNPs from modern European samples and showed that southern Europe exhibited greater heterozygosity than in northern Europe. They attributed these

[24] Krawczak and colleagues (2008) provide an overview of genetic studies relevant to the "German population", though none specifically address the Franks.

[25] There exist a number of studies using anthropological genetics for populations in Western Europe. However, they are often descriptive or forensic in nature (i.e., reconstruct kinship between two skeletons) or detail modern population interactions (i.e., 16th century immigration). For examples, see Gamba et al., 2011; Grumbkow et al., 2013; Rothe et al., 2015.

results to prehistoric patterns of population expansion from southern or southeastern Europe, or to a greater effective population size in southern Europe (for the importance of the Mediterranean region, see Sazzini et al., 2014).

Y-STRs are hypervariable portions of the Y-chromosome. Unlike Y-SNPs, they are argued to be better suited "to discriminate between closely related or co-localised male populations" (Roewer et al., 2005: 280; see also Kayser et al., 2003, 2005; Ballyntyne et al., 2014). In fact, Roewer and colleagues found that there were two sub-clusters of Western and Eastern Europeans Y-STR haplotypes. They argue that these results could be related to recent historical events such as the expansion of Early Medieval kingdoms, like the Franks, in Western and Eastern Europe.

Meanwhile, Ramos-Luis and colleagues (2014) used both Y-SNPs and Y-STRs to assess Y-chromosomal diversity in French (male) populations. These authors found that very little genetic differentiation exists between regional populations in modern-day France, although a number of regions do exhibit significant inter-population differentiation based on haplogroups (*ibid*: 166). Regardless, they also show that the Brittany region in northwest France is consistently distinct from the other regional populations, presenting two interpretations for this finding: 1) founder effect followed by genetic isolation; and 2) gene flow via migratory events from the British Isles during the first millennium AD.

The migration of peoples from the British Isles to Brittany and possible admixture with native Bretons is also discussed in an earlier work using mtDNA (Dubut et al., 2004). Here, the authors show genetic affinities between British, Irish, and Bretons resulting from successive migration and admixture of these peoples in Brittany beginning

in the 4th century AD (see also Richard et al., 2007). Interestingly, Dubut and colleagues also note some qualitative (though not statistical) differences between some regional populations in France, likely stemming from demographic events during pre-history (Dubut et al., 2004: 298).

4.4.0 SUMMARY

This chapter summarized the existing physical anthropological research that relates to population structure in Frankish Europe. Although not focusing directly on ethnogenesis *per se*, physical anthropologists have explored some of the effects of migration by presumed ethnic groups, like the Franks or Huns, on biological variation. This approach typically consisted of comparing "pre-migration" and "post-migration" skeletal assemblages to search for shifts in cranial "types". Only more recently have some physical anthropologists incorporated multivariate approaches to "population" comparisons. Regardless of the particular method, most interpretations concluded that Late Antique and/or Early Medieval migrations had little impact on population variation during these respective periods. Overall, true biodistance analyses incorporating population genetics are not employed or generally supported by established physical anthropologists studying the Early Middle Ages. Furthermore, molecular analyses with a focus on medieval continental Europe are remarkably rare. Clearly, the contribution of a bioarchaeological approach combined with population genetics to the question of Frankish ethnogenesis is a timely pursuit.

CHAPTER 5

POPULATION GENETICS AND BIODISTANCE

5.0.0 INTRODUCTION

This chapter presents a summary of the discipline of population genetics. Quantitative genetic traits and their relationship to physical traits are described in detail. I also define population structure, how population structure relates to population history, and the different kinds of models that may be used to relate different parameters of population genetics. Because the biodistance analysis that I employ in this work is based on concepts of population genetics, I also summarize how they relate to each other. The methods and assumptions underlying biodistance analysis are described, and the differences between model-bound and model-free approaches are also outlined.

Finally, I describe how changes in human behavior—including those of social identification—can manifest biologically. This biosocial understanding illustrates how biodistance analyses can be used to better understand social processes. To illustrate this biosocial approach, I present examples from recent work on Yayoi ethnogenesis (Hudson, 1999), Seminole ethnogenesis (Stojanowski, 2010), Mochica ethnogenesis (Klaus, 2008), and Tewa ethnogenesis (Ortman, 2010).

5.1.0 POPULATION GENETICS

Population genetics is the branch of genetics that attempts to infer aspects of natural selection, mutation, genetic drift, rates of recombination, and gene flow at the

population level. Biodistance analysis is, in a very basic sense, the application of principles of population genetics to past populations. However, biodistance analysis relies upon a thorough understanding of evolutionary and quantitative genetics within the field of population genetics. Most importantly, a comprehension of quantitative genetics allows scholars to address a key question regarding the application of biodistance techniques to past populations: how do we know that what we are measuring reflects an underlying genetic signal?

5.1.1 Quantitative Traits and Variation

Many of the traits relevant to bioarchaeologists, such as size and shape, do not correspond to a single genetic locus on human chromosomes. Rather, *multiple* genes contribute to the physical expression of such traits (i.e., phenotype). These traits can be thought of as polygenic and are often referred to as "quantitative traits." Quantitative traits can be further conceived of as 1) continuous, 2) meristic, and 3) discrete (see Hartl and Clark, 1989: 434). Finally, due to work by Rogers and Harpending (1983), scholars now recognize that a single, completely heritable quantitative trait can be just as informative as a single biallelic marker locus for understanding population relationships, as long as that trait is selectively neutral (Relethford and Blangero, 1990: 22).

Based on numerous experimental and observational examples, scholars have shown that genotypic frequencies tend to follow a normal distribution (e.g., the central limit theorem) within biological populations, especially when the number of loci contributing to a trait is large, as is the case for many polygenic traits (Konigsberg, 2000: 136). In other words, traits like tooth size and shape, as well as cranial size and shape, are

quantitative traits based on a large number of genes found across many different loci, but whose parameters can be estimated given their normal distributions within human populations. In fact, quantitative traits have the same laws of transmission and the same general properties as discrete traits, such that "a well-chosen polygenic trait may give equivalent information as single-gene traits" (Chakraborty, 1990: 149). Consequently, genetic drift and gene flow have the same effects on quantitative traits as on discrete traits at the population level (Relethford, 1991b: 156).

Since the physical expression of a quantitative trait is based on multiple loci, each of the individual loci contributing to the trait in question can be thought of as possessing a genetic value. The sum of the genetic values across all of the loci contributing to the trait is the additive genetic variance, or σ_G^2. However, the environment (i.e., cultural practices, diet) also contributes to the physical expression of the trait in question, and thus also has a certain amount of variance, σ_E^2, associated with it. As long as environmental and additive genetic effects are independent of each other, then the population variation of the physical expression of a particular quantitative trait (σ_P^2) can be expressed as

$$\boldsymbol{\sigma_P^2 = \sigma_G^2 + \sigma_E^2} \qquad \textbf{(Eq 1)}$$

Clearly, the bioarchaeologist performing a biodistance analysis must establish that a given physical trait is comprised mostly of additive genetic effects, rather than of environmental effects. This proportion of phenotypic variance due to additive genetic effects (as opposed to environmental variance; Hartl and Clark, 1989; Konigsberg, 2000) is known as narrow-sense heritability (h^2), or

$$h^2 = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_E^2} = \frac{\sigma_2^2}{\sigma_P^2} \quad \textbf{(Eq 2)}$$

Narrow-sense heritability is thus a value that ranges from 0 to 1; the higher the value, the greater the phenotypic variance that is contributed by the additive genetic variance, which is, in turn, subject to microevolutionary processes that can be estimated. Fortunately, for many multivariate anthropometrics, the environmental contribution to phenotypic differences appears to be minimal (Jamison et al., 1989).

5.1.2 Population Structure and Population History

Most studies of population genetics fall within two broad categories: population structure and population history. Population structure is a "study of the effects of internal migration, group composition, mating practices, and other factors on the amount and pattern of genetic drift within an area" (Harpending and Jenkins, 1973: 177). It is typically performed on small and/or homogenous areas that are assumed to be at genetic equilibrium relative to gene frequencies (for examples, see Blangero, 1990; Williams-Blangero, 1989; Williams-Blangero and Blangero, 1989, 1990; Relethford, 1991a,b; Relethford and Blangero, 1990; Relethford et al., 1997; Nystrom, 2006).

Population history, in contrast, is the "study of the degree of similarity among populations" due to shared common ancestry or to mate exchange (Harpending and Jenkings, 1973: 178) (for examples, see Relethford and Blangero, 1990; Relethford 1991b, 1996; Powell and Neves, 1999; Steadman, 2001; Relethford, 2003; Nystrom, 2006). However, it could be argued that a thorough study of population history also

encompasses an understanding of population structure (see Relethford and Blangero, 1990; Relethford, 1991b; Powell and Neves, 1999; Nystrom, 2006).

5.1.3 Population Genetic Parameters and Models

There are many different kinds of quantitative genetic parameters, such as the coefficient of relationship or genetic drift, which can be estimated. Likewise, there exist quantitative genetic models for explaining the relationship among these genetic parameters and for establishing expectations of different quantitative traits. Examples of quantitative genetic models include the island model (Wright, 1951, 1969), isolation by distance (IBD) model (Wright, 1943), the stepping stone model (Kimura and Weiss, 1964), the migration matrix model (Bodmer and Cavalli-Sforza, 1968), and the neighborhood knowledge model (Boyce et al., 1967).

5.2.0 BIODISTANCE ANALYSIS

Biodistance analysis is the study of microevolutionary processes in past populations using data from the skeleton and/or dentition (Buikstra et al., 1990; Larsen, 1997). Although they have a number of goals, biodistance studies ultimately fall into two broad categories: inter-population and intra-population (or intracemetery). Inter-population studies seek to reconstruct broad patterns of population affinity, migration and settlement patterns, and population origins (e.g., Buikstra, 1980; Turner, 1986; Howells, 1995; Konigsberg and Buikstra, 1995; Relethford et al., 1997; Steadman, 2001; Stojanowski, 2004, 2005a, b). Intrapopulation analyses tend to examine either: 1) the biological structure of cemeteries based on kinship analysis (e.g., Alt and Vach, 1992;

Pietrusewsky and Douglas, 1992; Byrd and Jantz, 1994; Corruccini and Shimada, 2002; Stojanowski, 2005a), temporal microchronology (e.g., Owsley and Jantz, 1978; Konigsberg, 1990a,b), and age structure (e.g., Perzigian, 1975; Larsen, 1983; Sciulli et al., 1988); or 2) the biological variability of cemeteries, such as postmarital residence (e.g., Corruccini, 1972; Lane and Sublett, 1972; Spence, 1974; Konigsberg and Buikstra, 1995; Schillaci and Stojanowski, 2003) and total phenotypic variability (e.g., Key and Jantz, 1990). Rather than focusing on "broad, taxonomic phenotypic" comparisons, intracemetery studies treat the site as a unit of analysis, thereby avoiding typological modeling (Stojanowski and Schillaci, 2006: 50). Overall, though, biodistance is inherently populational, not typological[26].

5.2.1 Methods and Assumptions

Biodistance analysis is based on the theoretical model of mate exchange and effective population size – populations who exchange mates become more phenotypically similar over time. Phenotypic data are used as proxies for genotypic data and have a long history of use and justification within the field due to their relatively high and consistent heritability estimates (e.g., Cheverud et al., 1979; Sjøvold, 1984; Devor, 1987; Cheverud, 1988; Konigsberg and Ousley, 1995; Scott and Turner, 1997; Sparks and Jantz, 2002; Stojanowski, 2004, 2005a; Carson, 2006). A heritability (h^2) around 0.55 is common for most skeletal phenotypic variables (Stojanowski and Schillaci, 2006), while odontometrics have a standard h^2 of 0.62 (e.g., Alvesalo and Tigerstedt. 1974; Townsend

[26] As noted by Mayr (1997), a populational perspective on human variation includes an awareness of the uniqueness of particular features of a population that can only ever be estimated, but not known. Not so for a typological perspective. "For the typologist, the type (*eidos*) is real and the variation an illusion, while for the populationist the type (average) is an abstraction and only the variation is real" (*ibid*: 28).

et al., 1986; Dempsey et al., 1995; Stojanowski, 2004, 2005a). The differences in average heritability estimates is not a critical aspect to most methods used today since they are robust to all but the lowest values ($h^2 < 0.20$) (Relethford and Blangero, 1990: 23).

Most data are obtained from continuous (or metric) (e.g., Martin, 1928; Howells, 1989; Buikstra and Ubelaker, 1994; Hillson, 1996) and discrete (or non-metric) (e.g., Hauser and DeStefano, 1989; Scott and Turner, 1997) observations of the crania and dentition. While continuous traits are appropriate for most types of biodistance analyses (where preservation allows), certain discrete traits are more suitable for regional and inter-regional analyses than intra-cemetery analyses[27]. However, this division is not mutually exclusive.

There are several assumptions underlying biodistance analysis (Stojanowski and Schillaci, 2006: 51). First, it is assumed that gene flow and genetic drift will affect the frequencies of alleles between and within geographically close populations sharing related environments only when mutation rates and selection effects are held constant. Second, the archaeological human skeletal samples used must be accumulated over an extended period of time (e.g., temporal aggregates or lineages) (see Cadien et al., 1974). Third, in order to measure changes in phenotypes, the changes in allele frequencies must result in changes in skeletal traits. These changes in skeletal traits (i.e., phenotypes) must then be capable of being mathematically assessed. Fourth, since the phenotype is a product of the genotype, environment, and the interaction between the genotype and environment, it is necessary for the effects of the environment to be negligible or

[27] Those discrete traits that are rare or unusual are quite suitable for identifying closely related individuals (Alt and Vach, 1998). In contrast, traits found to be in moderate frequency in several populations are less useful for intra-cemetery analyses since they are too common to delineate between families on such a small scale (Stojanowski and Schillaci, 2006: 53).

distributed randomly across the sample. Finally, phenotypic variation should be inherited in an additive manner (e.g., Blangero, 1988; Konigsberg, 1990a,b; Relethford and Blangero, 1990).

5.2.2 Model-Bound vs. Model-Free Approaches

The earliest biological distance analyses were based on the similarity between phenotypes without a corresponding foundation in evolutionary models (i.e., model-free). They relied on statistical analogies using continuous (e.g., Mahalanobis, 1936; Penrose, 1954) and discontinuous data (e.g., Smith, 1972; for a review, see Tyrell, 2000) to model specific population structures (Relethford and Blangero, 1990: 6). However, these model-free approaches could provide no basis for assessing interregional gene flow, since any increase in biological distance was typically interpreted as resulting from stochastic processes, like genetic drift (for Early Medieval examples, see Buchet, 1978; Alduc-Le Bagousse, 1980; Pilet et al., 1990). In addition, they were primarily classificatory in nature and provided a poor representation of population history. Subsequent work by scholars such as Relethford and Lees (1982) and Harpending and Ward (1982), however, provided testable evolutionary models by which to assess biodistance. These more recent model-bound approaches estimate actual genetic parameters from the direct application of the theoretical model to the data (e.g., Williams-Blangero and Blangero, 1989; Relethford and Blangero, 1990; Relethford, 1991b, 1996; Relethford et al., 1997; Relethford, 2003). Additionally, these biodistance methods allow for better calculations of population genetic parameters. Two examples of these parameters are 1) phenotypic $\boldsymbol{F_{ST}}$ which is a summary measure of regional genetic diversity (e.g., Relethford, 1991b;

Relethford et al., 1997); and 2) genetic distance, $\boldsymbol{d^2}$, which is similar to Mahalanobis's D^2 and permits an estimation of extra-local gene flow (e.g., Relethford and Blangero, 1990; Relethford et al., 1997; Relethford, 2003). Both can be derived from an R-matrix analysis (Relethford, 1991b; Relethford, 2003).

According to Armelagos and Van Gerven (2003), though, the field of biodistance analysis today remains typological and stagnates with its focus on migration and diffusion. Other scholars disagree (for example, see Stojanowski and Buikstra, 2004), and highlight current work on regional patterns (e.g., Buikstra et al., 1990; Larsen, 1997; Relethford, 2003; Vidoli, 2012; Byrd, 2014) and intrasite/intracemetery analyses (e.g., Gamble et al., 2001; Stojanowski and Schillaci, 2006; Serafin et al., 2014). According to these scholars, regional biodistance studies can be more effective than global ones. In other words, biodistance analysis performed at the regional scale "is not concerned with population origins or broad patterns of affinity but with local demographic variables such as population size, migration patterns, population turnover or replacement, and population aggregation, and their effect on the distribution of alleles within a mating network" (Stojanowski and Schillaci, 2006: 51). Given the narrower time span and smaller geographic regions analyzed, regional biodistance analyses are more effective at controlling for the effects of environmental variance than global biodistance analyses and consequently have a stronger methodological foundation than global biodistance analyses. Finally, regional approaches can provide important information on the relationship between genetic variation and linguistic and cultural variation, which may be more useful for studying ethnicity and ethnogenesis (for an example, see Stojanowski, 2009).

5.3.0 SOCIAL IDENTITY AND BIODISTANCE

As previously discussed, ethnogenesis is a complex, social process that is historically contingent. Although traditionally approached by examining changes and patterns in material culture and ethnolinguistics, ethnogenesis can also be assessed based on diachronic changes in population structure. This is because human behavior and mate choice *at the level of the group or community* can manifest itself in changes of population structure. In other words, much as changing conceptions of group identity may result in changes in archaeologically visible material remains (i.e., stylistic variation), ethnogenesis may also result in changes in gene flow and genetic drift that can be detected using biodistance techniques. Thus, as groups of people move along the continuum of ethnogenesis, their choices, like those of mate exchange, can have striking impacts on levels of genetic drift and gene flow (Stojanowski, 2010: 58-59).

Taken in this light, then, aspects of population structure, like gene flow, can passively reflect changing beliefs and behaviors by groups of people[28]. Most importantly, though, there is no causality implied in this process. Changes in phenotypic variation, such as tooth dimensions, are unconscious, non-deliberate results of ethnogenesis; they do not cause it. Furthermore, by being passive reflections of ethnogenesis, rather than active, changes in phenotypic variation viewed through population structure are less

[28] This approach presents an alternative to Halsall's (2010: 123) reasonable complaint regarding the use of biological data. Namely, Halsall questions how ethnicity, which he views as a state of the mind, could ever be ascertained by biological remains: "Even given the unlikely discovery that 'communities of belief' like late antique ethnic groups were *so* discrete as to be identifiable with particular physical anthropological traits of DNA patterns, an entire battery of modern scientific techniques would not, were we to find Stilicho's skeleton, reveal whether, or at which points of his life, he saw himself primarily as a Roman or a Vandal"

prone to active manipulation[29]. This is not to say that biological data are completely divorced from conscious decision-making. Rather, they form a product of the negotiated and heavily symbolic process of biological reproduction. Stojanowski (2010: 55) refers to this process as a reproductive *chaîne opératoire*, an identity discourse framework that socially constrains mate choice and marriage. Ultimately, this approach builds on the practice theory of ethnic identification and ethnicity and justifies the incorporation of biological data to studies of ethnogenesis.

5.3.1 Examples

A number of bioarchaeological studies on ethnogenesis have been published in recent years. Although not an exhaustive bibliography, these studies all share in common a reliance on human skeletal remains, an emphasis on social identity theory, the integration of a temporal component, and the application of biodistance techniques to answer questions related to ethnogenesis in the past.

Yayoi Ethnogenesis

Hudson (1999) addresses the issue of Japanese identity by examining the processes of ethnogenesis from an early agricultural period to the later Middle Ages. Confronted with modern ideologies of Japanese identity (e.g., Japanese are biologically, linguistically, and/or culturally homogeneous), Hudson uses the concept of Barthian identity formation (Barth, 1969) and world-systems theory (Hechter, 1975) to show how Japanese ethnic identity arose via a protracted process of multiple (im)migrations by past

[29] Forms of body modification, such as cranial or dental, are obviously excluded from this statement.

peoples to and within the Japanese islands, as well as core-periphery interactions of the developing Yamato state.

More specifically, ancient peoples migrated to the islands during the Pleistocene. According to Hudson, these peoples were the likely ancestors to the Jomon people. However, during the late first century BC, additional (im)migrations occurred by peoples that were the likely ancestors to Yayoi peoples. Although Hudson uses a comparative, phenetic approach and not a model-bound biodistance approach, he successfully shows how craniomorphology, dental morphology, and (to a lesser extent) modern DNA comparisons establish a distinct difference between skeletal assemblages attributed to the Jomon and Yayoi Periods. Furthermore, he points to evidence for admixture as well as gene flow and genetic drift in the current distributions of modern Japanese and indigenous Ainu and Okinawan populations. Finally, he bolsters these observations with linguistic and archaeological evidence, as well as evidence from changing patterns of body modification.

Hudson uses this foundation of population history to establish the importance of the distributions of people and agricultural subsistence systems to the eventual rise of the Yamato state in the 3rd-7th centuries AD. He argues that the interaction of the Yamato core with non-Yamato periphery—whether defined ideologically, politically, or economically—played a critical role in the eventual formation of Japanese "ethnicity" (*ibid*: 193). Ethnic differences in core regions were downplayed to emphasize state unification, while differences between those allied, assimilated, or identified with the Yamato with those who opposed to Yamato expansion (whether passively or actively) were institutionalized (*ibid*: 203-204). This core-periphery interaction is especially

interesting since many of those peoples included in the periphery were descendants of the original proto-Jomon migrants to the islands, regardless of the amount of admixture that occurred with immigrating Yayoi peoples.

Seminole Ethnogenesis

Stojanowski's (2001, 2004, 2005a, b, 2010) work on Southeastern Indians is particularly thorough and nuanced, using biological, archaeological, and historical data. With an eye on changing social identities in native and Spanish communities of Spanish Florida, he interprets various data sources within a social identity framework. More specifically, Stojanowski draws upon concepts of ethnic identity theory (Barth, 1969; Bentley, 1987; Jones, 2002), ethnogenetic life-cycles (Hickerson, 1996), material culture style (Voss, 2005), and historical ethnography (Hill, 1996) to understand changing patterns of regional phenotypic variation before, during, and after European contact in Spanish Florida. This goal was accomplished by collecting measurements on tooth size from a series of samples dating to pre-Spanish contact, early Spanish contact, and late Spanish contact. Using model-bound biodistance techniques, these odontometric data were analyzed using R-matrix methods that emphasized microevolutionary forces of genetic drift, gene flow, and migration to understand transformations in phenotypic variation.

Perhaps most importantly, though, was Stojanowski's compelling argument, and ultimately successful demonstration, for the cautious use of changing regional phenotypic variations as a signal for changes in social identities. More specifically, he argues that phenotypic variation is reflective of the choices made by individuals and groups (*ibid*:

55). Thus, microevolutionary forces and social practices of intermarriage, migration, and isolation can be bridged by using symbolically "invisible" reflections of human action (i.e., tooth size).

Mochica Ethnogenesis

Klaus's (2008) stated goal was to provide an initial description of the effects of culture contact and change on the health, diet, activity patterns, social structure and patterns of phenotypic variation of indigenous peoples in the Central Andes of Northern Peru. He uses the data to show how an existing Mochica group identity was transformed, actively and passively, through contact with Spanish colonialism. These interpretations formed just one part of an ambitious survey of burial patterns and skeletal remains for more than 1,000 individuals over a period of 850 years (*ibid*: 2).

Although his goal was broader than just an assessment of population structure, Klaus collected dental measurements from pre-Hispanic and contact-period samples and used model-bound biodistance techniques to generate estimate of gene flow and genetic drift (*ibid*: 354). Observing comparatively high amounts of between- group phenotypic diversity between pre-Hispanic ethnic Sican and Mochica groups, he argues that both groups differed by mating and possibly migration practices (*ibid*: 565). Furthermore, he showed how this pattern of elevated diversity reversed in the postcontact sample, when estimated genetic heterogeneity declines dramatically (*ibid*: 567). Klaus interprets this decline in between-group variability in two ways: 1) as a product of the effect of genetic drift as the population declined over time; and 2) as a result of changes in traditional

mating networks via processes like aggregation and an imposed religious system that aimed to control indigenous sexuality (*ibid*: 580).

Ultimately, Klaus suggests that the increase in genetic homogenization over time was a process of ethnic hybridization aided by Spanish economic and colonial policies. Specifically, strategies of population relocation and aggregation and imposed concepts of domestic spaces (e.g., *reduccion*) encouraged adaptive responses of mate exchange by the Mochica (*ibid*: 582). Although Klaus does not discuss social identity theory or establish an ethnogenetic framework by which he interprets these data, he does invoke a two-stage model of ethnogenesis by which groups first fused or amalgamated biologically (or "hybridized", see *ibid*: 586), followed by a second stage that involved syncretic Euro-Andean ritual and material domains.

Tewa Ethnogenesis

Interested in the intersections and disjunctures of biology, language, and culture, Ortman (2010) uses the mystery of Tewa origins as a means by which to explore ethnogenesis in prehistoric peoples. Specifically, Ortman argues that biology, language, and culture operate under different kinds of inheritance systems (*ibid*: 22). Much like Hudson (1999), Ortman also invokes the notion of Barthian identity formation and maintenance (Barth, 1969), as well as practice theory (Bourdieu, 1977; see also Jones, 1997), to support his argument for emphasizing cultural models of group identity over specific characteristics of group identity (i.e., objective group traits) (Ortman, 2010: 25-27).

To illustrate his approach, Ortman considers the sudden depopulation around AD 1275 of the once-densely populated area of southwestern Colorado and southeastern Utah (e.g., Mesa Verde region), the dramatic and concomitant increase in population of northcentral New Mexico (e.g., Rio Grande region), and the relationship of these processes to the ethnogenesis of modern Tewa peoples. Based on raw and aggregate data from more than 1200 individuals from 120 different sites (*ibid*: 164-169), he used model-bound biodistance techniques to show how post-AD 1275 Rio Grande region peoples were more similar to each other and to populations from the Mesa Verde region, than to peoples from the pre-AD 1275 Rio Grande region (*ibid*: 207). Furthermore, he shows that evidence for admixture is mixed between indigenous Rio Grande peoples and presumed immigrants from Mesa Verde peoples, and that genetic drift alone cannot account for differences in phenotypic variation in the Rio Grande region over time (*ibid*: 208).

With these patterns in mind, Ortman maintains that immigration and admixture—witnessed via the biological and linguistic data—formed an important part of the developing Tewa identity in the Rio Grande region after AD 1275. They molded part of a shared experience of migrants that included violence, upheaval, migration, and public surveillance (*ibid*: 596). Even the apparent lack of continuity in material culture over time can be understood as part of a negotiated discourse. Specifically, Ortman argues that changes and hybridization in material culture and practices reflect negotiated discourses that were enacted via the mechanisms of a religious movement (*ibid*: 621). Thus, Tewa ethnogenesis can only be understood by examining all of these facets together, especially when certain lines of evidence contradict each other.

5.4.0 SUMMARY

This chapter showed how a fundamental understanding of quantitative genetics could be used within the field of population genetics to estimate different parameters, such as gene flow and genetic drift. More specifically, certain measurable traits, like tooth dimensions, have an underlying heritable and quantitative nature that can be assessed at a supra-individual or population scale to reconstruct population structure and history. Ultimately, these concepts, as well as a theoretical model of mate exchange and effective population size, form the foundation of the model-bound biodistance analysis used in this study. Finally, and perhaps most importantly, this chapter provided a framework for understanding how human behavior could impact biological variation. No discussion of social identity could be possible without this critical linkage between behavior and biology. To illustrate this biosocial approach, a number of case studies were provided that used biodistance analyses to explore aspects of ethnogenesis.

CHAPTER 6

RESEARCH EXPECTATIONS

6.0.0 INTRODUCTION

Chapter 2 provided a summary of current theoretical approaches to ethnogenesis, including group fission and fusion, cultural accommodation and adaptation, group power differentials, to name a few. However, there is one heuristic style in particular—ethnogenetic life-cycles—which provides the framework used in this study. Emphasizing the transformative nature of ethnogenesis, Hickerson (1996) describes three phases in the creation and maintenance of ethnic groups: separation, liminality, and reintegration. These life-cycle transitions mirror those first developed by van Gennep (1909), who proposed that many of important rites of passage, such as marriage or death, in human societies share a common tripartite structure (e.g., separation, liminality, reintegration; see also Metcalf and Huntington, 1991:29-30).

Although van Gennep developed his schema of changing life stages in the course of studying Malagasy rituals, especially those surrounding death, his work clearly influenced the field of symbolic and interpretive anthropology (i.e., Turner, 1969; Geertz, 1973), as well as Hickerson's ethnogenetic life-cycles. This chapter, then, presents a description of each life-cycle phase and the expectations for population structure during these phases. I also discuss the historical and archaeological data used for assigning a particular phase to a time period[30].

[30] This latter approach is not intended to imply a strict adherence of specific time periods to specific life-cycle phases. Indeed, there is considerable "fuzziness" at the transitions between phases, much as there is

6.1.0 SEPARATION PHASE

Hickerson (1996: 70) describes the separation phase of ethnogenesis as one in which existing group loyalties disappear or are severed. Thus, in her example of the Jumano, regional and even long distance trade partnerships served as an existing mechanism to fuse any number of semi-nomadic hunters, traders, and pastoralists together during pre- and early-Spanish periods of central Texas (*ibid*: 72-73). These mechanisms were also combined with an implied similarity in culture and language, such that Spanish ethnohistoric documents could refer to "the Jumano". However, a period of intermittent but protracted warfare with "Apache" peoples would strain these Jumano ethnic connections during the 16th and 17th centuries AD (*ibid*: 74-79). Specifically, the Jumano were displaced from their territories, lost access to their hunting grounds, and lost access to trading routes and partners.

Similarly, Stojanowski (2005) proposed that a number of violent uprisings by indigenous peoples of *La Florida* and directed toward the Spanish are consistent with the separation phase of Hickerson's ethnogenetic life cycle. These uprising represent "tension internal to the Spanish system, caused by the ensuing demographic and social transition and resulting tribalization of communities competing for resources, whether they be actual or perceived (power)" (*ibid*: 426). In other words, Spanish reorganization of indigenous populations into the mission system (*congregacion* and *reduccion*), a decline in population sizes due to disease and poor health, a breakdown of shared aspects

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significant "fuzziness" between transitions and transformations from the Late Roman to Early Medieval world. People living during the 5-6th centuries AD, for example, could hardly be expected to view their lives during the transition from Late Antiquity to the Merovingian Period to be any more significant than how they lived the previous 50-100 years.

of social organization, and a shift in competition for resources resulted in the negation or severing of pre-existing group loyalties and socially integrating mechanisms.

6.1.1 Late Roman Period

In the same manner, several aspects of the Late Roman Period likely disrupted social mechanisms that once served to integrate "barbarian" groups. These events include 1) the effects of Hunnic expansion in the east during the late 4th century (Gibbon, 1830; Heather, 1995; Thompson, 1996; but see Goffart, 2006); 2) the successful (though short-lived) immigration of the Goths into the Roman Empire in AD 376 (Mócsy, 1974; Wolfram, 1990; Goffart, 2006); 3) the increasing importance of military support, especially of barbarians, in internal Roman disputes (Elton, 1996; Dixon and Southern, 2014); 4) the effects of nascent Christianization in the provinces (Hillgarth, 1986); and 5) the contraction of the Roman Empire and changing patterns of trade (Brather, 2005; Goffart, 2006; Halsall, 2010). Although referencing specific groups along the Danube, Goffart sums up this period of social disruption in the following manner:

> The Empire that supplied them with prestige goods that their leaders had come to rely upon was receding from the old frontiers and withdrawing to its core Mediterranean lands… [T]wo influences on the mid-Danubians acquire importance: a serious deterioration in the conditions of life along the Danube owing to disruptions of trade and gift exchanges with the Empire; and the sense that Rome, dependent on alien troops and receptive to alien labor was less restrictive to immigration than in the past. The mass admission of Goths had changed the outlook for life north of the Roman border. Once the door to the Empire was opened wide (even if shut again), life in *barbaricum* was profoundly devalued. (Goffart, 2006: 87)

Archaeologically, this period of change is distinguished by the adoption of a new burial rite across northern Gaul. According to Halsall (2010: 103) this was "basically the traditional late Roman funeral custom but with the addition of more lavish grave-goods." Many of these lavishly furnished burials (*früstengräber*) included symbols of authority, often that of military authority (Halsall, 2010: 103-106; see also Theuws, 2009). Due to intermittent and declining imperial presence in northern Gaul, a socio-political vacuum was created in which local elites—whether Roman, barbarian, civilian, or military—used grave goods to compete for community leadership (Halsall, 2010: 103-106; see also James, 2014: 117). Both Halsall (2010) and James (2014) argue that these changes in burial practices signal a period of social stress and political insecurity.

6.2.0 LIMINAL PHASE

During the liminal period, any surviving social and/or economic ties are severed, and alternative connections are forged (Hickerson, 1996: 70). In other words, group identity is being actively renegotiated in such a manner to emphasize new in-group similarity. For the Jumano, Hickerson points to this renegotiation in the form of active alliance-seeking and trade solicitation during the 18th century (*ibid*: 79-83). Additional groups, mainly the Apache, increasingly absorbed those that did not migrate or relocate when faced with warfare and territory loss. Others appeared to have successfully allied themselves with Spanish missions and towns, while still more maintained ties to friendly confederacies further east (*ibid*: 82). These eastern ties are thought to have brought bands of Kiowa into contact and perhaps eventual merger with those of the Jumano (*ibid*: 83).

Using the example of indigenous peoples in *La Florida*, Stojanowski (2005) showed how an intensification of repopulation and relocation of previously Christianized populations along the *camino real*, or mission road, followed the devastating declines in population sizes due to disease and fugitivism (*ibid*: 426). Increasing demands for labor by Spanish authorities only intensified the frequency of fugitivism, as many indigenous males fled to areas far from the reach of Spanish colonial taxation. According to Stojanowski (*ibid*: 426), this process of relocation and demographic collapse essentially produced a "motive of opportunity" for mate exchange in mission villages beyond the prescriptions structuring social norms between groups. This emerging 'hybridized group coalition' (*sensu* Albers, 1996: 93) could then be said to reflect a social adaptation by indigenous communities in this postcollapse environment (Stojanowski, 2005: 426).

6.2.1 Early Frankish Period

Although there is no evidence in the early Frankish Period for a dramatic demographic collapse or forced relocation as in the example by Stojanowski (2005), new and active forms of social integration were being negotiated by people, especially those inhabiting the northern region of Gaul. Starting in the mid-4th century, although possibly earlier (see Wood, 1993: 38), a multi-ethnic confederation of people, the "Franks", were firmly established in what is modern-day northern France, Belgium, and southern Netherlands. By the mid-5th century, one particular family of this multi-ethnic confederation—the Merovingians—rose in dominance, eventually uniting most of Gaul in the 6th century. Their rise and consolidation in power thus began in the Late Roman Period (i.e., Separation Phase) and extended to the middle of the Frankish Period.

The Merovingian dynasty cultivated a complex ideology, one that combined elements of the Roman past. Thus, elaborate burials of locally power families included symbols of Roman or martial authority (Halsall, 2010: 211-212). Similarly, Roman law codes and administrative systems relying on the *civitates* were maintained, although not uniformly across the kingdom (Wood, 1993). Yet, this ideology also emphasized new elements of integration. These included 1) a new origin story[31] (Goffart, 2006: 18; Wood, 1993: 33-35; Broome, 2014: 37-43); 2) further incorporation and expansion of Christianity throughout the kingdom[32]; 3) the establishment of new trade routes, goods, and emporia (i.e., Dorestad, Quentovic) (Wood, 1993: 295-299); 4) marriage alliances (Crisp, 2003); and 5) the centripetal nature of internal Merovingian politics (Wood, 1993: 88-102, 140-159, 221-239).

Indeed, this latter point was elaborated by Wood (1993), who argued that "the authority of the Church, and particularly that of the bishops, was connected with the power of the king, especially in the urban centres of the Frankish kingdoms (*ibid*: 71). Similarly, the landed elite, whether Gallo-Roman, one of the multi-ethnic groups comprising the Frankish confederacy, or members in any of the Merovingian *teilreichen* (i.e., Neustria, Austrasia, Burgundia), relied on royal patronage.

> The relationship between the centre and periphery in the Merovingian kingdom was thus extremely complex, because the connections between the two regions were exploited by the Gallo-Roman aristocracy and by the northern rulers for their own ends up until the eighth century. There was,

[31] It could be argued that the elements of the story—one that traces the Frankish origins to Troy—were not actually new. However, the narrative and the message being conveyed were new. See Broome (2014: 37-43).

[32] Commonly, though perhaps inaccurately, attributed to the conversion of the Merovingian king, Clovis I, in AD 496.

> therefore, a balance between court and country, and the civil wars helped to maintain this balance, by providing a central focus for local conflict. Certainly the civil wars were destructive… Nevertheless, the Merovingian civil wars did not pose a threat to the survival of the kingdom. Indeed, in a sense, they were a unifying part of the structure of the Frankish state in the sixth century and for much of the seventh. (Wood, 1993: 101)

Marriage alliances also served to unite those living in the Frankish realm, perhaps in line with maintaining the focus of social and political interactions on the royal court (Crisp, 2003). Thus, rather than serving the goal of creating peace, these marriages served to bolster the royal status of the Merovingian dynasty. Specifically, "marriages to prestigious foreign spouses raised a king's status in the eyes of his follower, which allowed him to assert greater control over the resources of his own kingdom, and beyond (*ibid*: 225).

6.3.0 REINTEGRATION PHASE

The reintegration phase is characterized by a shared ideology that is used to validate the emergent identity Hickerson (1996: 70). In other words, rituals and associated mythologies (usually an origin story) are developed and maintained. In some cases, they may be used to "overwrite" existing histories. She points to traditional Kiowa histories that reveal a syncretic emergence myth of the tribe, one that emphasizes the composite nature of the Kiowa people themselves (*ibid*: 83-85). Likewise, the possible fusion of the Jumano, and any number of other groups, with the Kiowa produced diverse rituals in which these disparate peoples would participate. These iterative practices ultimately promoted group cohesion and identity and eventually helped shape the nature of Kiowa ethnicity.

In his example of indigenous peoples in *La Florida*, Stojanowski (2005) points to the possibility for this to have occurred. However, the reintegration phase of this ethnogenetic process among indigenous peoples actually subsided or was curtailed due to changing global politics between the Spanish and English (*ibid*: 428). Ultimately, the internalization and reification of an emergent ethnic identity implied by events (both circumstantial and necessary) in the liminal phase collapsed as the Spanish mission system finally contracted. The resulting diaspora of indigenous peoples eventually split along pre-contact ethnic lines, suggesting the persistence of ethnic identity and the transient nature of the liminal identity that was in the process of forming (*ibid*: 427).

6.3.1 Late Frankish Period

The late Frankish Period included a dynastic shift (i.e., coup) from Merovingian to Carolingian rule. In AD 751, the last Merovingian king was exiled to a monastery, and the former mayor to the palace, Pippen III, was crowned king. Under the Carolingians, much of the administrative aspects of the kingdom (*civitas*) continued as they had been under the Merovingians. Likewise, the role of Christianity in the kingdom followed in the same direction as implied under the Merovingians. The Carolingians even used the same or similar origin story as their predecessors (Broome, 2014).

However, a focus on the similarities not only masks changes, but it also obscures the intensification of these changes (see Reimitz, 2008). For example, Carolingian authors still used Trojan origins as the basis of Frankish community (Goosmann 2013: 55-56). Yet, they also added to it and emphasized a narrative of Frankish community that *began* with the Carolingian rise in power. In other words, just as “Merovingian authors

tied the emergence of their rulers to the origins of the Franks, so Carolingian authors were imagining a community that emerged from the actions of its rulers" (Broome, 2014: 35).

Overall, both the Merovingian and Carolingians had complex ideologies that impacted many political and social aspects of their kingdom, as well as influenced the maturing concept of Frankish identity. However, the form of Frankish identity that coalesced under the Carolingians appeared more definitive than what was present in the early Frankish Period (McKitterick, 1983; Reimitz, 2008; Broome, 2014). Arguably, the "hardening" of this once viscous Frankish identity was promoted by a Carolingian ideology that emphasized unity, loyalty to the king, and religion. Thus, this ideology included 1) an appropriation of a mainly western Frankish history (i.e., Neustria) to the exclusion of the other *Teilreichen* (i.e., Austrasia, Burgundia) (Reimitz, 2008: 64-65); 2) the absence of references to, or de-emphasis of, internal divisions in the Frankish kingdom (Broome, 2014: 83); 3) the institutionalization of Frankish identity in Carolingian capitularies and law codes (Nelson, 2008: 81-83); 4) an increasing emphasis on Christianity and Christian behavior (McKitterick, 2004: 245-264; Halfond, 2008: 215-216; Broome, 2014: 87; see also McKitterick, 1977); and 5) the purposeful definition of Frankish territory and integrity, and the use of armed conflict to achieve or maintain it (Bachrach, 2001, 2013; see also Broome, 2014: 83, 87, 98-150).

6.4.0 POPULATION STRUCTURE

On the basis of the summarized ethnogenetic life-cycle described above, as well as well as historical and archaeological knowledge of the transition from Late Antiquity

through the Early Middle Ages, several expectations concerning population structure can be generated.

1) **I expect a difference in population structure for groups in the north and south of Gaul.** Archaeologists and historians have often pointed out the differences that occurred between northern and southern Gaul. Much of the Roman administrative system based on the *civitates* in the south remained unchanged when the Frankish confederation was settled in the north and solidifying their position of authority. Indeed, some provinces in southern Gaul, such as Aquitaine and Burgundy, were not conquered until the early- and mid-sixth century AD, respectively. These differences have the potential to impact many aspects of population structure, both synchronically and diachronically.
2) **I expect that inter- and intra-group phenotypic variation to be high in the Gallo-Roman Period.** The presence of barbarian confederations and Gallo-Roman settlements imply a high degree of inter- and intra-group genetic variation.
3) **I expect that inter-regional phenotypic variation will be lower in the Merovingian Period than in the preceding Gallo-Roman Period.** As existing social ties break down, and new forms are forged, genetic variation between groups will decrease.
4) **I expect that inter- and intra-regional phenotypic variation will be low in the Carolingian Period.** As a new group identity more fully coalesces, inter-regional phenotypic variation will decline relative to the previous periods.

5) **I expect that Late Roman populations experienced greater levels of extra-local gene flow than those in the Merovingian and Carolingian Periods.** I also expect this pattern to change as Frankish identity develops over time.

These expectations are not intended to predict all changes in population structure in an exhaustive manner. Rather, the goal is to establish theoretically informed expectations that promote further explorations.

6.5.0 SUMMARY

In this chapter, I described the main ethnogenetic model employed in this study and the historical and archaeological data supporting each phase. In the Separation Phase, existing group loyalties are severed. When viewed through an historical lens, several aspects of the Late Roman Period, such as Hunnic or Gothic expansion or migration, likely contributed to a large degree of social disruption. During the Liminal Phase, alternative social and/or economic ties are forged. This phase is consistent with many syncretic characteristics of early Frankish administration and ideology. Finally, during the Reintegration Phase, an emergent identity is validated by a shared ideology, much like the rhetoric of Frankish identity during the later Frankish Period. Finally, the generalized expectations for changes in population structure were outlined.

CHAPTER 7

MATERIALS

7.0.0 INTRODUCTION

This chapter outlines details on the materials used in this study. Primary skeletal collections, from which all odontometric data were generated, include the following sites: Frénouville, Giberville, Sannerville, Réville, Verson, Larina, La Granède, Champlieu, Chelles, Mareuil-sur-Ourcq, and Précy-sur-Oise. Archaeological details on these sites were generated from published and unpublished reports (i.e., archaeological field reports, physical anthropological reports) (see Table 1). All sites date to the Late Antique and/or Early Middle Ages, whether based on relativistic dating methods or on absolute dating methods (i.e., radiocarbon). The use of relativistic dating was very common in the mid-to-late twentieth century, and it is still considered an acceptable means of dating material due to well-established dating sequences (i.e., numismatics). Most of these reports stemmed from excavations and analyses during the 1970s. Consequently, details that are pertinent for modern research questions and relevant to more recent (bio)archaeologists are often lacking or are arguably dated in their interpretations. However, they still present valuable insights, which are discussed below and summarized in Table 2.

Secondary skeletal collections include contemporaneous sites from the same regions as those in the primary skeletal collection (see Figure 4). The goal of such an enterprise was largely to elucidate any additional information about changes in phenotypic variation. While the raw craniometric data, sex estimates, and age estimates

were mined from published and unpublished anthropological reports, information on each site or, in some cases, museum collection (e.g., grave goods, grave orientation), was not possible given their large number.

Figure 4. Map of the skeletal collections used in this study. Sites are grouped by region: Green=Normandy, Blue=Paris Basin, Yellow=Rhône-Alps, Orange=Midi-Pyrenées.

Table 1

Odontometric Collections

Site Name	Associated Reference(s)
Frénouville	Buchet, 1977, 1978; Pilet, 1980; Carver, 2012
Granède	Naji, 2011; Saint-Pierre et al., 2011; Carver, 2012
Larina	Porte, 1984, 2011; Carver, 2012
Champlieu	Viollet le Duc, 1860; Broca, 1864; Cauchemé, 1900-1902; Durand, 1986; Carver, 2010
Chelles	Broca, 1864; Cauchemé, 1900; Malsy, 1972; Carver, 2010
Mareuil-sur-Ourcq	Verneau and Ripoche, 1898; Auboire, 1982; Carver, 2010
Précy-sur-Oise	Duvette, 2000, 2001; Gressier, 2001; Derbois, 2003, 2004; Redjeb et al., 2005; Carver, 2010
Réville	Scuvée, 1973; Buchet and Torre, 1981; Carver, 2012
Sannerville	Pilet, 1983; Pilet et al., 1992; Carver; 2012
Verson	Alduc-le Bagousse, 1980; Lemière and Levalet, 1980; Carver, 2012
Giberville	Pilet, et al. 1990; Carver, 2012

Note: Those references marked as Carver (2010) or Carver (2012) were observed personally by the author in the year indicated.

7.1.0 PRIMARY SKELETAL COLLECTIONS

7.1.1 Normandy

Frénouville

Excavated in 1970, the site of Frénouville covers roughly one hectare and is located in a field near the modern village of the same name in Lower Normandy. Over 650 burials from the late 3rd century AD until the end of the 7th century AD were uncovered (Figure 5). The long occupation of the site is manifested on the ground by a "radical difference" in the orientation of the graves: those in the south portion of the cemetery are oriented north-south, while those in the north portion of the cemetery are oriented east-west (Pilet, 1980: 2). Surrounding the necropolis is the medieval church of St. Martin, a Roman road linking Vieux to Lisieux, two Roman villas, and the ancient village of Criquetot.

Despite the close association to the St. Martin church, there does not appear to be any link between the cemetery adjacent to it and discoveries at Frénouville (*ibid*: 2). According to regional archaeologists, it is common to find two Merovingian-period cemeteries in close proximity with each other – one isolated and located more remotely in the countryside, the other located around the village or settlement church. Numerous churches in Normandy at this time were founded and dedicated to St. Martin, and the apparent abandonment and foundation of new cemeteries is probably related to this process of church foundation and relic pilgrimages (*ibid*: 4). Pilet also speculates that this cemetery "shuffling" may be related to a re-Christianization of the region during the Early Middle Ages (*ibid*: 4).

Historically, the site of Frénouville is known to have had Frankish influence, but its Gallo-Roman origins are also noted (*ibid*: 4, 171). Evidence from toponyms attests to the mixture of Frankish and Gallo-Roman influences (*ibid*: 5). However, there is delayed evidence of Frankish influence relative to other areas known historically to be occupied/ruled by the Franks (*ibid*: 172). Pilet suggests that early Frankish arrivals may have been rebuffed by the coastal zone that offered little economic advantage, or possibly by a pre-existing Anglo-Saxon presence (*ibid*: 172).

Grave reuse is rare in the Gallo-Roman sector of the cemetery (i.e., those burials oriented north-south) and quite common in the Merovingian sector of the cemetery (i.e., those burials oriented east-west). Consequently, of 650 burials, roughly 801 individuals were identified anthropologically, while many graves were void of any human skeletal remains (*ibid*: 6, 7). Although preservation was poor, the majority of the skeletons were supine, arms extended along the sides or gathered on the pelvis.

Grave organization is seemingly disordered, but does possess a certain amount of patterning (*ibid*: 7). Clearly remarkable is the change in orientation of the graves mentioned previously. Also of note is the presence of a possible charnel house and Gallo-Roman villa. The edges of the cemetery are fairly well delineated, despite the fact that nothing in the actual topography of the site can explain the abrupt halt in horizontal extent (*ibid*: 7). Often, short rows and groups of graves are visible and for those oriented north-south may be explained by the manner of excavation as well as by evidence of above-ground markers in the form of stelae and wooden stakes (*ibid*: 8).

Preservation of grave goods and other material remains is quite poor. In fact, Pilet (1980: 8) remarks on the overall evidence for “calm and stability” in the material

remains. For those graves attributed to the end of the 3rd through the first quarter of the 6th century, material remains consist almost exclusively of metallic, glass, or ceramic dishes, belt buckles, knives, tweezers, scissors, keys, sac bands, necklaces, bracelets, and fibulae (*ibid*: 9). For those graves attributed to the second quarter of the 6th century, there are a number of weapons. Pilet (1980: 8) takes this as evidence of the general integration of these "arm-bearers" into a generally peaceful community. Also of note is the presence of five cupeliforme fibulae that are Anglo-Saxon in style, seeming to confirm links between Kent and the lower Norman coast at this time period (*ibid*: 8, 171).

The overall impression, however, is that Frénouville was "a small village of middling economic importance", as evidence by the near total absence of precious metals (*ibid*: 170). Anthropologically, 163 Gallo-Roman skeletons (137 adults, 26 sub-adults) and 638 Merovingian skeletons were observed (617 adults and 21 sub-adults), although considerably less were sufficiently preserved to allow further analysis (Buchet, 1977, 1978). Regardless, Buchet finds no evidence of "foreigners", as based on craniometrics. In fact, he argues that the Gallo-Roman population at Frénouville was no different than the population of Fontenay-le-Marmion II (3500 BC). Likewise, he concludes that there is nothing to suggest that the Merovingian population is any different than the Gallo-Roman population. In other words, populations in Normandy were quite homogeneous and had their origins in the Neolithic.

Figure 5. Plan of the cemetery at Frénouville (adapted from Pilet, 1980).

Giberville (Le Martray)

Giberville was excavated between 1975 and 1980. Consisting of two cemeteries, one is located around the church of Saint Martin, the other is located around the church of Saint-Germain (Le Martray). Both are in proximity to settlement ruins from the 4th-6th centuries, suggesting that the community at that time was split into two nodes (Pilet et al., 1990: 12).

There are an estimated number of 482 graves, 394 of which were excavated at Le Martray (Figure 6). Such elevated numbers of graves are similar to other contemporaneous sites, like Frénouville. Although in a slightly different manner as Frénouville, the graves are organized by groups into irregular rows of pits. Unfortunately, the majority of the graves were pillaged in antiquity, yet it is evident that the dead were interred with heads to the west and feet to the east. Likewise, individuals were placed supine with their arms extended alongside the body or joined over the pelvis, and only rarely crossed on the chest. The sole exception to this mortuary practice is individual 253 who is buried on the right side.

Despite the abandonment of the cemetery at the end of the 7th century, there is a well-preserved funerary enclosure evident at the site, which is indicative of a *martyrium*. Other indications of mortuary practices include funerary meals and fires—practices thought to be exclusive to the Gallo-Roman Period. However, the cemetery itself was only used for two centuries—from the end of the 5th to the end of the 7th century. Given that the dating of the cemetery is based primarily on material culture, the superposition of graves, and aspects of grave orientation, excavation, and depth, it is of course possible that the dates for use are broader than first indicated.

Unlike Frénouville, the cemetery is oriented around two contemporaneous groups of “founding graves” spaced apart from each other by approximately 30 meters. The first founding group located in the south central portion consists of the following burials: 29, 37, and 3A. The second founding group located in the north central portion consists of the following burials: 283, 286, and 289. The most well preserved portion of the cemetery is for the first group. Within it are groupings of notable burials with material culture like swords and an axe. Burial 29 is considered the cemetery founder, a male, and is surrounded by a palisade. Burials 28 and 30 overlap and cut into the circular ditch of the palisade. There is also a rectangular enclosure to the west and to the east of the cemetery founder, as indicated by postholes. These contain burials 37 and 294 respectively. Other postholes exist, as well as stelae, demonstrating their use as grave markers. Unfortunately, poor skeletal preservation prohibits the evaluation of kinship based on the apparent groups within the cemetery.

Remains of material culture are fairly common at Giberville, and the authors assert that social status can be inferred based on the large number of graves containing “rich” grave goods. Interestingly, one grave, although pillaged, still contained the remains of a yew bucket with Gallo-roman motifs engraved on it. Other evidence of Gallo-roman material culture was present in burials 153 and 67 and consists of buckles and belts. The authors state that local stationing for Roman troops near Giberville would have been Bénouville (Pilet et al., 1990: 33). Giberville itself is at least seven kilometers straight-line distance from this Roman encampment with evidence of Roman baths along the bank of the Orne River. Nothing else is known about the organization or the length of

use of Bénouville, although the military installation likely continued to play an important role after the withdrawal of the army.

Evidence for Anglo-Saxon contact is also present at Giberville, consisting of female burials with Anglo-Saxon style fibulae. Likewise, there is a cremation in grave 294, which the authors also argue is evidence Anglo-Saxon influence. The founder of the second group is surrounded by the following graves: 283, 286, 289, and 178. The development and organization of this group is harder to reconstruct due to the number of secondary interments and pillaging that occurred. Postholes do suggest, however, the presence of a rectangular wood building, the perimeter of which was interrupted/cut by burials 206, 207, and 209. Grave goods include buckles and coins from Justinian's reign. According to the authors, these material remains suggest the presence of nobles (Pilet et al., 1990:35). The presence of other goods like goblets, jewelry, and fibulae, is interpreted as signs of wealth and as indications of economic exchange distinct from what was in place during the Roman conquest of the same region (*ibid*: 35-36).

The number of observable skeletons available for study from those interred in the 6th century is only 173 adults and 24 sub-adults, with 71 estimated to be female and 41 to be male. However, some of these sex estimates were generated based on the presence of associated grave goods, and so the resulting distributions may be inaccurate. Roughly one-third (n=65) of the 202 graves attributed to the 6th century contained no remains. Grave re-use was common, often reaching multiple periods of exploitation. The majority of individuals are quite gracile, especially females (i.e., "pedomorphic"), although males were found to be more robust. Comparisons of craniometric measurements from Giberville with those from the contemporaneous site of Martin-de-Fontenay found little

difference between males of both sites. Interestingly, a greater distinction was found between females, with females from Giberville being more “dolichocephalic”.

During the 7th century, the general disposition and orientation of the graves did not change. A handful of graves from this period were marked by postholes, possibly indicating the presence of burial markers. Sometimes in small groups, the burials more frequently intrude upon one another in the latter period of the cemetery than in the earlier period. Material remains that were recovered were typically dated using relativistic methods and were widespread in the north and northwest of France. For example, a number of fibulae are similar to ones also found at Frénouville, Verson, and Hérouvillette.

Since only two recovered objects bear the symbol of a cross, the principal evidence of the Christianization process in the community is taken from sarcophagus style. There are 19 sarcophagi, 16 of which are concentrated in the northern portion of the cemetery. The remainder is dispersed in a southeasterly angle. All sarcophagi are superimposed over older burials, and are constructed from limestone found on the Caen Plain. These sarcophagi were pillaged and reused, with only five conserving their covers. Two sarcophagi have a portion carved specifically for the shape of the head.

Finally, at the end of the 7th century, the cemetery was abandoned in favor of graveyards associated with two churches – one dedicated to Saint Germain, the other to Saint Martin. This schema of displacement of older cemeteries toward new centers closer to a living community and a church is witnessed in several sites in the area, including Hérouvillette, Frénouville, Sannerville, and Saint-Martin-de-Fontenay. The graves dated to the 7th century are less numerous than for the preceding period. There are only 189, but

this smaller number could easily be attributed by an incomplete excavation of the eastern portion of the cemetery where grave reuse was quite intense. Eighty graves were void of any material or osseous remains, but at least a third were likely for children due to their small size. Of the remaining 175, 158 were for adults and 16 for sub-adults. There are roughly equal number of males (n=43) and females (n=41), and 74 individuals of unknown sex. According to the physical anthropologist who examined the skeletal material, the females during this phase were quite gracile, much as in the preceding period. However, there appeared to be an overall decrease in sexual dimorphism relative to the 6th century inhabitants. Metopism also completely disappeared, with only one individual expressing this heritable variant.

Craniometrics were also compared to the contemporaneous sample from St. Martin-de-Fontenay using *t*-tests. There were no differences between males from both sites, although there were differences post-cranially. There was a greater distinction for females – Giberville females had longer, lower heads than those from St. Martin-de-Fontenay. A comparison of individuals using craniometrics and morphology from Giberville from each time period suggests that these chronological samples are distinct, yet it cannot be verified statistically when sexes are separated (Pilet et al., 1990: 52). These results are interpreted as a result of progressive change, but with no way to determine if it was due to extralocal gene flow.

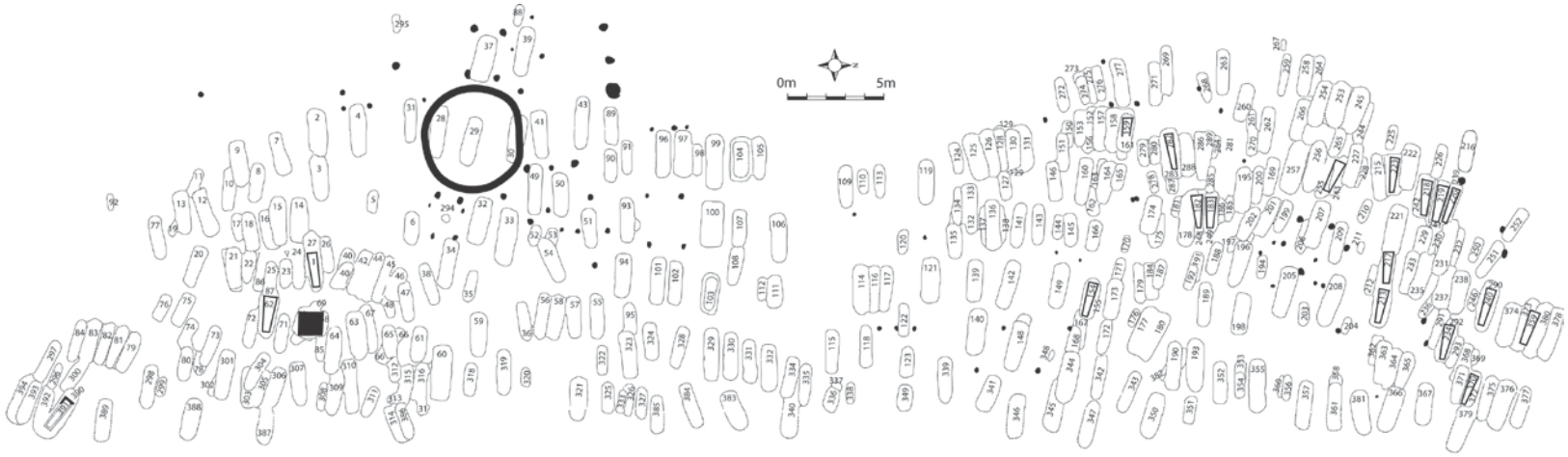

Figure 6. Plan of the cemetery at Giberville (Le Martray) (adapted from Pilet et al., 1990).

Sannerville

Excavated from 1979 to 1984, the cemetery was in use from the 6th-7th centuries AD with burials evident from the Early Middle Ages. Two-thirds of the cemetery is located on the "Delle Saint-Germain", while the remainder was excavated from a parcel of land that was once a dirt path. A few postholes indicate the existence of a kind of aboveground marker signaling the presence of the cemetery enclosure to individuals passing along the path. Similar to a structure found at the contemporaneous cemetery of Saint-Martin-de-Fontenay, it would have been visible to voyagers taking the nearby route to the sea, called the "chemin Saulnier" (Pilet et al., 1992: 22).

There are a total of 121 graves, with 55 having traces of wood indicating the presence of coffins (Figure 7). Forty-seven individuals were interred in earthen graves; the remainder of the graves is unclassifiable due to ancient pillaging and/or poor preservation. Much like other cemeteries from the area, Sannerville consists of irregularly arranged graves with the occasional small groupings of individuals, presumably based on kinship. Unlike other cemeteries from the area, however, Sannerville yields more clearly demarcated groupings of males and females. Also of interest is the presence of a rectangular void within the graveyard, but having no discernible function or even presence of postholes or stones.

Individuals are principally interred with their heads to the west and feet to the east, except for S. 23 and S. 60 who were interred north-south. All were interred supine on their backs and with their upper limbs placed alongside the body, gathered on the lower pelvis, or rarely, crossed on the chest (n=1; S.81), with the exception of S. 72, 81, 93, and 110 who were interred on their right sides (*ibid* 25). Twenty-three graves were

empty of all osseous material, 19 were pillaged, and seven were disturbed by an intercutting from another grave. There is no correlation between the absence of osseous material and pillaging or grave re-use (*ibid* 25). The geology of the soil (loess) is ultimately responsible for the overall poor preservation of skeletal material. Despite the absence of above-ground markers generally, there was little overlapping of graves that actually occurred (*ibid* 25), thereby suggesting some kind of grave signaling in the past. During the 6th century, the graves reached the limit of the "enclosure" in all four directions, despite the fact that it was often difficult to discern the edges of the cemetery itself.

Much like Giberville, the space is organized around two "founding" groups of graves separated by about 15 meters. The first is defined by S. 113 and 115; the other by S. 24, 25, 27, 36. Both groups are contemporaneous (*ibid* 27). Archaeologists have suggested that S. 113 and 115 are "masculine" graves associated with females in S. 112, 119, and 120. However, preservation issues prevent any systematic verification of biological relationships within this first group. Regardless, the use of two presumed heritable variants (e.g., "pyramidal roots", enamel extensions) were used to suggest possible biological linkages. In the second group, four males with "rich" goods were buried, while the associated female graves were pillaged. Overall, the individuals interred during the 6th century appear to be "wealthier" than those at other contemporaneous cemeteries (based on graves with weapons and ornate jewelry). The authors suggest they may have had an "easier" life of sorts (*ibid* 39), perhaps functioning as salt merchants or as customs agents of sorts. Moreover, the authors argue for the continual presence of Anglo-Saxons in the area and at Sannerville in particular based on certain styles of grave

good and documentation of the *litus saxonicum* (*ibid*: 40, 42*)*. However, the physical presence at Sannerville of "outsiders" has not been verified anthropologically.

During the 7th century, the limits of the cemetery were only expanded a small amount. Much as in the previous century, the graves are grouped together into small packets that are fitted between older graves (*ibid* 42). Grave intercutting is rare, thus supporting the argument that grave location was visibly signaled. Certain styles of material remains (i.e., fibulae, pottery, weapons) were used to "date" the graves from this time period. Burials 55 and 63 are females, each possessing a fibula and glass bead necklace, and each interred near males with weaponry. The authors suggest that this weak pattern may be significant (*ibid* 45).

Evidence of Christianization is stronger for this time period than the previous 6th century, noted in symbolism on certain grave goods, such as a belt buckle with the theme of Daniel in the lion's den. This evidence is consistent with the abandonment of the cemetery in favor of the installation of a new one around the Saint-Germain church during the 7th century. Moreover, the schema of cemetery displacement to churchyards has been verified at other contemporaneous cemeteries in the area, including, Hérouvillette, Frénouville, Sannerville, Giberville, and Saint-Martin-de-Fontenay. Based on its topographical position, grave 92 with the "Christian" belt buckle can be dated to the early 7th century, and with it, a mark of early Christianization in a rural location.

Although possessing some ideal conditions for an anthropological study, the skeletal material from Sannerville exhibits poor preservation, thus preventing a more detailed study. The nearly complete obliteration of some osseous material seems somewhat restricted to the middle axis of the cemetery, with preservation improved

peripherally. Regardless, few individuals present enough material to study. Moreover, poor preservation often prevented sex and age estimations. Of the 98 graves with observable skeletal material, only 32 could be assigned an age and sex. Graves with presumed gender-specific grave goods were more numerous (n=77), thus allowing the authors to assign a sex estimate in unknown cases.

Due to such poor preservation, the morphological analysis treats both time periods together unless otherwise specified. Both males and females are characterized by hyper-gracility, common to the Caen Plain at this time period. In fact, the sample from Sannerville is virtually indistinguishable from contemporaneous populations. Demographically, sub-adults are underrepresented at Sannerville (n=12), but consistent with other sites like Giberville, Hérouvillette, and Verson. The absence of any trace of neonates and infants less than 3 is a pattern also seen at other sites on the Caen Plain and has been suggested to represent a significant social status threshold for these individuals (*ibid* 54). It has been estimated that the village sustained 150-170 inhabitants while the cemetery was in use, or roughly 150 years, and would likely have not exceeded 34-40 persons each generation. Finally, only two heritable variants have been used to suggest some kind of biological relationships: 1) the fusion of molar roots, and 2) enamel extensions on molars. A net increase in the frequency of molar root fusion from one period to the other is interpreted as a possible sign of endogamy. In contrast, the appearance of enamel extensions in the 7^{th} century is interpreted as a possible sign of gene flow.

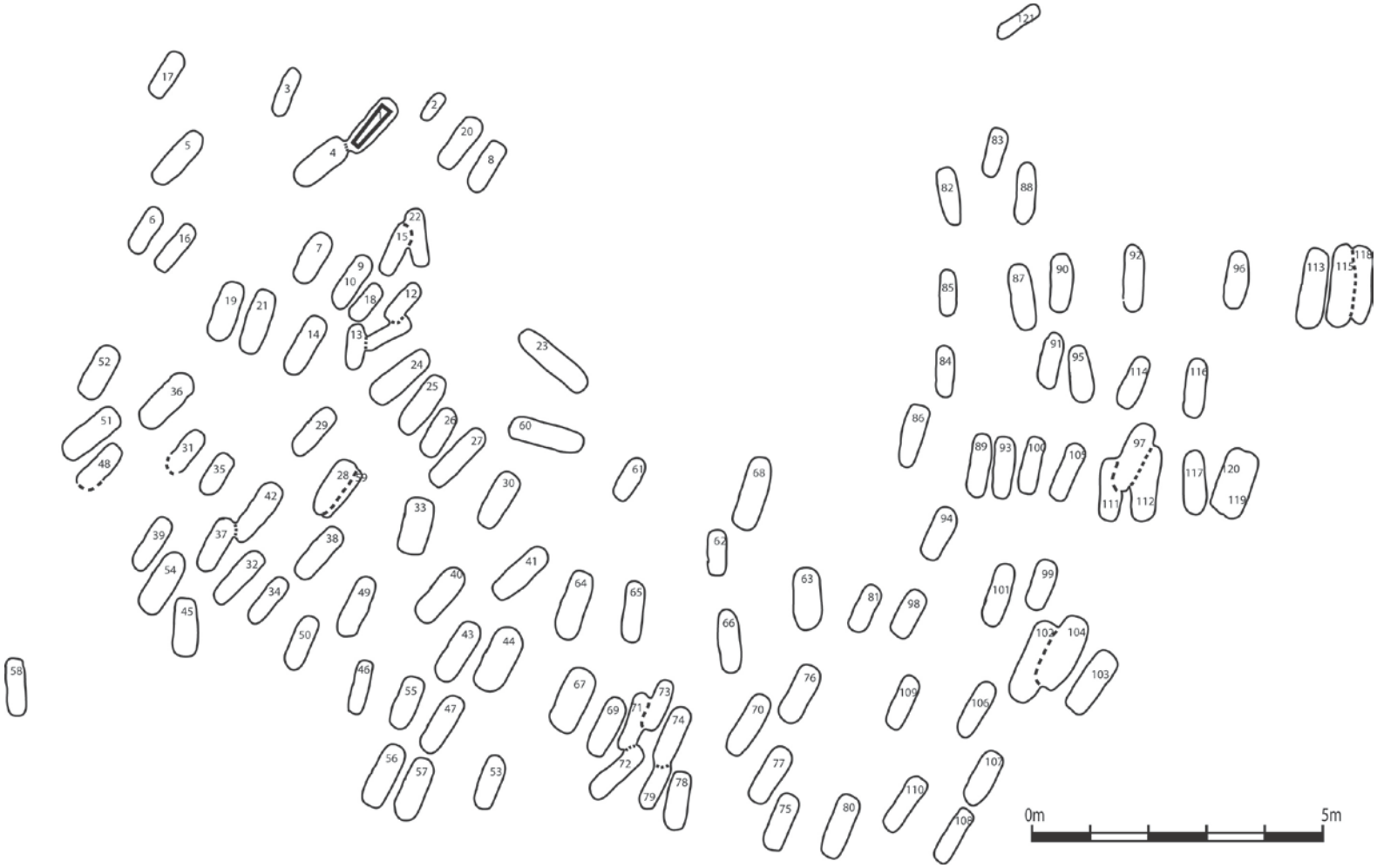

Figure 7. Plan of the cemetery at Sannerville (adapted from Pilet et al., 1992).

Réville

Réville and its environs have been occupied since prehistory. Traces from the Gallo-Roman period are quite frequent and includes the possible presence of a Roman road along the coast linking Barfleur to Saint-Vaast-la-Hougue (Scuvée, 1973: 7). During the "barbarian invasions" of the 4th century, Scuvée has argued that Germanic peoples "without a doubt" were amongst the immigrants, often at the behest of the Romans themselves. These peoples were thought to have formed a *laetus* (i.e., community of barbarians) in the area. Saxons were also likely in the area, having settled near Bayeux and its environs. At least from the 3rd century, Saxons from northern Germany were known to have traveled via the sea to this peninsula and settled there, despite preexisting Roman fortifications that were clearly inadequate to repel all of them, thus suggesting a mixing with the autochthonous Gallo-Romans. Regardless, from the 5th century, it was the Franks who became the most important and dynamic group to establish themselves in the region (*ibid*:8). The author, however, argues that any truly "Frankish" influence had little real impact in the region until much later.

The cemetery of Réville was established on a dune that continued to "move" over time due to wind and water. This cemetery formation lends itself to arguments of religious significance, although Scuvée also suggests that practical reasons should not be excluded (e.g., the preservation of cultivatable land) (*ibid*: 14, 17). Preservation at the site is variable, due to the sandy and watery conditions, so the extent of the cemetery will never be known. However, based on observations, it is thought that burials extended on the western flank of the dune from the 3rd-4th centuries (Figure 8). The rocky point upon

which the cemetery is located forms a kind of crescent shape, which may be significant (*ibid*: 16).

Cemetery organization, despite being quite difficult to reconstruct, consists of a series of rows of graves. Moreover, despite the time period of its foundation, it consists of regularly arranged rows, without any "family islands" (i.e., cemetery founders), indicating a Gallo-Roman influence (*ibid* 17, 19). In other words, Réville is a "classic" Reihengräber (e.g., row-grave cemetery) with occasional interruptions of the rows. It is unclear whether grave markers existed, as no evidence for them remains, and it is unlikely that they were preferentially destroyed since the older part of the cemetery covered over by the migrating dune surface contains no evidence of any markers either (*ibid*: 21). However, the cemetery does consist of burials interred in two successive layers that are superimposed, occasionally overlapping/intermixed, and chronologically distinct (*ibid*: 23).

Grave orientation is structured by four groups: 1) oriented to the North (n=?); 2) oriented with feet to the East (n=?); 3) head oriented North-Northeast (n=4); and 4) oriented with head between North and North-Northeast (although this is probably insignificant). There are 135 inhumations and 10 cremations, however the cremations present characteristics that are entirely distinct from cremation rites common to the Gallo-Roman period and the Bronze Age (*ibid*: 67). Individuals were overwhelmingly interred supine with their limbs extended, and there are only a few instances of individuals having their arms crossed or slightly bent. One individual, a female, was interred on her left side, right hand extended and resting on the legs of a child interred

next to her. The authors refer to this practice as a kind of a throwback, a “germanism” (*ibid*: 171).

The placement of the hands of the deceased are more variable: alongside the body, arms extended; hands joined on the lower abdomen or between the thighs; right hand extended along the right thigh, left hand on the lower abdomen or between the thighs, and vice versa; right hand on the left elbow or higher up, left arm extended alongside the body; forearms crossed, hands on opposite sides of thighs. In general, it was noted that 1) symmetrical positions one and two (see above) occur more frequently after about AD 600, 2) females exhibit more of positions one and two, and 3) males exhibit more of positions three and four. However, no statistical testing was performed.

A comparison of sub-adult (n=23) and adult (n=119) graves does not reveal any explicit patterns for funerary rites or deposition of material culture, other than the observation that more sub-adults are buried in earthen graves with rocks or rubble than adults (*ibid*: 174). Overall, however, sub-adult graves appear to be less “rich” in material culture than adult graves. For adults, males are more frequently interred in earthen graves, and females tend to have more stones, rubble, caches of pebbles, flint, and pottery shards in theirs. Females have more seashells in their graves, while males have more snail shells, ash and carbon deposits indicating ritual fires in theirs. Bronze belts and money were more often found in male graves, while belt buckles and fibulae were exclusive to females.

These observations and interpretations should be taken with caution, since Buchet and Torre (1981) did not perform an anthropological assessment of individual burials until after the publication of the site report. There were a total of 162 adult skeletons

recovered from Réville: 41 males, 30 females, and 91 of unknown sex. Attempts were made to ascribe an "ethnic" affiliation to the remains – a common practice at the time (*ibid*: 5). General characteristics indicate a Mediterranean "type": short stature, large cranial capacity, and overall gracility (*ibid*: 6). The authors admit to being surprised at the resemblance of the population at Réville to other Norman populations and to absence of so-called "Nordic" traits, especially since Saxons were thought to have traveled to the Cotentin Peninsula and settled there some time in the 3rd and 4th centuries AD (*ibid*: 6). Consequently, they propose two hypotheses to account for these patterns. The first hypothesis states that the population of Réville originated from the same Neolithic "parent" population as others located from Caen plain (i.e., Frénouville), as suggested by the similarity to the Neolithic population of Fontenay-le-Marmion II. Any arrival of "Nordic" peoples would then be insufficient to change this biological substrate. The second hypothesis put forth by Buchet and Torre (1981) stated that the population of Réville was not a descendant of Neolithic peoples from the Caen plain, but that the similarity is a result of migrating peoples to the area during the early centuries AD, and any biological differences are not anthropologically distinct enough to detect (*ibid*: 6).

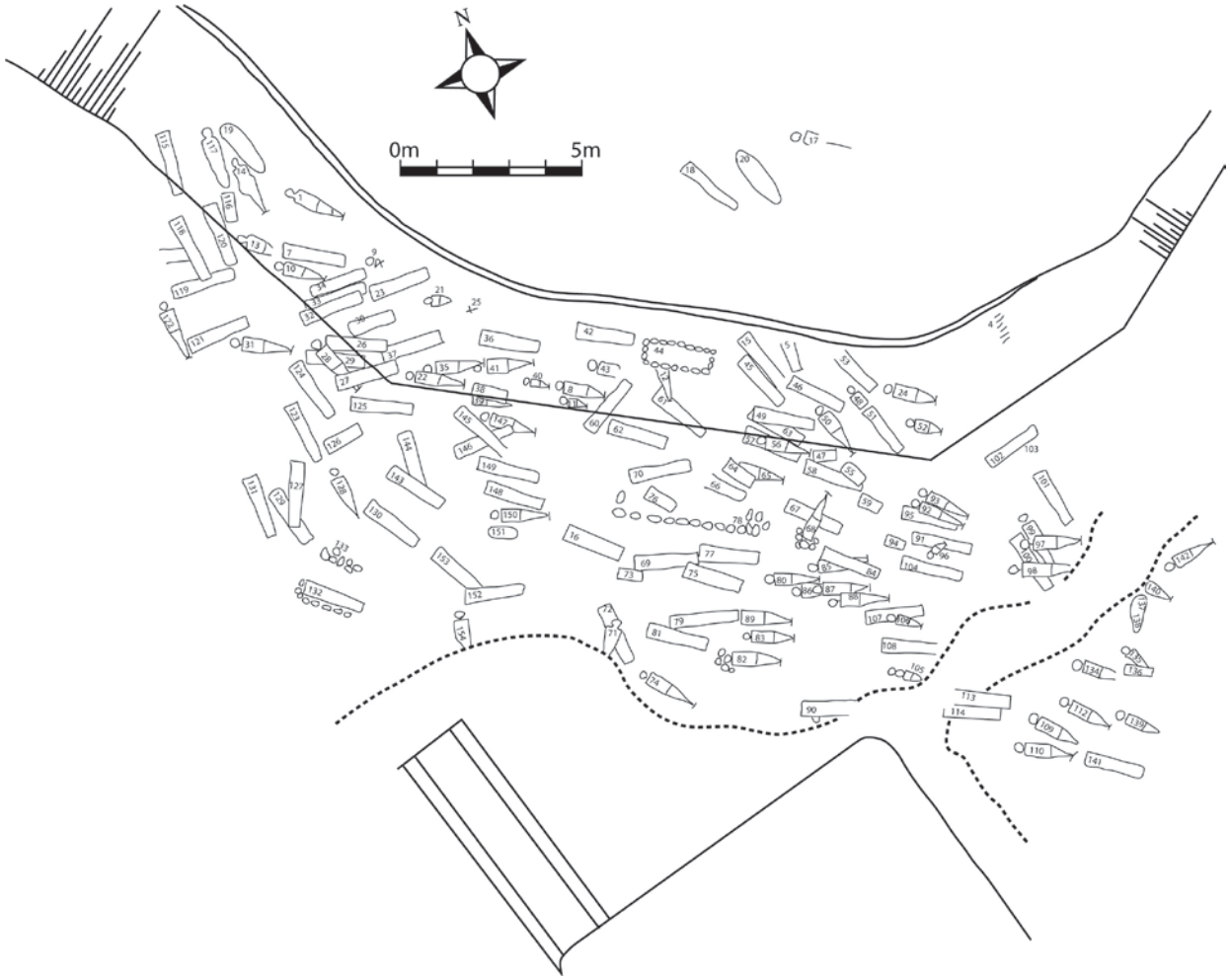

Figure 8. Plan of the cemetery at Réville (adapted from Scuvée, 1973).

Verson

Excavated in the early 1970s, Verson is cemetery of 186 graves and 296 individuals, a higher percentage of which are sub-adults (Figure 9). All graves were oriented east-west, and the majority was dug directly into the underlying calcareous rock. Very few grave goods were discovered; those that were recovered consist primarily of jewelry and clothing-related items.

The site is consistent with the time period from the late 7th to the early 8th century (see Decaens, 1972: 95) and is thought to have been founded by "gallic" peoples. There was a Frankish "fisc" composed of three parishes that would eventually become a ducal fisc during Norman times situated on the Delle St. Martin (a grassy area just outside of the current village of Verson). It is known that the *mansus indominicatus* was also situated around the Delle, thus indicating the presence of a religious edifice until the 14th century.

Although considered a "rowed cemetery" or *reihengräber*, the organization of the graves is not always orderly. Indeed, the only order that is apparent for the outer portion of the cemetery is formed by graves 141, 140, 25, 26B, 27, 30, and 31. In the center it is much more disorganized, with many graves overlapping each other and often sharing the same grave wall on a single side (Lemière and Levalet, 1980: 62). A study of the skeletal remains, however, indicates the presence of three main groups of burials that are primarily of females. These groups are also situated with a central axis that is west-east, somewhat isolated and being more dense. Group 1 is S.140, 106, 46, 45, 47, and 147 (all females). Group 2 is S. 96, 80, 87, and 97 (5 females, 2 males). Group 3 is S. 72, 48, 82, 35, and 34 (all females).

Regardless of the actual composition of each group, their range in number from five to 16 interments and beg the question of how the people from the time period actually recognized burials on the surface. It is known that other cemeteries from the region and time period had stelae, and even at Verson, there is evidence of marker. For example, graves 53, 13, and 175 bear evidence of stelae. However, there is no evidence of any reliefs or engravings on them. The presence of three postholes near graves 7(11) and 172 and 17 could also support an argument for wooden markers. Similarly, the high frequency of re-used graves would also imply that graves were marked in some way. The re-exploitation of some graves resulted in the enlargement of the graves to accommodate larger or more numerous burials, while others were reduced inside by the use of stones or fill in order to fit the shape of particular burial.

Interestingly, though, most cases of grave re-use appear to be done expeditiously, with little evidence of caution. There is occasional evidence that bodies were placed to fit into previously used graves (*ibid*: 66). There were also several instances of the superimposition of bodies. The oldest burial(s) in such cases of superimposition typically lack any grave goods. There are also a few cases of burial treatment that included the severing of the femurs and the replacement of each half into the grave. It is unclear whether this body treatment occurred pre- or peri-mortem, but the grave was large enough to accommodate the full body length, so grave size does not appear to be a factor (*ibid*: 67). Another case (S.84) consists of a headless skeleton and a grave that lacks the space necessary for the head itself.

There does not appear to be a relationship between grave construction and wealth or social status. This conclusion is based on the lack of grave goods found in most

burials. There were only four stone sarcophagi at Verson, one of which bears the only piece of evidence for Christianity in the cemetery—a stone relief of a cross. Orientation of the graves is east-west, with head to the west and feet to the east. Interestingly, the cemetery exhibits a consistent shift to the south during its use, which the archaeologists argue was a means by which graves would track the rising sun. There are two burials oriented north-south, with the head to north. Bodies are typically placed supine on their backs, faces up, legs parallel and extended. No burial (n=86) has arms crossed on the chest. Thirty have arms folded on the pelvis, 28 have arms extended along the body, and 28 have one arm extended and the other on the pelvis. There is no relationship between arm position and the presence or absence of grave goods.

Remains of specific mortuary rites are scarce. Although ritual fires may have occurred, the proof is somewhat equivocal. Indeed, there is only one clear example of a funerary deposit (a ceramic container with grave goods inside), but this is not wholly unexpected given the comparatively "late" date of the cemetery (e.g., 7th century) and is consistent with the same pattern witnessed in lower Norman cemeteries from the same time period, like Fleury-sur-Orne (*ibid*: 67).

While faunal remains and flint are rare, grave goods are present. Of the 185 observable graves, about a third contained grave goods, consisting primarily of clothing and jewelry accessories. Based on sex estimates of some of the skeletal remains, females appear to be associated with more grave goods. However, these goods are characterized by their simplicity and utilitarian nature, which the archaeologists interpret as evidence of relative poverty for those buried at Verson. One burial in particular, though, had a scramasax and was associated with a female. There is some evidence of burial shrouds

based on shoulder pins being found, as well as some examples of coffins based on the presence of nails. Overall, the quasi-absence of funerary deposits, the progressive disappearance of grave goods, and the superimposition of graves fit well with other cemeteries from the late Merovingian Period.

The cemetery dating was performed on relativistic dating techniques using grave goods, particularly items with "precise" stylistic dates. Specifically, 45 burials were used to establish the chronology of the site. About 15 were dated to the second half of the 7th century specifically, and the 7th century in general. A few elements were attributed to the debut of the 8th century (e.g., fibule ansée symétrique en bronze S. 18(2), plaque-boucle en bronze à dix bossettes S. 34). Other grave goods have very simple styles with broad chronologies. However, the archaeologists believe it unlikely that they are earlier than the 7th century. Overall, two-thirds of the graves lack any material remains that can be stylistically dated. Moreover, when only a single grave is used for multiple contemporaneous burials, it can be impossible to date them. However, in certain cases, the reuse and superimpositions afford certain possibilities. For example, there are several groupings of graves that can be observed, possibly family groupings. While a hypothesis, it does appear as if there are very clear separations in material remains (between/among them). Four of the groups do not contain any goods or contain only very poor material remains. These are: 1) 134, 135, 136, 137, 127; 2) 123, 130, 124, 126, 109, 116, 117, 118, 126; 3) 111, 112, 113, 114, 115, 121, 102; 4) 6, 74, 94, 88, 89, 90, 91, 11, 79, 92. The four other groups, in contrast, have some of the most beautiful examples of damasquinée belt buckles in the cemetery and the richest female burials. These are: 1) 63, 54, 53, 51,

52, 50, 38; 2) 85, 76, 84, 84bis, 96, 81, 80, 87, 77, 75, 66, 78, 61, 62, 58, 60; 3) 49, 71, 72, 48, 34, 35, 82; 4) 47, 46, 45, 105, 103, 143, 144.

Overall, the community that created the cemetery appears to have been poor, with many objects like belt buckles showing signs of repair. It is also difficult to reconstruct the chronological development of the cemetery itself. Burial 164 is the extreme eastern burial; burial 172 is the extreme western burial. There is no chronological difference between the two and many of the graves were reused at least one time. The population (much like at Frénouville) appears to be homogenous.

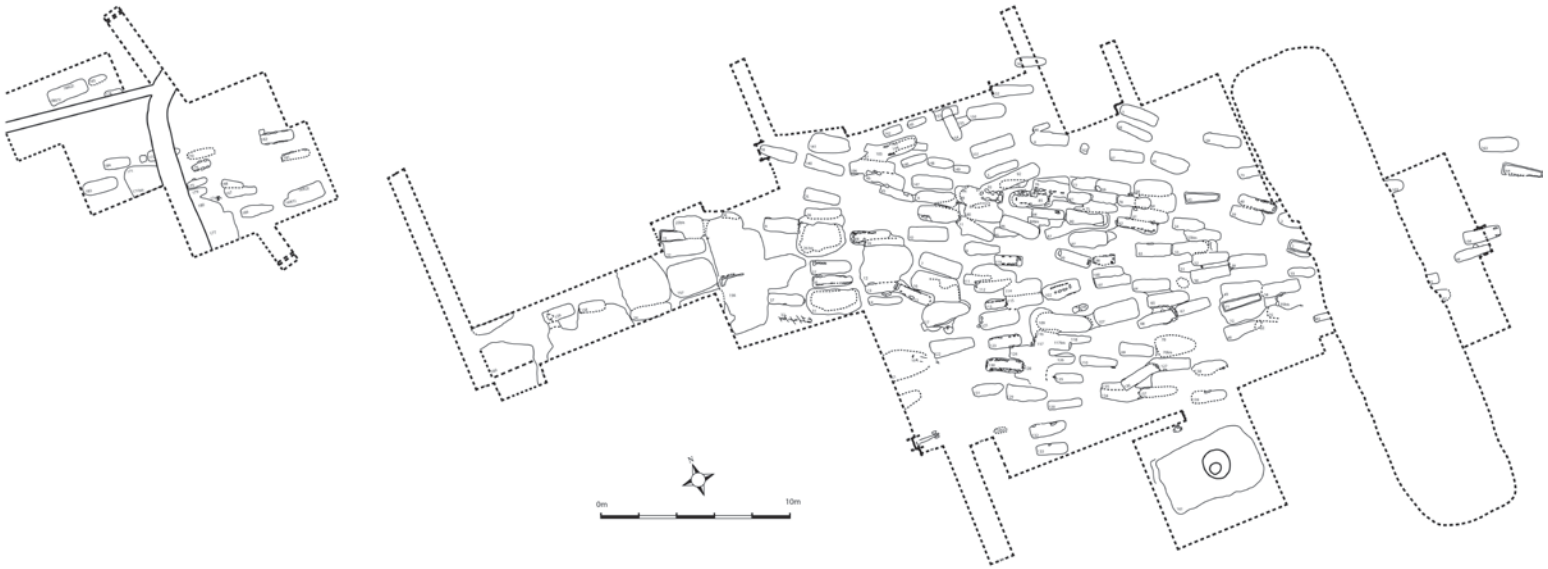

Figure 9. Plan of the cemetery at Verson (adapted from, Alduc-le Bagousse, 1980).

7.1.2 Rhône-Alps

Larina

The cemetery of Larina has two overlapping phases of use that are distinguished by name, La Motte (ca. 380-550 AD) and Le Mollard (ca. 500-700). Odontometrics were collected from Le Mollard only. Consequently, the phase coinciding with La Motte is summarized briefly.

Larina: La Motte

La Motte consists of 136 individuals interred in 115 burials. However, there are likely double that number since much of the site was quarried in the past. Of the 126 adults, only 49 crania were observable for craniometrics. There were 52 males, 58 females, and 16 of undetermined sex. Furthermore, there were 12 sub-adults. There does not appear to be any organization in the cemetery relative to sex, but according to the archaeologist, individuals of the same sex were more likely to be interred near each other than to those of the opposite sex. The only double interment contained two males. Sub-adults are scattered throughout the cemetery, but are more numerous at the summit of the moraine. There are 21 cases of reinhumation, often combining individuals of opposite sex and sometimes combining adults and sub-adults.

A discussion of biological relationships for La Motte is based on the concept of heterogeneity and homogeneity. As understood by Buchet (presented in Porte, 2011: 448), the biological evolution of populations is due to genetic, social, and environmental factors with their source(s) in population history. The complexity of these evolving contexts can be expressed by the homogeneity or heterogeneity of human groups and

described using measurements and observations. Multivariate analyses were performed in order to look at intrapopulation variation. Factor analysis revealed two morphological groups, but there was no association with any archaeological variable. The two groups are distinguished by cranial shape: 1) Narrow and long; and 2) Round and short. Members of both "groups" are found throughout the cemetery without any kind of organization. Buchet does acknowledge that cranial morphology cannot prove that "barbarians" settled in Larina, but notes the perceived morphological variation during this phase. He insists that the arrival of even a small number of immigrants of unknown origin can still be inferred. This small number would have accounted for an increase in morphological variation while "rupturing" group endogamy. The presence of one artificially modified crania would, according to Buchet, also suggest the presence of migrants, since this particular a trait was attributed to central Asian and eastern European peoples. Furthermore, this particular burial is oriented differently relative to the others surrounding it.

In summary, the author hypothesizes that the first occupants of the site had regional origins. Females had a strong homogeneity, while males appear to show a rupture of endogamous practices by revealing an increased heterogeneity, but without significantly modifying the greater morphological characteristics. Nothing seems to indicate that the original population was notably changed by the settlement of any migrants between the 4th and 6th centuries.

Larina: Le Mollard

There are 258 graves with a total of 378 skeletons – the difference is due to the large number of reinhumations (Figure 10). Historic excavations emptied portions of the cemetery, so there were probably more graves than what was actually uncovered. There are 344 adults, 29 sub-adults, 138 males, 96 females, and 33 of undetermined sex. Using Howell's statistic, there is a greater heterogeneity at Mollard than Motte. Cranial morphological differences between males and females has been attributed to changes in biological structure and standards of living for females. Buchet also says that the difference could be attributed to a change from endogamy to exogamy. Females at Mollard are more heterogeneous than males. Buchet speculates that some kind of endocrine dysfunction (hypothyroidism) could lead to an early cessation of growth, although he presents no evidence to support this supposition. He goes on to state that endogamy plays an important role in this, since it increases the proportion of homozygotes sensitive to this particular environmental influence. Buchet then speculates that the de-brachycranization was linked to disappearance of endogamy (i.e., the increase of exogamy) and an increase in standards of living from Motte to Mollard. Stature for males and females at the site is greater at Mollard than at Motte, an increase of 16 and 14 cm respectively. Buchet says that this is much too great an increase to be accounted for by internal variation, thus lending greater weight to arguments for migration. The location of two of the tallest individuals at the chapel entry also seems significant. One particular burial, 714, has evidence of tooth brushing (supposedly a rare practice), and "negroid" cranial morphology. The cranium and post-cranium also exhibit a lot of

trauma. Burial 776 is a female of greater stature buried in the chapel with grave goods, with an age estimate of 25-30.

A number of burials were found outside the “bounds” of the cemetery, but in overall poor condition. One burial in particular is interesting because the cranium was disarticulated and placed on the pelvis of the skeleton, possibly an indication of decapitation (grave under building VII). Changes in diet or possibly food production may also be inferred, according to Buchet. Sixty individuals exhibit some form of trauma or another, 28 of whom were interred in the chapel/church. Buchet claims that the patterns of trauma for many of these individuals are consistent with cavaliers. Paleodemographic analyses suggest a population of 97 at any particular time for Mollard, while Buchet speculates that it was probably greater given the historical excavations and pillaging that destroyed parts of the cemetery. He insists that the increase in population size from Motte to Mollard cannot be attributed to a natural demographic increase, rather some kind of immigration must have occurred.

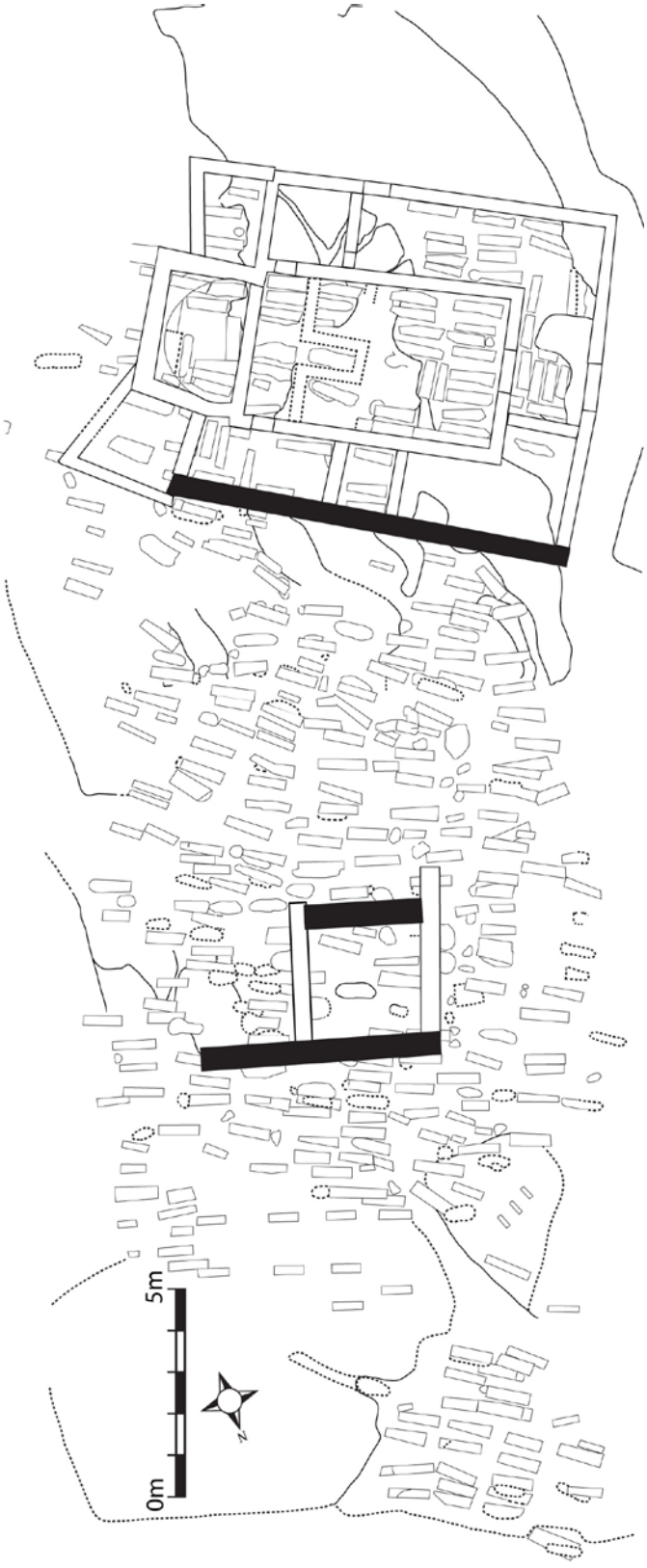

Figure 10. Plan of the cemetery at Larina (Le Mollard) (adapted from Porte, 2011).

7.1.3 Midi-Pyrénées

La Granède

One of the most recently excavated sites, La Granède, is located on the northern border of a plateau situated between two rivers in the department of Aveyron. A fortified and elevated site (i.e., *oppidum*), La Granède may have played an important role in local territorial organization. Excavations revealed a church with an associated cemetery, and radiocarbon dates give a chronological horizon spanning from the 5th to the 10th centuries AD.

The plateau itself, with the exception of a small "isthmus" of land, covers roughly four hectares (Saint-Pierre et al., 2011: 1), two of which show human occupation. Accessibility to the summit would have been extremely difficult, if not impossible, from the west and southwest. Of relevance to this research are three phases determined at the site: Phase VI (5th-7th centuries AD), Phase VIa (8th-10th centuries AD), and Phase VII (11th-13th centuries AD) (*ibid*: 5). Interestingly, material remains associated with Phase VI are the first tangible indication that the site was in use during Late Antiquity and the Early Middle Ages, and that it was isolated from the ramparts and "cultural space" (*ibid*: 81). Also of note is the marked lack of use of the site during Phase VIa, based on a study of the ceramics and radiocarbon dates (*ibid*: 81). Phase VI is contemporary with the first phase of church construction at the site. Yet, during Phase VIa when the church was undergoing reconstruction, there is no indication of site use based on material remains. However, inhumations continue at the site and become relegated to the exterior of the church building (Figure 11). The authors speculate that there had to have been an event sufficiently important both to provoke the abandonment of the settlement while also

encouraging the reconstruction of the place of worship for a population that was no longer present (*ibid*: 81).

After the 2011 field season, a total of 136 burials were uncovered, consisting of 155 individuals. The vast majority of the burials are primary interments of individuals oriented west-east with the head to the west. Age and sex observations by Stephan Naji yielded 20 females, 24 males, 111 of indeterminate sex, 71 sub-adults, 85 adults, and one of unknown age. Radiocarbon dating of various interments span from AD 388 to AD 1265.

Figure 11. Plan of the cemetery at La Granède (adapted from Saint-Pierre et al., 2011).

7.1.8 Paris Basin

The Paris Basin consists of an assortment of sites originally excavated in the late 19th or early 20th centuries and donated by scholars to the Musée National d'Histoire Naturelle / Musée de l'Homme. These include samples from the following sites: Chelles (n=57), Champlieu (n=14), Mareuil-sur-Ourcq (n=7), Précy-sur-Oise (n=7) (Figure 12). A more detailed provenience of the human skeletal remains is unknown. However, most archaeologists and physical anthropologists (see Auboire, 1982), as well as museum curators, are confident in the relative chronology for the remains and date them firmly within the Early Medieval Period. The skeletal remains from Champlieu, Chelles, and Précy-sur-Oise are Merovingian in origin; those from Mareuil-sur-Ourcq are Carolingian.

Chelles

Under orders from Napoleon III, Chelles was excavated in 1863 (Cauchemé 1900). Although there are some minor variants in recorded information by the principal excavators of the site (i.e., Choron, A. de Roucy, and Cauchemé; see Malsy, 1972), it is agreed that Chelles represents a large Merovingian site, at least 6400 m^2. In fact, the number of burials estimated for the site during these initial excavations exceeded 2300, and due to the prevalence of reinhumation Choron suggested that approximately 7000 individuals could have been buried here (cited in Malsy, 1972: 77). However, only 1775 burials were excavated, and 290 of these were children.

The preservation of artifacts was common, as well as remnants of clothing, leading Choron to suggest that individuals were interred fully clothed (cited in Malsy, 1972: 77). Many of the burials were contained in sarcophagi with carved lids, while

above ground stelae marked others. Malsy (1972: 83) argues that the carvings of crosses on coffin lids and stelae imply evidence for early "Christianization" of the region. However, he also notes that "pagan" symbols were likewise prevalent at the site (*ibid*: 83).

Unfortunately, the exact location of the site is now unknown, but it has been established that Chelles was close to a church and to an important Gallo-Roman settlement located along a critical trade route to the north. Although no Gallo-Roman burials were noted by the original excavators, the presence of Gallo-Roman motifs on stone coffin lids, as well foundations and walls older than the Merovingian burials, would suggest a greater antiquity to the site.

Finally, there is a general lack of conserved skeletal remains from the site, likely due to the destruction and loss of several wars and to the regrettable preference for artifacts that was typical of the 19th century archaeological inquiry. The few skeletal remains that were conserved at that period, however, were likely analyzed by Paul Broca (1864), although the author has found no published records of his assessment. Eventually, Broca and/or Bourgeois (one of the excavators at the site) donated some or all of those remains to the Musée de l'Homme.

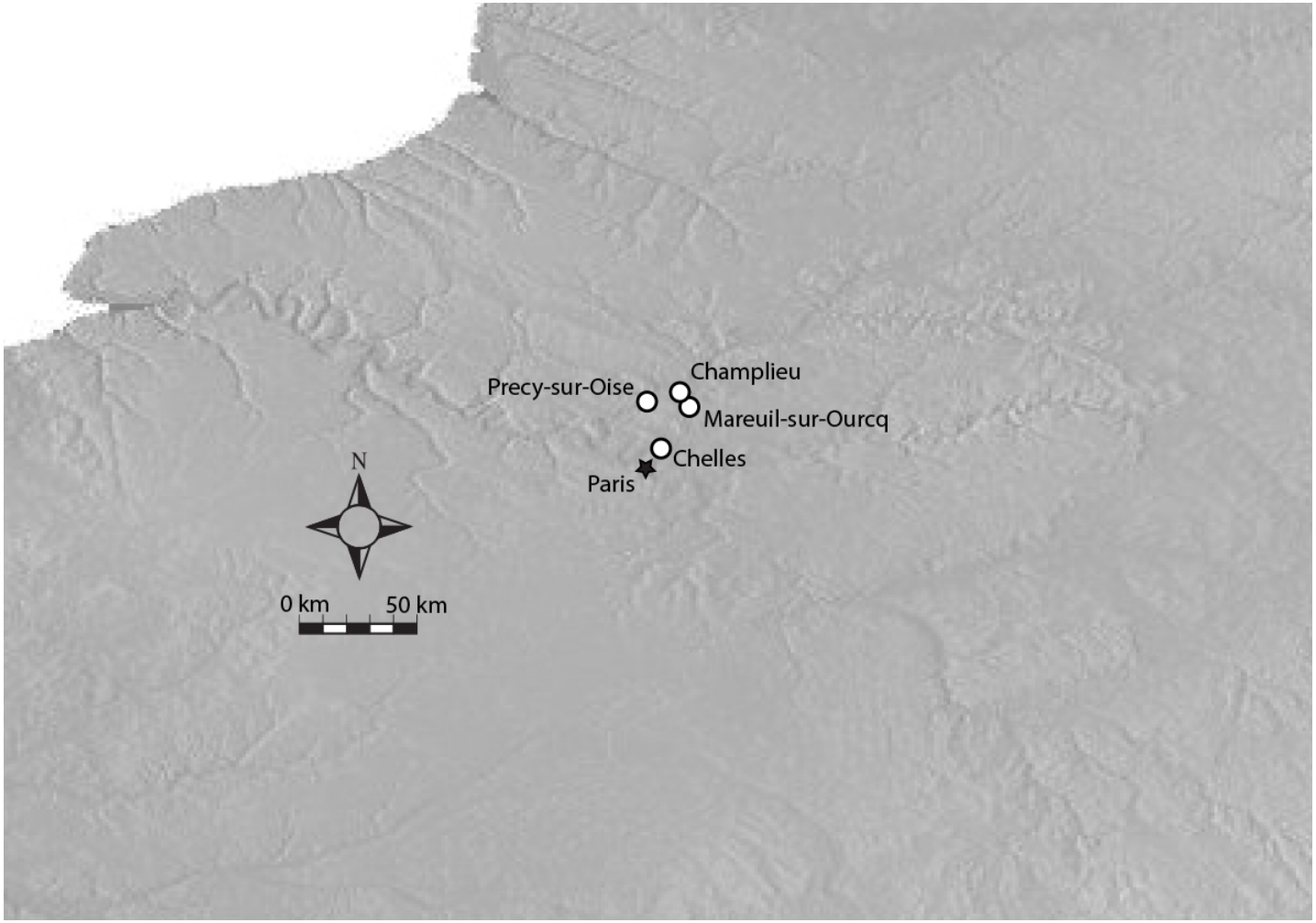

Figure 12. Map of the skeletal collections originating from the Paris Basin.

Champlieu

Champlieu, much like Chelles, was excavated under the auspices of Napoleon III in the mid-19th century (Viollet le Duc, 1860), although observation and recording of the site dates as early as the mid-18th century (Carlier, 1764). Located at the junction of multiple trade routes and in the same region as Chelles, Champlieu is perhaps best known for a Gallo-Roman temple and thermal bath at the site. However, excavations also yielded evidence for a Gallo-Roman cemetery that was eventually replaced by a Merovingian cemetery and associated church (Durand, 1986).

Most of the burials excavated, approximately several hundred (see Durand, 1986: 55), were likely chosen due to artifact accompaniments. However, at least some of the excavated skeletal remains were preserved and ended up at the Musée de l'Homme in Paris. Unfortunately, the author has located no further information or analysis of these remains.

Mareuil-sur-Ourcq

Commissioned in 1897, Verneau and Ripoche (1898) excavated Mareuil-sur-Ourcq over the course of two years. Numerous Neolithic remains were discovered at the site, as well as artifacts and remains from the Gallo-Roman Period. The excavators also note the prevalence of grave goods and sarcophagi from the Merovingian Period, causing them to argue that the transition from Gallo-Roman to Merovingian use of the cemetery was accomplished within two hundred years at most (*ibid*: 511).

Overall, the Merovingian burials were oriented east-west, with head to the west. Much like other cemeteries from the same time period, multiple-inhumation and

reinhumation was common. Interestingly, though, the excavators record the presence of secondary reburial and sometimes the stacking or assembling of crania atop Merovingian burials (*ibid*: 514-515). They argue that these crania were from the antecedent Gallo-Roman Period, were disinterred as the cemetery became crowded, and were re-buried in a ritualistic fashion such that all crania faced east. Exact numbers of these crania are not indicated.

Although the excavators state with certainty that these burials date to the Merovingian Period, they do not estimate when the cemetery was abandoned. This omission of information is critical because the skeletal remains used in the odontometric analysis are attributed to the Carolingian Period by the Musée de l'Homme. Unfortunately, no accompanying documentation has been found that would suggest why or how the remains used in this manuscript were associated with the Carolingian Period rather than the Merovingian Period. Given a propensity by 19th century excavators and historians to emphasize the Merovingian Period over the Carolingian Period, it is perhaps not surprising that no mention would be made of continuing use of the cemetery. Despite this uncertainty, the author accepts the chronological attribution provided by the Musée de l'Homme.

Précy-sur-Oise

It is unclear when Précy-sur-Oise was originally excavated and by whom, although it was likely during the mid-20th century when high-speed rail lines were constructed across the region (see Gressier, 2001: 79). Curators at the Musée de l'Homme identify the skeletal remains analyzed for the odontometric portion of this

manuscript as Merovingian. This attribution is also consistent with more recent excavations at Précy-sur-Oise by salvage archaeologists (Duvette, 2000, 2001; Gressier, 2001; Derbois, 2003, 2004). Despite the regrettable lack of information on the site, it is known that Précy-sur-Oise originated as a Gallo-Roman villa (Duvette, 2000: 82), and later developed as a Merovingian settlement with an associated cemetery.

Table 2.

Key Characteristics of Sites in the Odontometrics Collections.

Site Name	Time Period	Number of Burials Observed at Site	Number of Individuals Observed at Site
Frénouville	Gallo-Roman	163	801
	Merovingian	638	
Giberville	Merovingian	394	372
Sannerville	Merovingian	121	108
Réville	Merovingian	135	162
Verson	Merovingian	186	296
Larina	Merovingian	373	514
Granède	Gallo-Roman	3[a]	155
	Merovingian	20[a]	
	Carolingian	13[a]	
Chelles	Merovingian	2300[a]	7000[b]
Champlieu	Merovingian	14[a]	100[b]
Mareuil-sur-Ourcq	Carolingian	7[a]	?
Précy-sur-Oise	Merovingian	7[a]	?

Notes: Due to incomplete documentation, those fields marked with “a” should be considered minimum estimates. Those fields marked with a “b” indicate projected estimates made by the original excavator(s).

7.2.0 COMPARATIVE SKELETAL COLLECTIONS

Primary data collection was supplemented using comparative craniometric data found in the published literature, including gray literature and museum reports. As stated previously, the goal of such an enterprise was to elucidate any aspects of population structure and how it may have changed from Late Antiquity to the Early Middle Ages that was not captured using the odontometric data alone. Sources were selected upon availability and the osteometric standards used by the researchers (i.e., Martin, 1957; Buikstra and Ubelaker, 1994). The standardization of cranial measurements was established as a criterion to control for inter-observer error. (A more thorough discussion on inter-observer error is provided in Chapter 8). Colleagues at CRAHAM provided additional craniometric data in the form of a digital spreadsheet for the following sites: Cherbourg, Évrecy, Frénouville, Giberville, Mondeville, This process yielded phenotypic information on roughly 1200 additional individuals that were contemporaneous to those in the primary data collection (Table 3; see also Figure 4).

Table 3

Craniometric Collections

Site Name	Associated Reference(s)
Andrésy	Manouvrier, 1890, 1897
Baye	Vallois, 1925
Bellengréville	Dastugue and Torre, 1964
Bourgogne	Chabeuf; 1976, 1977, 1987
Caen-St. Martin	Dastugue and Torre, 1965
Chaumes	Baudouin, 1923
Cherbourg	CRAHAM, 2012
Créteil	Ferembach and Clement, 1958
Énnery	Heuertz, 1957, 1966; Simmer, 1993
Évrecy	CRAHAM, 2012
Frénouville	Buchet, 1977, 1978; Pilet, 1980; CRAHAM, 2012
Giberville	Pilet et al., 1990; CRAHAM, 2012
Hérouvillette	Dastugue and Torre, 1971
Mondeville	Musset, 1963-1964; CRAHAM, 2012
Poitou-St. Gelais	Billy, 1970
Réville	Scuvée, 1973; Buchet and Torre, 1981; CRAHAM, 2012
Saint-Laurent	Leroi-Gourhan, 1949
Sannerville	Pilet, 1983; Pilet et al., 1992; CRAHAM, 2012
Savigne	Patte, 1937
Strasbourg	Straub 1881
Verson	Alduc-le Bagousse, 1980; Lemière and Levalet, 1980; CRAHAM, 2012

Note: Those references marked as CRAHAM (2012), indicate those sites for which raw data were provided directly to the author.

7.3.0 SUMMARY

As detailed in this chapter, the primary skeletal collections used in the odontometric analysis derive from four regions in modern-day France (Normandy, Paris Basin, Rhône-Alps, Midi-Pyrénées). Each site included in these regions was outlined, the general characteristics of the cemeteries were described, and important interpretations drawn by the original field archaeologists and physical anthropologists were summarized. Unfortunately, preservation of field notes and other information on archaeological context were not always available for those sites in the Paris Basin. Regardless, it is accepted that all of the sites forming the primary skeletal collection derive from the Early Middle Ages, likely spanning no more than 500 years. For a summary of the key characteristics of each site, see Table 2.

The craniometrics portion of this analysis stems primarily from published literature of raw data. These data were verified to have originated from other sites from the first millennium A.D. and to have been recorded using accepted measurement standards. Given the larger number of samples used for this portion of the analysis, a detailed discussion of individual sites was prohibitive. However, a detailed bibliography was provided in Table 3.

CHAPTER 8

METHODS AND ANALYSES

8.0.0 INTRODUCTION

In this chapter I relate the mechanisms by which teeth form, and how they reflect underlying genes. Given their unique developmental and morphological qualities, as well as their dimensions possessing an underlying quantitative nature, teeth are particularly well suited for studies of biodistance. Similarly, as discussed in Chapter 5, they can be used to explore *generally* the intersections of biological variation and social identity within a biosocial interpretive framework. Consequently they are employed in this manuscript to provide an understanding of population structure during the transition from Late Antiquity to the Early Medieval Period and of temporal changes in patterns of group interactions. These goals are accomplished by following established protocol for their observation and measurements, by performing appropriate statistical analyses, and by establishing how they fit into more traditional biodistance approaches (e.g., craniometrics).

8.1.0 DENTAL DEVELOPMENT

Research from the mid-twentieth century established that much of the variation in dental morphology is explained by genetic factors (Scott and Turner, 1997: 131-164; see also Rizk et al., 2008). Likewise environmental perturbations have been shown to have an effect (i.e., Potter et al., 1979, 1981). Recent work by molecular biologists however has

also revealed a "dynamic interplay" of molecules, cells, and tissues during dental development (Townsend et al., 2012: 2). This is referred to as "epigenetics" – the way in which genes are expressed on a molecular, cellular, and local tissue level – and is used along with genotype and environment to explain variation in dental morphology (i.e., phenotype).

Understanding the impact of epigenetics on teeth includes an understanding of the developmental processes controlling morphogenesis. For example, how is tooth size controlled? How is tooth number controlled? These aspects of evolutionary development can be subdivided into major categories (macro-patterning and micro-patterning; see Cai et al., 2007) and will be discussed below. However it is critical to note that these categories function in parallel as part of a continuum of reiterative signaling that influence each other.

8.1.1 History of Study on Dental Development

During the early 20th century the interpretive concept of the "morphogenetic field"[33] provided the formative basis for understanding the ordered forms and patterns in skeletal and dental development (Scott and Turner, 1997: 82). While the governing principles and causes were unknown (Townsend et al., 2009: S35), it was observed that teeth at the terminal region of a dental field were the most morphologically and metrically diverse (Bateson, 1894). Butler (1939) applied this concept further by suggesting that morphogenetic fields accounted for morphological variation in mammalian dentition. More specifically he proposed that dental morphology was controlled by "morphogens"—molecules that induce differentiation and that were strung

[33] A gradient by which an unknown morphogen-like field substance operated on mammalian development

out along the dental lamina constituting a morphogenetic field. Progressively, morphogens clumped along the dental lamina with fewer occurring distally. Different tooth classes comprised three kinds of morphogenic fields corresponding to the presumptive incisors canine and (pre)molars. Each field had a morphogenic-diffusing gradient such that each field had a center or pole about which it was expressed more strongly. Teeth at the poles then possessed less variability in size and shape while those further from the pole possessed greater size and shape.

Building on this concept Osborn (1978) proposed a complementary theory that the development of specific teeth arose by clones. Specifically a "single clone of pre-programmed cells led to the development of all the teeth within a particular class" of teeth – incisors canines and (pre)molars (Townsend et al., 2009: S35). He suggested that primordial cell clones of particular tooth classes were found in the mesenchyme and would induce the dental lamina to initiate tooth development for its respective tooth class. As the dental lamina grew the cell clones of primordial tooth germs were deposited. Likewise, as each primordial tooth germ was formed, a zone of inhibition was also produced around it. This inhibition zone delayed the formation of subsequent primordia and ultimately determined the spacing between adjacent teeth. Over time the cell clone lost its potency to form a primordium thus constraining the number of teeth.

8.2.2 Odontogenic Homeobox Code

Although critical in the early study of dental development, neither the Field Theory (Butler, 1939) nor the Clone Theory (Osborn, 1978) was sufficient "explanation for how the dentition develops as a whole with different tooth classes displaying different

shapes" (Townsend et al., 2009: S35). Likewise, they could not detail the cellular mechanisms controlling tooth size and shape or cusp size and shape. However, with the relatively recent explosion of research within the field of developmental biology (see Berger et al., 2009), an Odontogenic Homeobox Code was proposed as a model to explain how dental patterns develop (see Sharpe, 1995). Rather than simple gene expression being the root cause for odontogenesis it was asserted that the dentition develops in the same manner as other ectodermal organs—by homeobox genes (McCollum and Sharpe, 2001: 481). Homeobox genes are defined as relatively short gene sequences that consist of conserved regions of DNA and are present in the developing jaws of many animals including mammals and birds. Thus, mechanisms of reaction and diffusion of activator and inhibitory genetic signaling pathways account for the serial formation of teeth in specific regions (Townsend et al., 2009: S35-S36). Relevant for odontogenesis are several primary signaling pathways involved in cellular communication (e.g. Fgf Bmp Shh Wnt and Tnf) (Townsend et al., 2012: 2).

Overall, a "series of reciprocal tissue interactions that occur between an epithelium and its underlying mesenchyme" (McCollum and Sharpe, 2001:481). It is multi-level (molecular cellular and tissue levels) and multi-dimensional (size shape and time) in nature. "The reciprocal interactions between the ectodermal and ecto-mesenchymal tissues regulate key stages in the process of odontogenesis including initiation morphogenesis and differentiation" (Townsend et al., 2012: 2). A more detailed explanation of these complex processes is provided below.

8.2.3 Macro-patterning

During tooth initiation (bud stage) the dental lamina, which is comprised of condensed oral epithelium, thickens and invaginates the underlying ectomesenchyme forming a tooth bud. “This stage is critical in determining the number of teeth that will form and in ensuring that the different tooth types i.e. incisors canines premolars and molars develop in the appropriate regions within the oral cavity” (Townsend 2012: 2-3). All tooth buds (including those for supernumerary teeth) from along the dental lamina never outside of it[34].

The dental lamina itself exhibits a nested proximal-distal and rostral-caudal pattern whereby the maxilla and mandible are divided into different domains—oral aboral distal and proximal—each of which expresses specific transcription factors (Catón and Tucker, 2009: 504; see also Tucker and Sharpe, 2004: 501). For example certain signaling pathways and transcription factors (i.e., Bmp4) are expressed and overlay the distal[35] and presumptive incisor region and others (i.e., Fgf8 Fgf9) are expressed and overlay the proximal and presumptive molar region (Tucker and Sharpe, 2004: 501). These signaling molecules then operate to control the expression of other regulatory molecules in the ectomesenchyme (Msx1/2 Dlx1/2 Barx1 Pitx1), which in turn promote and maintain a kind of mutual antagonism between the proximal and distal regions (Catón and Tucker, 2009: 504). The end results are areas of partially overlapping zones

[34] Teeth can actually form in any place where the epithelium and ecto-mesenchyme come into contact necessary for the iterative signaling process.

[35] The orientation of the maxilla and mandible (specifically the pharyngeal arch) in embryological development are “opposite” of what they are in a fully developed fetus. Thus in this case the distal portion of the maxillary and mandibular ectomesenchyme give rise to what will become the proximal deciduous and adult dentition.

of expression that ultimately aid in determining the resulting tooth class (Tucker and Sharpe, 2004: 502; see also Tucker and Sharpe, 1999).

The number of teeth that form results from a reaction-diffusion mechanism of key activator and inhibitory molecules in the ectomesenchyme (Cai et al., 2007: 506) and is proportional to the size of the tooth field (Tucker and Sharpe, 2004: 503). The size of the tooth field is established by the activation and inhibition of signaling molecules (i.e., Eda) in the oral epithelium and of their receptors (i.e., Edar) in the ectomesenchyme (*ibid*: 503). Furthermore, transcription factors in the ectomesenchyme regulate the expression of reciprocal signals in the oral epithelium resulting in multiple signaling networks that possess different but specific intracellular cascades (Jernvall and Thesleff, 2000: 22). These signaling cascades promote the formation of the dental organ or cap. Thus, as the invagination of the oral epithelium into the ectomesenchyme continues the ectomesenchyme surrounding this invagination begins to condense (Tucker and Sharpe, 2004: 501). Activation of molecules (i.e., Bmp4) in this condensed ectomesenchyme are then promoted that induce the formation of the primary enamel knot at the tip of the dental organ.

The enamel knot plays a critical role as a signaling center for further tooth development. Indeed the enamel knot expresses a number of important signaling molecules (i.e., Shh Fgf4 Bmp4 Wnt10b) that promote the proliferation of cells outside the knot while other signaling molecules (ectodin) are expressed that inhibit the proliferation of cells within the enamel knot itself (Laurikkala et al., 2003). This process of high exterior proliferation and low interior proliferation leads to the folding of the oral epithelium and to the two distinct layers of epithelium (inner and outer) described earlier.

Ultimately the primary (and any secondary) enamel knot determines the final *shape* of the tooth (Catón and Tucker, 2009: 504) but not necessarily its size.

To understand tooth size, which is relevant to this manuscript, one has to understand the role of the ectomesenchyme and the dynamic interplay of signaling molecules in the ectomesenchyme between teeth. According to Cai and colleagues (2007), the size of a tooth that results from this cascade of network signaling is primarily based in the ectomesenchyme. In fact, the transplantation and recombination of an embryonic rat's ectomesenchyme to an embryologically synonymous mouse's oral epithelium resulted in a tooth size that was *larger* than the mouse control (*ibid*: 502). Likewise the transplantation and recombination of an embryonic mouse's ectomesenchyme to an embryologically synonymous rat's oral epithelium resulted in a tooth size that was *smaller* than the rat control (*ibid*: 502). Thus the activation and inhibition signals in the ectomesenchyme direct an individual tooth's size. These authors also suggest that the dental ectomesenchyme possesses some kind of "intrinsic memory" of its own final tooth size (*ibid*: 504).

In addition, the size of an individual tooth regulates the size of subsequent teeth in the same tooth row. Specifically, signaling molecules in the ectomesenchyme of one tooth regulates the development of subsequent teeth (Kavanagh et al. 2007). This dynamic balance of activator and inhibitory signaling molecules between teeth determines how quickly a subsequent tooth will form and how large it will be relative to antecedent and subsequent teeth (Kavanagh et al., 2007; see also Polly, 2007). This is known as the Inhibitory Cascade Model. Thus, teeth that form first will inhibit teeth that form later. These earlier-forming teeth may also be larger than subsequent teeth. This can

arise due to an inhibition by one tooth's ectomesenchyme on the activation of enamel knot formation for the subsequent tooth (Kavanagh et al., 2007: 428-429).

8.2.4 Micro-patterning

While the reiterative signaling between activator and inhibitory molecules in the oral epithelium and ectomesenchyme help determine tooth number and tooth size, tooth shape also relies on the activation and inhibition of various molecules (BMP FGF Hh Wnt) and their signaling cascades (Jernvall and Thesleff, 2000: 23). Specifically it is during the transition from the bud to the cap stages that tooth shape is generated. As previously described the primary enamel knot expresses a number of important molecules that promote the proliferation of cells outside the knot while cell proliferation inside the enamel knot is prohibited (Jernvall et al., 1994). This process "folds" the oral epithelium around the condensed ectomesenchyme eventually forming the cervical loop (Tucker and Sharpe, 2004: 505; see also Jernvall and Jung, 2000).

Due to high levels of apoptosis within the primary enamel knot (possibly due to the expression of Bmp4), the knot eventually disperses after the cap has formed (Jernvall et al., 1998). In the case of posterior dentition especially, this programmed cell death effectively removes the inhibitory signaling molecules that suppress the formation of secondary enamel knots (Jernvall et al., 1994). Secondary enamel knots form quickly via the same manner as primary enamel knots appear at the location of future cusp tips and are also removed apoptotically (Jernvall and Jung, 2000: 178).

Based on the concept of dynamic patterning mechanisms (like that derived for feather primordia) the number shape and relative size of future cusps derive from an

understanding of the spatial and temporal controls of secondary enamel knot formation (Jernvall and Jung, 2000: 179; see also Weiss et al., 1998). As the first enamel knot promotes cell growth around itself it also inhibits the formation of other enamel knots via the diffusion of inhibitory molecules through the ectomesenchyme (but see Hammer, 1998). The larger the cusp formed by the first enamel knot, the greater will be the inhibition zone around it. This broader zone of inhibition delays and displaces the formation of new secondary enamel knots further away (Jernvall, 2000). As secondary or tertiary cusp formation is delayed shorter cusps will result. Thus there is a cumulative effect on the later-developing cusps (Jernvall, 2000). This is referred to as the Patterning-Cascade Model of cusp development and it has been used to explain the development of supernumerary cusps and tooth shape overall (i.e. Hunter et al., 2010; Moormann et al., 2013; but see Cai et al., 2007 and Morita et al., 2014).

8.3.0 DATA COLLECTION METHODS

8.3.1 Odontometrics

Dental measurements have a long history of use by physical and dental anthropologists, dentists, and biologists for assessing a broad range of subjects, including human evolution health and disease and biological development. Since the mid-20th century the human dentition has been used to investigate biological affinity, a critical aspect of this manuscript. Primarily based on tooth crown dimensions (see Kieser, 1990), recent work has also highlighted the utility of measuring dimensions at the cervical-enamel junction (CEJ) (i.e., Hillson et al., 2005), inter-cusp dimensions (i.e., Townsend

et al., 2003), 3D morphometrics (i.e., Teaford and Ungar, 2006), and even measurements based on micro-CT scans of dental elements (i.e., Macchiarelli et al., 2003).

Due to their resistance to taphonomic processes and *in vivo* mechanical stimuli, along with their lack of biological remodeling after formation, teeth are valuable for studies of (pre)historic population structure and biodistance. Furthermore, tooth dimensions and morphology are quantitative, making them amenable to studies based on population genetics (see Chapter 5). Overall, the human dentition is remarkably genetically conserved possibly due to the critical role it plays in processing the food necessary for survival (see Ungar, 2010). Despite the conservative nature of teeth, it is clear that there are a number of cultural and idiopathic practices that can serve to alter them (Alt and Pichler, 1998), although this subject will not be detailed here nor was it found to be relevant for this study. It should also be noted that teeth are capable of experiencing biomechanical forces during development (i.e., Hatton et al., 2003), which may also subject them to epigenetic effects during development (i.e. Townsend et al. 2005). These effects can be as simple as slight differences in the spatial arrangements of cells that result in missing or extra teeth. Although it is possible that tooth number anomalies could impact crown size (see Brook, 2009), the genetic mechanisms between tooth number anomalies and crown size are unclear. Given the sample sizes employed in this study, it is assumed that minor epigenetic effects on tooth crown size are insufficient to alter the underlying patterns in group heritability.

Numerous narrow-sense heritability studies show that observable phenotypic variations, including those of teeth, act as suitable proxies for genetic relatedness (e.g. Goose and Lee, 1971; Alvesalo and Tigerstedt, 1974; Townsend and Brown, 1978;

Corruccini and Potter, 1980; Harris and Smith, 1980; Potter et al., 1983; Kieser, 1990; Scott and Turner, 1997 Stojanowski and Schillaci, 2006). However, heritability estimates are always population- trait- and time period-specific (see Konigsberg, 2000; Vitzthum, 2003), which explains the broad range of heritability estimates for the dentition—from 0.38 (Scott and Potter, 1984; see also Townsend et al., 1992) to 0.80 (Dempsey et al., 1995; Townsend et al., 2003). Despite this range in heritability estimates, many cluster around the moderate value of 0.55 (Stojanowski and Schillaci, 2006: 53). Thus, the analyses outlined in this manuscript employ a narrow-sense heritability of both 0.55 and 1.0. The former reflects the most likely heritability for the dentition, while the latter provides a more conservative estimate that yields minimum genetic distances among regional populations (Williams-Blangero and Blangero, 1989; Relethford and Blangero, 1990; Relethford, 1994). Using a narrow-sense heritability estimate of 1.0 also permits cross-cultural comparison of genetic differentiation regardless of the data type used (for example, see Steadman, 2001).

Tooth Wear and Non-Metric Variants

Although there are number of advantages in employing the dentition for studies of population structure and human variation, the dentition also has a number of inherent limitations. First and foremost teeth are subject to wear and pathologies that serve to obscure and complicate data recording. Ante-mortem tooth loss, caries, and calculus can prevent taking precise and accurate measurements. In some cases, caries and other oral health sequelae (i.e., ante-mortem tooth loss due to dental abscesses) can completely

obliterate a tooth or teeth (Hillson, 1996: 269-284). Likewise, wear of the occlusal and interproximal surfaces of teeth can progressively destroy a tooth crown.

Even small amounts of occlusal and interproximal wear/attrition can negatively impact the measurements of a tooth's crown and/or CEJ (Van Reenen, 1982; Hillson, 2008). Any negative impact on accurately and precisely measuring a tooth crown or CEJ also adversely impacts the reliability of using crown or CEJ dimensions as phenotypic proxies for the underlying genotype of tooth size. Consequently, standard procedures dictate that any teeth exhibiting heavy wear would be excluded from study (Van Reenen, 1982; Hillson, 1996; Mayhall, 2000). All teeth were recorded for occlusal surface wear based Smith's (1984) stages, and any tooth exhibiting a stage of four or greater was not included in subsequent analyses.

A second, though less critical, limitation to using tooth size for studies of population structure and human variation is the possibility that morphological variants can alter tooth crown dimensions (see Reid et al., 1991). Although not a significant issue for the CEJ, the varying degree of expression of certain dental morphological traits such as Carabelli's cusp or protostylids can differentially impact the placement of calipers. Whether this potential alteration serves to obscure aspects of the underlying genotype is not clear, especially given the close relationship between tooth/cusp size and shape as explained by the odontogenic homeobox code. Likewise, given the threshold and continuous expression of many of these traits, it is unclear at which stage of expression they would have a negative impact. Consequently, no "correction" for this issue was introduced here.

Crown Dimensions

Measurements of crown diameters are based on the length (mesial-distal) and breadth (buccal-lingual or labial-lingual) of a fully erupted deciduous or adult tooth crown (Kieser, 1990). For this study the measurement techniques of Moorrees (1957) Goose (1963) and Kieser (1990) were followed. Specifically maximum mesiodistal (MD) and buccolingual (BL) adult tooth crown dimensions were recorded to the nearest hundredth of a millimeter for both the maxillary and mandibular dental arcades using Mitutoyo Absolute Digimatic (500-196-20) sliding calipers. The MD dimension reflects the maximum length of a tooth crown and is made parallel to the occlusal plane. The BL dimension represents the breadth of the tooth and is measured perpendicular to the plane used for the MD dimension (Figure 13).

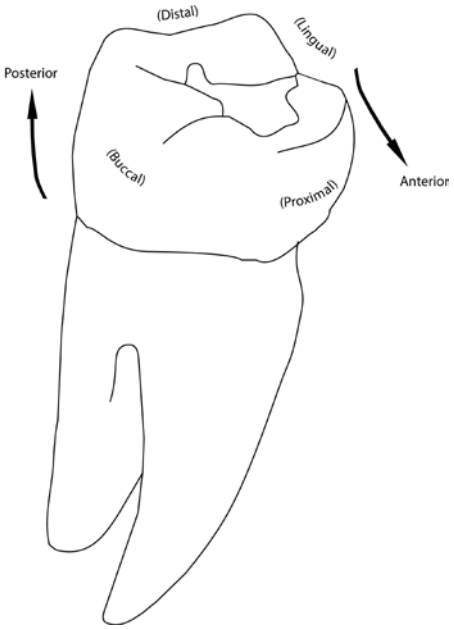

Figure 13. Human tooth showing anatomical directions.

Cervical Dimensions

As demonstrated by Hillson and colleagues (2005) and confirmed by Stojanowski (2007) measurements of the CEJ are highly correlated with crown measurements. They are also much less likely to be affected by wear (Fitzgerald and Hillson, 2008) than traditional crown dimensions thus increasing the potential sample size of any odontometric study. Furthermore they may be more representative of the underlying genotype than crown measurements, since their dimensions are better suited to distinguishing between various fossil hominin taxa than tooth crowns (see Skinner, 2002).

Measurements of cervical diameters are based on the length (mesial-distal) and breadth (buccal-lingual or labial-lingual) of a fully erupted deciduous or adult tooth's cervical-enamel junction. Measurement techniques were modeled after Hillson and colleagues (2005) and Fitzgerald and Hillson (2008) although alternatives have also been proposed by Aubry (2009). Specific measurements of the MD and BL cervical dimensions were taken using Paleo-Tech Hillson-Fitzgerald calipers and were recorded to the nearest hundredth of a millimeter for both the maxillary and mandibular dental arcades. The use of these calipers requires skill since all measurements require the placement of the caliper points on the enamel surface just occlusal to the cervical margin. In other words they should not be allowed to slip off the enamel surface and onto the cementum.

8.3.2 Craniometrics

Much like those of the dentition, craniometric variables are both heritable and quantifiable (Susanne, 1975 1977; Cheverud et al., 1979; Sjøvold, 1984; Devor, 1987; Cheverud, 1988; Konigsberg and Owsley, 1995; Spark and Jantz, 2002; Carson, 2006). Their history of use in the field of anthropometrics physical anthropology and human biology is extensive (for relevant reviews, see Buikstra and Beck, 2006). Although not without critique (i.e. Armelagos and Van Gerven, 2003), cranial dimensions continue to provide a useful and informative foundation for the study of human variation and biodistance (for examples, see Roseman and Weaver, 2004; Stojanowski and Schillaci, 2006; Konigsberg et al., 2009; Byrd, 2014).

The author took no cranial measurements. Rather all cranial measurements referred to in this manuscript were supplied in one of two manners. Firstly, A. Alduc-le-Bagousse from CRAHAM provided extensive digital spreadsheets of cranial measurements (Table 3). These measurements were likely taken by a small number of researchers over several decades. However, all measurements were firmly based on clear inter-landmark distances from Martin (1959), and the author has confidence in their combined ability to capture aspects of a sample's underlying genotype. Similarly, a search through published and gray-literature sources yielded further raw craniometric data (Table 3). These reports also followed the measurement protocols established by Martin (*ibid*) and were compiled into a single digital spreadsheet.

The acquisition of raw data in this manner obviously lends itself to issues of inter- and intra-observer error (see Utermohle and Zegura, 1982; Utermohle et al., 1983). Unfortunately, there is no way to determine whether any particular researcher was or

would be consistent with him- or herself without some form of self-reported error measurement. Nor is there a clear manner by which to assess the consistency of two or more researchers at measuring the same cranial dimension using already published data. Although the preferred method would be to quantify the technical error of measurement (TEM), the only way of doing this is by repeated measurements of the same object (Harris and Smith, 2009: S109), which is not practically possible for a comparative study this large.

It is important to note that error tends to increase the dispersion of a measured variable (i.e., variance, standard deviation), which thereby increases the chances of accepting the null hypothesis when it should be rejected (e.g., Type-II error). In other words, more error decreases the likelihood of finding a statistically significant difference (Harris and Smith, 2009: 109; see also Lakens, 2015). Given the goals of the craniometrics portion of the analysis and this study overall, the increased possibility for Type-II error is superior to that of Type-I error—rejecting the null hypothesis when it should be accepted. For example, accepting the null hypothesis of no difference between two "populations" is a more conservative "risk" than rejecting the null hypothesis, especially given the tendency for "biological continuity" over time that most physical anthropologists studying this time period have already determined using traditional model-free biodistance approaches (see Chapter 4).

However, without dismissing the issues surrounding inter-observer measurement error, one way of reducing the negative effects of error is by having large sample sizes. Although no formal power analysis was performed prior to data collection to determine the minimum sample sizes necessary to avoid Type-II error, sample sizes used in the

craniometrics range from 2 to 809, with an average of 63 individuals representing a "population". These numbers are consistent with (and in many cases exceed) other biodistance studies of (pre)historic peoples that focus on questions of ethnicity and ethnogenesis (i.e., Stojanowski, 2004; Klaus, 2008; Kurin, 2012). Thus, given that the authors providing the raw craniometrics used the same underlying measurement protocol, that generally large sample sizes were involved, and that cranial dimensions are normally distributed, the likelihood of statistical "noise" swamping a statistical "signal" is low.

8.4.0 ANALYTICAL METHODS

8.4.1 Pre-Analysis Data Treatment

Odontometrics

Pre-analysis data treatment of all crown and cervical dimensions included tests for outliers and for normality. Specifically P/P plots for normality were generated in SPSS (version 20 SPSS Inc. Chicago IL) and any non-normal variables were eliminated. Likewise box-plots of individual measurements were used to identify and eliminate any statistical outliers defined as those points two standard deviations above or below the mean.

Next, the odontometric data were tested for age-related correlations using Pearson's R in SPSS. Because age estimates were not always reported (e.g., poor preservation; no record), and skeletal and chronological age may not always coincide (e.g., stress/nutrition affects skeletal growth), I used a proxy for "age"—tooth wear. More specifically, there are strong correlations between molar wear and adult age at death (e.g., Mays, 2002). Thus, all teeth were recorded for occlusal surface wear based on Smith's

(1984) stages, and the composite wear scores of maxillary and mandibular first molars were correlated with crown and cervical dimensions. Any significantly ($p \leq 0.05$) correlated variables were eliminated from further analysis.

Unfortunately, a similar test for correlations between sex and odontometric variables was not possible due to 1) a lack of reported sex estimates based on skeletal morphological traits for a large number of individuals, and 2) the author making no estimates herself. However, tests were performed to assess whether the available sex estimates based on skeletal morphological traits yielded equal ratios between males and females for each site, region, and temporal phase of those sites and regions. Accordingly, a X^2 Analysis with Yates Corrections or an analysis of Log-Likelihood Ratios (depending on sample size) was performed. Results indicate that sex ratios by site, region, and time period were mostly equal. Only the Paris Basin Region exhibits statistically unequal frequencies of males and females, and this outcome is due to two sites in particular: Chelles and Champlieu. These results are potentially informative, since unequal sex ratios could indicate a bias in burial practices and/or that these skeletal assemblages differed in their biological "catchment areas" (see Stojanowski and Schillaci, 2006). A more likely explanation for Chelles and Champlieu, however, is a tendency by nineteenth century excavators to have prioritized the recovery and curation of skeletal material with associated grave goods, like belt buckles and swords, which were indeed more common in the graves of males.

In addition to testing for normality, outliers, age correlations, and sex ratios, all crown and cervical dimensions were subject to an assessment of intra-observer error. A random selection of individuals (n=60) were re-measured and recorded. Corresponding

measurement sets of each variable were assessed using paired sample *t*-tests and F-tests in Excel (version 11 Microsoft, Redmond WA). These tests were run for each dental measurement at both the site- and regional-scale. Any variable exhibiting a significant difference $(p \leq 0.05)$ was eliminated from further analysis. Furthermore, any case or variable having missing values greater than or equal to 85% of the total were eliminated from further analysis. These combined processes ultimately yielded 63 dimensional variables (out of a total of 128) used in further analyses (Table 4).

Because an R-matrix Analysis (R-Model Evaluation Toolkit (RMET) 5.0 Relethford) requires a complete data matrix, missing values for all cases and variables were imputed using the Expectation-Maximization (EM) Algorithm in SPSS. Each site was then subjected to a Factor Analysis in SPSS in order to produce new variables that are orthogonal and thus un-correlated to each other. Factor scores having eigenvalues greater than one were saved and incorporated as the new data matrix of values coded by site region and time period. This dataset was then subjected to an R-matrix Analysis.

Table 4

Odontometric Variables

Dimension	Tooth
Crown:	
Maxillary:	
Mesio-Distal	LM^3, LM^2, RP^3, RM^2, RM^3
Bucco-Lingual	LM^1, LC, LI^2, RI^2, RC, RP^4, RM^2, RM^3
Mandibular:	
Mesio-Distal	LM_3, LM_2, LM_1, RC, RM_1
Bucco-Lingual	LM_3, LM_2, LM_1, LP_4, LI_2, RI_1, RI_2, RP_3, RP_4, RM_3
Cervical:	
Maxillary:	
Mesio-Distal	LP^3, LI^2, RC, RP^3, RP^4, RM^1
Bucco-Lingual	LM^2, LP^4, LP^3, LC, LI^2, RI^1, RI^2, RC, RP^4, RM^1, RM^2
Mandibular:	
Mesio-Distal	LM_3, LM_2, LM_1, LP_4, LP_3, LC, LI_2, RC, RP_3, RP_4, RM_2
Bucco-Lingual	LP_3, RI_2, RP_3, RP_4, RM_2, RM_3

Note: These represent the culled variables after pre-analytical data treatments.

Craniometrics

Much like the odontometric data, all craniometric data were assessed using box-plots in SPSS (version 20 SPSS Inc Chicago IL) to identify and eliminate statistical outliers ($\pm 2\sigma$). Likewise P/P plots were generated to evaluate normality. Any variables with non-normal distributions were removed. Since the author did not perform any age estimates, tests for age-related correlations could only be performed on those individuals having a published age estimate. Numerical ages and nominal age grades were "converted" into an ordinal age category using the ranges in Table 5. An ANOVA using the ordinal age categories as a fixed factor was then performed on the craniometric variables of those individuals possessing a published age estimate. All significant ($p \leq 0.05$) variables were removed from further analysis.

Initial *t*-tests for sex-correlations showed that all variables were significantly correlated with sex (when this estimate was provided). Given the likely influence of sexual dimorphism to size, the Geometric Mean was used as a size correction (see Jungers et al., 1995). Next, any remaining case or variable having missing values greater than or equal to 85% of the total were eliminated from further analysis. Each remaining variable was log-transformed, and the log geometric mean of all measurements for each individual was calculated. The difference between the log-transformed mean of each case and its variable formed the basis for further data imputation using EM to eliminate any remaining missing data. Table 6 lists the concluding craniometric variables. Finally the resulting covariance matrix was subjected to Factor Analysis. Factor scores with eigenvalues greater than one were saved and used as the new data matrix.

Supplementary codes for region and time period were also noted in this final data matrix. Given the large numerical size of the craniometrics dataset, as well as its geographic breadth (Figure 4), it was necessary to combine sites into larger geographic regions while also keeping temporal components separate. This was done to avoid an overly burdensome dataset[36] for the main statistical analyses, as well as to prevent singletons from representing a single region. The pooling of geographically close samples has precedence (i.e., Stojanowski, 2004; Ragsdale and Edgar, 2015) and is considered an appropriate technique when faced with low sample sizes (Relethford and Blangero, 1990: 21).

[36] RMET can handle 62 populations or less (http://konig.la.utk.edu/relethsoft.html)

Table 5

Age Variables

Category	Age Range	Order
Adolescent	16-18/20	1
Young Adult	18/20-35	2
Mature Adult	35-50	3
Older Adult	50+	4

Note: These were used to test for age-related correlations.

Table 6

Craniometric Variables

Dimension	Martin Number
Glabella-Opisthocranion Length (GOL)	1
Basion-Nasion Length (BNL)	5
Minimum Frontal Breadth (WFB)	9
Maximum Frontal Breadth (XCB)	8
Basion-Bregma Height (BBH)	17
Porian-Bregma Height	20
Nasion-Bregma Arc	26
Bregma-Lambda Arc	27
Frontal Chord (FRC)	29
Parietal Chord (PAC)	30
Occipital Chord (OCC)	31
Nasion-Prosthion Height (NPH)	48
Dacryon-Ectoconchion (OBB)	51a
Orbit Height (OBH)	52
Nasal Breadth (NLB)	54
Nasion-Nasospinale Height (NLH)	55

Note: These represent the culled variables after pre-analytical data treatments.

8.4.2 Statistical Analysis

The same statistical analyses were performed for both the odontometric and craniometric data. These analyses included R-matrix analysis, Mantel tests, and their associated tests for significance to be discussed below. Furthermore principal coordinates were employed to visualize the genetic relationships generated by the R-matrix. All R-matrix analyses were performed using RMET version 5.0 (Relethford et al., 1997). All Mantel tests were performed using XLSTAT (Addinsoft 2015)

Relationship Matrix (R-Matrix) Analysis and the Relethford-Blangero Model

Chapter 5 outlined the nature of quantitative variation biodistance techniques and the relationship between these topics and ethnic identity. Quantitative traits such as cranial and dental dimensions can be used 1) to assess *specifically* aspects of population structure and 2) to explore *generally* the intersections of biological variation and social identity within a biosocial interpretive framework. The Relethford-Blangero Model[37] (Relethford and Blangero, 1990) is important for understanding population structure and the microevolutionary forces (i.e. gene flow, genetic drift) that contribute to it.

The Relethford-Blangero Model was a modification of a model initially developed by Harpending and Ward (1982). These authors used allele data to provide a model of intra-regional genetic heterozygosity that assumes the following null hypothesis (H_0): if all subpopulations of a given region exchange mates with the same outside (e.g. extra-local) source at an equal rate then there should be a linear relationship between average within-group variance and the genetic distance to the regional centroid (*ibid*:

[37] The following derivations of the R-matrix and its expansion to multivariate quantitative traits are found in Relethford and Blangero (1990) and Relethford et al. (1997), unless otherwise stated.

217). Thus one can compare observed (sub)population genetic variance/heterozygosity to an expected level of regional heterozygosity; any deviations from expectation would suggest that a subpopulation experienced greater than average gene flow and became more genetically diverse (i.e., more heterogeneous) or experienced less than average gene flow and became more genetically isolated (i.e., more homogeneous) (Relethford and Blangero, 1990: 6).

Harpending and Ward's (1982) model specifically used a Relationship Matrix (R-Matrix) of standardized variances and covariances of (sub)population allele frequencies. Thus, each element r_{ij} of the R-matrix is computed as

$$r_{ij} = \frac{(p_i - \bar{p})(p_j - \bar{p})}{p(1 - \bar{p})} \quad \textbf{(Eq 3)}$$

where p_i and p_j are the allele frequencies of a given trait in (sub)populations *i* and *j* respectively. The weighted mean allele frequency is $\bar{p}$. The average weighted element of the R-matrix is equal to 0 and the weighted average diagonal of the R-matrix (e.g., F_{ST}) acts as an indicator of microdifferentiation.

For *n* loci having two alleles at each locus the expected heterozygosity $E(H_i)$ of a (sub)population *i* is

$$E(H_i) = H_t(1 - r_{ii}) \quad \textbf{(Eq 4)}$$

where H_t is the heterozygosity of the total region. The distance of (sub)population *i* from the regional centroid (r_{ii}) is generated from the diagonal of the R-matrix in Equation 3.

Under an assumption of complete panmixia the heterozygosity of the total region is defined as

$$H_t = \sum \frac{2\bar{p}_k \bar{q}_k}{n}. \quad \textbf{(Eq 5)}$$

The variables $\bar{p}_k$ and $\bar{q}_k$ are defined as the weighted mean allele frequencies for locus *k* and

$$\bar{p}_k = \sum w_i p_{ik}$$

$$\bar{q}_k = 1 - \bar{p}_k$$

where w_i is the ratio of the census size of (sub)population *i* to the total census size of all groups combined and p_{ik} is the frequency of one allele at locus *k* in (sub)population *i*. Finally, the observed heterozygosity (H_i) of (sub)population *i* is computed as

$$H_i = \sum \frac{2p_{ik}q_{ik}}{n} \quad \textbf{(Eq 6)}$$

Thus, should a (sub)population deviate from the expected level of heterozygosity for a region either receiving greater (e.g., where $H_i > E(H_i)$) or less (e.g., where $H_i < E(H_i)$) than the expected/average external gene flow one can better characterize any increase or decrease in biological distance as well as detect differential admixture (Relethford and Blangero, 1990: 8). In other words if the rate or source of extra-local

gene flow is different for a specific (sub)population, then the null hypothesis would be violated and the (sub)population in question would exhibit either greater or less than expected extra-local gene flow.

Despite the obvious benefits afforded by the Harpending and Ward (1982) model allele frequencies for many traits of interest are virtually unknown. It was for this reason that Relethford and Blangero (1990) extended it to apply first to univariate quantitative traits and then to multivariate quantitative traits. The process for doing so is fairly simple. First, the trait(s) in question should be subject to equal and additive effects of genetic variance (a safe assumption, see Chapter 5). Given a polygenic trait with additive effects over multiple loci and two alleles *p* and *q* the genotypic values of each genotype of locus *k* can be written as

$$\alpha_k \; 0 \; -\alpha_k.$$

However since we assume a model of genetic variance having equal effects over all loci then

$$\alpha_k = \alpha.$$

If we take that the additive genetic variance (σ_G^2) within (sub)population *i* is

$$\sigma_{Gi}^2 = \sum 2\alpha^2 p_{ik}(1 - p_{ik}) \qquad \textbf{(Eq 7)}$$

(Falconer, 1981), then assuming panmixia the additive genetic variance for the total region in question would be

$$\sigma_{Gt}^2 = \sum 2\alpha^2 p_{ik}(1 - \bar{p}_k). \quad \textbf{(Eq 8)}$$

Assuming that heterozygosity and additive genetic variance are proportional to each other (see Chapter 5), then the heterozygosity for (sub)population *i* is

$$H_i = \frac{\sigma_{Gi}^2}{n\alpha^2}. \quad \textbf{(Eq 9)}$$

Furthermore the heterozygosity for the total panmictic region is

$$H_t = \frac{\sigma_{Gt}^2}{n\alpha^2}. \quad \textbf{(Eq 10)}$$

This straightforward projection then permits us to compute the expected levels of heterozygosity based on a quantitative trait for a (sub)population *i* by using Equations 4 and 8, which gives us

$$E(\sigma_{Gi}^2) = \sigma_{Gt}^2(1 - r_{ii}). \quad \textbf{(Eq 11)}$$

Since the additive genetic variance (σ_{Gi}^2) of the panmictic region is a product of within- and among-group variance it cannot be actually be directly observed (Relethford and Blangero, 1990: 9). Rather it must be estimated. Thus,

$$\sigma_{Gt}^2 = \frac{\sigma_{Gw}^2}{1 - r_0} \quad \textbf{(Eq 12)}$$

where σ_{Gw}^2 is the pooled within-group genetic variance and r_0 is the weighted average genetic distance to the centroid of the R-matrix defined by contemporary alleles. This latter parameter, r_0, is computed as

$$r_0 = \sum w_i r_{ii} \quad \textbf{(Eq 13)}$$

where w_i is the relative census size of (sub)population *i*. Similarly the pooled within-group genetic variance (σ_{Gw}^2) must be weighted due to the effects of differential (sub)population sizes. Thus

$$\sigma_{Gw}^2 = \sum w_i \sigma_{Gi}^2. \quad \textbf{(Eq 14)}$$

The expected heterozygosity based on a quantitative trait for a (sub)population *i* can now be expressed as

$$E(\sigma_{Gi}^2) = \frac{\sigma_{Gw}^2(1 - r_{ii})}{1 - r_0} \quad \textbf{(Eq 15)}$$

where r_{ii} is the genetic distance of the quantitative trait from the centroid. This latter parameter is determined in the following manner: first the phenotypic mean of the total region ($\bar{x}_t$) is defined as

$$\bar{x}_t = \sum w_i \bar{x}_i \quad \textbf{(Eq 16)}$$

where $\bar{x}_i$ is the phenotypic mean for (sub)population *i*. We can determine the phenotypic mean since environmental effects are assumed to be negligible (see Chapter 5), so $\bar{x}_i$ is also understood to be the genetic mean of the trait in question. Thus, for *g* groups/subpopulations we can define a *g x g* matrix *C* having elements

$$c_{ij} = (\bar{x}_i - \bar{x}_t)(\bar{x}_j - \bar{x}_t) \quad \textbf{(Eq 17)}$$

Now the elements r_{ij} of the R-matrix can be written as

$$r_{ij} = \frac{c_{ij}(1 - r_0)}{2\sigma_{Gw}^2} \quad \textbf{(Eq 18)}$$

with the genetic distance of (sub)population *i* from the regional centroid given by

$$r_{ii} = \frac{c_{ii}}{(2\sigma_{Gw}^2 + \sum w_i c_{ii})}. \quad \textbf{(Eq 19)}$$

The weighted average genetic distance to the centroid can now be rewritten as

$$r_0 = \frac{\sum w_i c_{ii}}{2\sigma_{Gw}^2 + \sum w_i \, c_{ii}}. \quad \textbf{(Eq 20)}$$

Because the genetic variance of a trait should include the proportion of additive to environmental effects (h^2, see Chapter 5) the genetic variance of a trait in (sub)population *i* can be written as

$$\sigma_{Gi}^2 = h_i^2 \sigma_{Pi}^2 \quad \textbf{(Eq 21)}$$

where σ_{Pi}^2 is the phenotypic variance. Furthermore, by assuming (for an explanation, see Relethford and Blangero, 1990: 11) that h^2 is the same over all populations, then the additive genetic variance of a trait in the total region subject to panmixia is

$$\sigma_{Gt}^2 = h^2 \sigma_{Pt}^2. \quad \textbf{(Eq 22)}$$

Thus, by substitution, the expected phenotypic variance of a trait in (sub)population *i* is

$$E(\sigma_{Pi}^2) = \frac{\sigma_{Pw}^2(1-r_{ii})}{1-r_0} \quad \textbf{(Eq 23)}$$

and the sample variance can be used to estimate the observed phenotypic variance (σ_{Pi}^2) of (sub)population *i*. Finally the elements of the R-matrix can be rewritten as

$$r_{ij} = \frac{c_{ij}(1 - r_0)}{2h^2\sigma_{Pw}^2}. \quad \textbf{(Eq 24)}$$

Up to this point the expected and observed levels of heterozygosity for a single quantitative trait have been generated. Likewise the elements of the R-matrix and its centroid have been calculated for a single quantitative trait. However, the data used in most bioanthropological analyses are multivariate in nature. Consequently, Relethford and Blangero (1990) continued to adapt the Harpending-Ward (1982) model to include multivariate data. By considering *m* variables for *g* (sub)populations they establish a number of functional steps for determining the elements of the R-matrix and the expected and observed heterozygosities for these *m* variables.

First, they denote P_i as the phenotypic covariance matrix of (sub)population *i* having *m* variables. Because this phenotypic covariance matrix consists of both additive and environmental effects, P_i can be decomposed into an additive genetic covariance matrix G_i and a random environmental covariance matrix E_i, which is likely to be held constant (see Equation 1). Thus, the expected heterozygosity of (sub)population *i* is denoted by

$$E(G_i) = \frac{G_w(1 - r_{ii})}{1 - r_o} \quad \textbf{(Eq 25)}$$

where G_w is the pooled within-(sub)population additive genetic covariance matrix. Given the proportionality between (sub)populations and G_w, there is a common genetic correlation matrix (i.e., R-matrix or R_G) between them. In other words there is an R-matrix that can be generated for multivariate quantitative traits for all (sub)populations g. The challenge stems from finding a way to describe or represent its properties and elements in terms of population parameters.

The solution is eigenvectors, which Relethford and Blangero (1990: 12-13) detail extensively but will not be discussed here. Regardless they show that the expected average genetic variance can be calculated as

$$E(\bar{v}_{Gi}) = \frac{\bar{v}_{Gw}(1 - r_{ii})}{1 - r_0}. \quad \textbf{(Eq 26)}$$

The genetic distance of (sub)population *i* to the regional centroid can be computed as

$$r_{ii} = \frac{c_{ii}}{2m + \sum w_i c_{ii}} \quad \textbf{(Eq 27)}$$

while the average genetic distance is given as

$$r_0 = \frac{\sum w_i c_{ii}}{2m + \sum w_i c_{ii}}. \quad \textbf{(Eq 28)}$$

Furthermore by assuming 1) that the heritabilities (h^2) for the *m* quantitative traits are constant across all (sub)populations (or substituted for a single estimate of an average heritability as in this manuscript; see Cheverud, 1988), and 2) that environmental variance has no effect, then the additive genetic variance of (sub)population *i* is computed such that

$$G_i = h^2 P_i - E_w$$

$$G_i = h^2 P_i. \quad \textbf{(Eq 29)}$$

The estimated distances from the regional centroid (r_{ii}) are then taken to be the minimum genetic distances between (sub)populations and are conservative in nature, lending themselves to cautious cross-comparison with other studies (for example, see Stojanowski, 2004: 324).

The elements of the R-matrix can now be written as

$$r_{ij} = \frac{c_{ij}(1 - r_0)}{2h^2 v_P^2} \quad \textbf{(Eq 30)}$$

where v_P^2 is the phenotypic variance. Moreover, because r_0 is a measure of the variation of distances from a regional centroid it is equivalent to Wright's (1951) F_{ST}. So, Equation 30 can be rewritten as

$$r_{ij} = \frac{c_{ij}(1 - F_{ST})}{2h^2 v_P^2} \quad \textbf{(Eq 31)}$$

where

$$F_{ST} = \sum_{i=1}^{g} w_i r_{ii}. \quad \textbf{(Eq 32)}$$

Finally a return to the null hypothesis (H_0 = if all subpopulations of a given region exchange mates with the same outside source at an equal rate then there should be a linear relationship between average within-group variance and the genetic distance to the regional centroid) shows that the expected/average within-group/(sub)population heterogeneity can finally be written as

$$E(\bar{v}_{Pi}) = \frac{\bar{v}_{Pw}(1 - r_{ii})}{1 - F_{ST}}. \quad \textbf{(Eq 33)}$$

Thus, one can now compare observed (sub)population phenotypic variance/heterozygosity to an expected level of regional heterozygosity. Any resulting difference is known as the ***residual***. A scatterplot showing the line of expected heterozygosity with the distance to the centroid against observed (sub)population variances is a convenient means of displaying residuals and is employed in this manuscript.

Estimated Parameters of the R-Matrix

There are a number of potentially informative population genetic parameters that can be estimated from the R-matrix (see Chapter 5). The first of these is $\boldsymbol{F_{ST}}$, which is a measure of regional genetic diversity. As demonstrated by Equations 28 and 32, F_{ST}provides a summary measure of the genotypic heterozygosity for a given region. The Relethford-Blangero model uses this statistic to determine the *residuals* as shown in Equation 30-33. The residuals provide a way to estimate differential gene flow an important aspect of population structure.

Another key population parameter is genetic distance $\boldsymbol{d^2}$, which can be estimated from the R-matrix (Harpending and Jenkins, 1973). Measures of genetic distance combine large amounts of data and are comparable to geometric distance (Hedrick, 2011: 378). Specifically the genetic distance between (sub)population *i* and (sub)population *j* can be calculated as

$$d_{ij}^2 = r_{ii} + r_{jj} - 2r_{ij}. \qquad \textbf{(Eq 34)}$$

This estimate of genetic distance is similar to Mahalanobis's D^2 which is itself a generalized expression of the distance between two statistically normal populations based on a matrix of variances and covariances for any number of traits (Mahalanobis, 1936). These distances actually represent the minimum possible genetic distances as demonstrated by Williams-Blangero and Blangero (1989: 4-5).

Interestingly, a principal coordinates analysis can be performed on this d^2 matrix to assess patterns of phenotypic relationships between and among (sub)populations. This

approach (Gower, 1966) uses the latent roots or eigenvalues of the d^2 matrix to plot complex patterns of biological relationships in just two or three dimensions (see Harpending and Jenkins, 1973 for an early visual example; for an explanation of eigenvalues and matrix algebra, see Manly, 1995). This approach not only permits a visual representation of the d^2 matrix but it also facilitates further interpretation of the factors that may be responsible for population similarity and differentiation.

Bias Correction and Standard Errors

Both F_{ST} and the elements of the d^2 must be statistically corrected for bias that arises from small sample size (see Relethford, 1991a). This step is important since small sample sizes (used as population proxies) can potentially skew the results and suggest greater amounts of genetic drift and regional heterogeneity than actually occurred.

Thus a bias corrected F_{ST} can be calculated as

$$unbiased\ F_{ST} = \sum_{i=1}^{g} w_i(r_{ii} - \frac{1}{2n_i}) \qquad \textbf{(Eq 35)}$$

where n_i is the *relative* size of (sub)population *i* and where any negative bias-corrected estimates are truncated to zero. Similarly, the bias-corrected elements of the d^2matrix can be computed as

$$unbiased\ d_{ij}^2 = (r_{ii} - \frac{1}{2n_i}) + (r_{jj} - \frac{1}{2n_j}) - 2r_{ij}. \qquad \textbf{(Eq 36)}$$

Another important step is ensuring statistical significance. Just how variable is the estimated F_{ST}? In other words, if we take the null hypothesis that F_{ST} does not differ significantly from zero, then the division of F_{ST} by its standard error provides a test of significance. This is because the results follow a *t*-distribution where *g* are the number of (sub)populations/samples in the R-matrix analysis and the degrees of freedom are computed as

$$\nu = n_g - 1 \qquad \textbf{(Eq 37)}$$

Similarly, if we take the null hypothesis that the estimated genetic distance between two (sub)populations d_{ij}^2 is not significantly different from zero (in other words they are genetically the same) then following the same process as F_{ST} above the division by its standard error would provide a test of significance.

The standard errors of F_{ST} are calculated by taking the square root of the following equation:

$$\sigma_{F_{ST}} = \sqrt{\sigma_{F_{ST}}^2} = \sqrt{\left(\frac{2}{m}\right)(1 - F_{ST})^3 \left(\sum \frac{w_i^2 r_{ii}}{n_i}\right)} \qquad \textbf{(Eq 38)}$$

where *m* is the number of quantitative traits. Likewise the standard errors of d_{ij}^2 can be calculated by taking the square root of its variance:

$$\sigma_{d_{ij}^2} = \sqrt{\sigma_{d_{ij}^2}^2} = \sqrt{\frac{2(1 - F_{ST})d_{ij}^2}{m}\left(\frac{1}{n_i} + \frac{1}{n_j}\right)}. \quad \textbf{(Eq 39)}$$

Factors Affecting Heterozygosity

As outlined previously a deviation from the expected regional heterozygosity can result from differential gene flow to one or more (sub)populations. However changes in regional heterozygosity may also arise due to other factors (see Hedrick, 2011: 98). Specifically a *decrease* in regional heterozygosity may be due to the following: 1) natural selection for homozygotes; 2) inbreeding; 3) positive-assortative mating; 4) gene flow of zygotes; 5) the Wahlund Effect; and 6) mutation. Similarly an *increase* in regional heterozygosity may be due to the following: 1) natural selection for heterozygotes; 2) outbreeding; 3) negative-assortative mating; 4) gene flow of gametes; 5) mutation; and 6) geographic distance or ecological barriers.

Given the relatively short time period (~1000 years) involved in this study, the similar ecological setting shared by the people represented in the study samples, as well as evidence for stabilizing selection on the functional morphology of the human skeleton and dentition (Weaver et al., 2007; Betti et al., 2010), natural selection for or against heterozygotes is unlikely to be a major factor contributing to any variability in observed heterozygosities for this study. Likewise, given the rarity of mutation events—especially mutations resulting in changes in allele frequencies and/or observable and viable changes in phenotypes—mutation rates can be safely assumed to be shared equally across space and time for all (sub)populations used in this study.

Inbreeding and outbreeding both have the potential for influencing heterozygosity. Inbreeding is the result of non-random mating in which two individuals share alleles due to close common descent. Inbreeding does not result in changes in allele frequencies; it shifts the relative proportion of homozygotes to heterozygotes increasing the frequency of homozygotes and decreasing heterozygosity. Outbreeding is also a result of non-random mating, but it is the opposite of inbreeding and also does not change allele frequencies. Outbreeding increases the frequency of heterozygotes and thus increases heterogeneity. However, these two types of non-random mating are not expected to have a serious and lasting influence on genotype frequencies (see Hedrick, 2011: 442) especially since changes in genotype would affect *all* loci in the genome increasing the frequency of deleterious traits upon which selection would act. Similarly any changes in non-random mating practices can "erase" the effects inbreeding or outbreeding in the span of a single generation.

Other forms of non-random mating are positive- and negative-assortative mating. Based on phenotypes rather than genotypes, these forms of non-random mating likely do play a role in the observed differences in heterozygosities in this study because mate-choice is based on phenotype (i.e., hair color choice of religion) rather than on genotype for these forms of non-random mating (see Alavarez and Jaffe, 2004). Positive-assortative mating occurs when an individual chooses a mate with the same phenotype more often than would be expected by chance; negative-assortative mating is when an individual chooses a mate with the same phenotype less often than would be expected by chance (Hedrick, 2011: 516).

A distinction between the gene flow of zygotes versus that of gametes may also result in a decrease or increase in heterozygosity. The gene flow of zygotes (i.e., an egg fertilized by a sperm) would progressively remove variation from a (sub)population whereas the gene flow of gametes (i.e., an egg or a sperm) would progressively introduce variation into a (sub)population. In simpler terms, a pregnant female that migrates from a group effectively reduces that group's heterogeneity because she is removing from that group any variation due to genetic recombination. In contrast, a male or female that migrates outside of his/her group will carry gametes with him/her such that successful mating with individuals from another group will introduce new alleles and thus increase genetic variation.

The Wahlund Effect, substructuring that may be present within a population but which is not evident to the observer, may also serve to reduce genetic variation within a population. Thus, if two (sub)populations that are individually quite different from each other and possess differing allele frequencies are (unknowingly) combined into a single sample, the resulting frequencies of heterozygotes are reduced (for an explanatory computation, see Hedrick, 2011: 376). The Wahlund Effect is unlikely to be a factor in decreased heterogeneity here due to the close geographic proximity of the communities sampled for this analysis, as well as the relatively constrained time periods. Furthermore, a decrease in heterogeneity can only be attributed to the Wahlund Effect if the differences in allele frequencies between the combined samples are quite large (Hedrick, 2011: 376).

Finally, the presence of ecological barriers such as mountains or bodies of water serves to disrupt the flow of alleles thereby increasing heterogeneity. Likewise large geographic distances can also prevent the homogenizing flow of alleles. It is much easier

to find a mate who lives close by than one who lives farther away. Indeed a generalized observation in population genetics is of gene flow when populations are randomly distributed across the landscape (see Wright, 1943). Because those (sub)populations who are geographically proximate likely share more alleles in common there is a linear relationship (i.e., a genetic cline) between allele frequency and geographic distance. However, this prediction must be tested, as described below.

Isolation-By-Distance and the Mantel Test

As previously stated, geographic distance can serve to isolate (sub)populations from each other, resulting in increased heterogeneity. This concept is known as isolation by distance, and it can be explicitly tested by creating a matrix of geographic distances and comparing it to an analogous matrix of biological distances (d^2 matrix). This technique was first developed by Mantel (1967) to test for time-space correlations within epidemiology. Smouse and colleagues (1986) elaborated the method to include the definition of a geographic distance matrix *Y*. The elements of this matrix Y_{ij} represent the geographic distance between (sub)populations *i* and *j*. Thus, *X* represents the genetic distance matrix (d^2 matrix) generated by the R-Matrix Analysis, and X_{ij} represents the genetic distance between (sub)populations *i* and *j*. The null hypothesis is that X_{ij} and Y_{ij} are not correlated; the alternative hypothesis (H_a) is that there is a positive correlation between both matrices.

If we let Z represent the sum of the cross-products between X_{ij} and Y_{ij} then the expected product of the summation of all pairs *i* and j can be computed as

$$E(Z_{XY}) = \sum_{ij} X_{ij}Y_{ij}. \quad \textbf{(Eq 40)}$$

The observed product of the summation of all pairs *i* and j can be written as

$$O(Z_{XY}) = \sum_{ij} X_{ij}Y_{ij}. \quad \textbf{(Eq 41)}$$

Given that the Mantel Test is essentially a linear regression (without requiring any knowledge of the underlying statistical distribution of each variable) of X_{ij} on Y_{ij} the regression coefficient can be written as

$$b_{YX} = \frac{SP(XY)}{SS(X)} \quad \textbf{(Eq 42)}$$

where

$$SP(XY) = O(Z_{XY}) - N\left(\sum_{ij}\frac{X_{ij}}{N}\right)\left(\sum_{ij}\frac{Y_{ij}}{N}\right)$$

$$SS(X) = \sum_{ij}\left(X_{ij} - \left(\sum_{ij}\frac{X_{ij}}{N}\right)^2\right)$$

$$N = K(K-1)$$

and *K* is the number of (sub)populations or groups forming the analysis. Furthermore, the correlation coefficient can be computed as

$$r_{YX} = \frac{SP(XY)}{\sqrt{SS(X) * SS(Y)}} \quad \textbf{(Eq 43)}$$

where

$$SS(Y) = \sum_{ij} \left(Y_{ij} - \left(\sum_{ij} \frac{Y_{ij}}{N} \right)^2 \right). \quad \textbf{(Eq 44)}$$

Finally, using a null distribution based on Monte Carlo sampling, one can calculate the probability of obtaining a particular $E(Z_{XY})$ relative to $O(Z_{XY})$ based on chance alone. This last step involves the randomization of the rows and columns for 1000 iterations and looks for significant ($p \leq 0.05$) correlation coefficients (Smouse et al., 1986).

Fortunately, the comparison of X and Y can be accomplished using XLSTAT. Initially, matrices of inter-site and inter-region walking-distances were generated using Google Maps (2015). Complete precision was not always possible, especially when recording inter-region walking distances. However given the process for calculating correlation coefficients described above, relative geographic distances are of primary importance. It should also be noted that the walking-distances computed from Google Maps (*ibid*) may not reflect the true routes by which individuals travelled during the Gallo-Roman and Early Medieval Periods. Regardless, many of the routes forming the Roman road network are now under modern European roads (for example, see

Codrington, 1909) and may thus be sufficient for this part of the analysis. Future research could include a GIS study based on the *Tabula Peutingeriana* (Figure 14), a 4th century AD map of the Roman road network for Europe North Africa and parts of Asia (see Talbert, 2010). Next, the geographic distance matrix is combined with the genetic distance matrix in the manner prescribed by XLSTAT and results were recorded.

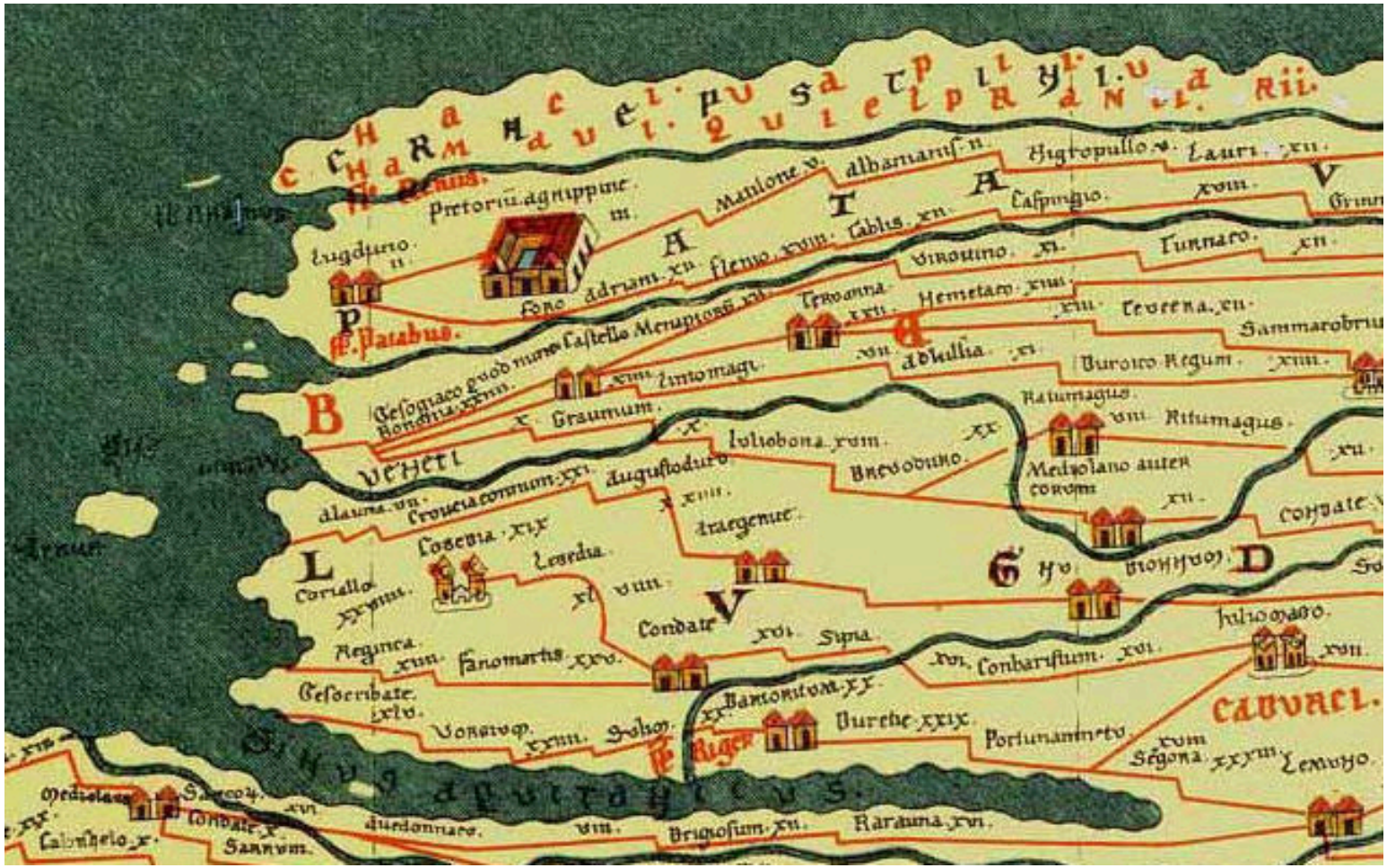

Figure 14. Portion of the *Tabula Peutingeriana*, a Roman-era map of Western Europe and Northern Africa (by Conradi Millieri (Ulrich Harsch Bibliotheca Augustana) [Public domain], via Wikimedia Commons).

8.5.0 ORGANIZATION OF ANALYSES AND RESULTS

8.5.1 Analytical Organization

To assess Early Medieval population structure and how it changed over time, the odontometric and craniometric data were analyzed synchronically and diachronically using the temporal divisions outlined in Table 7. Thus, two key analyses were performed, each of which possesses synchronic and diachronic components (Table 8).

8.5.2 Demographic Scenarios

Each analysis was performed using two different estimates of narrow-sense heritability (h^2): 1) $h^2 = 1.0$; and 2) $h^2 = 0.55$ (see Table 9). An h^2 of 1.0 would yield the most conservative estimates of biological distances and regional heterogeneity. Furthermore an h^2 of 1.0 facilitates comparison with other published biodistance studies. Although representing a more balanced proportion of additive genetic effects to environmental effects for the quantitative traits in question, a h^2 of 0.55 would also yield less conservative estimates of biological distances and regional heterogeneity. More accurate estimates of h^2 for each quantitative trait likely fall between these two values and thus using 1.0 and 0.55 should provide a justifiable range for estimates of biological distances and regional heterogeneity.

Changes in effective population size (N_e) also have potential effects on estimates of biological distance and regional heterogeneity generated by an R-matrix analysis (see Equation 35; Relethford, 1991a). Knowledge of actual N_e is impossible for the Gallo-Roman and Early Medieval Periods. However, it is *relative* population size that is most critical for these analyses since genetic drift is more likely to affect a smaller population

than a larger one. Consequently, each analysis was also performed using two different models of relative population size where: 1) all populations were equal in size synchronically and diachronically; and 2) populations differed in relative size synchronically and diachronically (see Table 9). Although it is unlikely that all populations were of equal size, this approach provides a baseline by which further comparisons and interpretations may be made.

Relative population sizes were generated from published sources on Early Medieval demography (for examples, see Russell, 1958; Durand, 1977). For most synchronic and diachronic analyses inter-site and -regional relative population sizes were based on the prevailing view that population sizes differed between northern and southern Gaul and that overall population sizes increased from AD 1 – 1000 (Russell, 1972: 25-71; see also Zimmerman et al., 2009)[38]. Likewise, these estimates were tempered by assessing archaeological proxies for population size, such as settlement size and number of burials (for a review on archaeological demography, see Chamberlain, 2009). Although estimating population sizes is a contentious subject, the analytical methods used in this study afford a certain amount of latitude for differences in relative population size. In other words, it is enough to know that one population was bigger than another. Any unorthodox differences between analyses using equal or relative population sizes would then warrant further examination. Consequently all results unless otherwise specified are also structured in the manner displayed in Table 9.

[38] Specifically, population sizes in the more mountainous southern portions of Gaul were much less than those in the north following the possible migration and settlement of "barbarians" into northern Gaul and due to distinct ecological differences between these broad regions (see Devroey and Jaubert, 2011).

Table 7

Chronology

Time Period	Year Range
Gallo-Roman:	AD 1-450
Early Roman	AD 1-200
Late Roman	AD 200-450
Frankish:	AD 500-900
Merovingian	AD 450-750
Carolingian	AD 750-900

Note: The year ranges for this chronology are approximate.

Table 8

Organization of Analyses

Analysis	Scale
Odontometric:	
Synchronic	Inter-Site, Inter-Region
Diachronic	Inter-Region
Craniometric:	
Synchronic	Inter-Region
Diachronic	Inter-Region

Table 9

Demographic Scenarios

Number	Narrow-Sense Heritability (h^2)	Population Size
1	1.0	Equal
2	0.55	Equal
3	1.0	Relative
4	0.55	Relative

8.6.0 SUMMARY

In this chapter, I illustrated how teeth form via a continuum of reiterative signaling throughout the human jaw. The number of teeth, their size, and their shape can be understood within the context of an odontogenic homeobox code. Furthermore, given their underlying quantitative variation, lack of remodeling after formation, resistance to taphonomic processes, and relatively high estimated heritabilities, teeth are particularly well suited to biodistance analyses

This chapter also outlined the methods employed for measuring tooth crowns and cervixes, the pre-analysis data treatments applied to them, and the final odontometric dataset subject to a biodistance analysis. The similar methods used to treat cranial measurements, their standards and pre-analytic data treatments, and their limited incorporation into this study, were also discussed.

Finally, a thorough exposition of the analytical techniques used in this study was established. Specifically, the mathematical basis of the R-matrix analysis, the Relethford-Blangero Model, and the Mantel Test were all explored. The structure of each analysis, their results, and their final configuration in subsequent chapters was also outlined.

CHAPTER 9

RESULTS: ODONTOMETRIC SYNCHRONIC ANALYSIS

9.0.0 INTRODUCTION

This chapter introduces the results for the synchronic biodistance analysis performed on the odontometric dataset. Relevant pre-analytical data treatments were performed (see Chapter 8), resulting in a total of 63 dimensional variables (see Table 4) for the four regions comprised of 11 sites and outlined in Chapter 7 (Tables 10 and 11). The goal of this portion of the analysis was to establish overall "snapshots" of the relationships between site and regions, regardless of their respective time periods.

Results are presented using individual sites as the subpopulations/units of the R-matrix analysis (site-level), and then by regions (regional-level). Both levels of analysis were performed using four different demographic scenarios (see Table 9). These scenarios are based on different permutations of population sizes (equal or relative) and of narrow-sense heritability estimates ($h^2 = 1.0$ or $h^2 = 0.55$). Each report includes details on the following: 1) the percentage of variation accounted for by the relationship matrix; 2) the spatial relationship among the analytical units/subpopulations depicted by a scatterplot of principal coordinates; 3) the results of the Mahalanobis d^2matrix; 4) the results of the Mantel Test; 5) the estimate of between-unit variance (i.e., the estimate of genetic diversity; F_{ST}); and 6) the Relethford-Blangero residuals (i.e., estimate of gene flow).

Table 10

Odontometric Sample Sizes: Sites

Site	Relative Population Size	Sample Size (n)
Frénouville (Normandy)	1	339
Réville (Normandy)	1	66
Sannerville (Normandy)	1	46
Verson (Normandy)	1	124
Giberville (Normandy)	1	72
Champlieu (Paris Basin)	1	14
Chelles (Paris Basin)	1	57
Mareuil-sur-Ourcq (Paris Basin)	1	7
Précy-sur-Oise (Paris Basin)	1	7
Granède (Midi-Pyrénées)	0.5	42
Larina (Rhône-Alps)	0.5	78
Total		852

Table 11

Odontometric Sample Sizes: Regions

Region	Relative Population Size	Sample Size (n)
Normandy	1	647
Paris Basin	1	85
Rhône-Alps	0.5	78
Midi-Pyrénées	0.5	42
Total		852

9.1.0 SITE-LEVEL

9.1.1 Demographic Scenario 1

Results for the first demographic scenario (equal population weights, h^2=1) are shown below (Figure 15). The first two eigenvectors account for 98.2% of the variation in the sample of 11 sites. As seen in the scatterplot of the principal coordinates for the sites, a subtle geographic north-south gradient can be seen in the dispersion of points along the second eigenvector, with sites from the north (Frénouville, Réville, Sannerville, Verson, and Giberville) being less than 0.0. Sites farther south have values greater than 0.0 along the second eigenvector. An exception to this trend is Champlieu from the Paris Basin. Figure 15 also shows the clear distinction that sites from the Paris Basin have in comparison to the remaining seven sites – they all possess values less than 0.0 along the first eigenvector. Four sites originating from the Paris Basin region (Champlieu, Chelles, Mareuil-sur-Ourcq, and Précy-sur-Oise) appear to form a group. Likewise, the five sites from the Normandy region (Frénouville, Réville, Sannerville, Verson, and Giberville) also form a group. While the first eigenvector seems to distinguish the Paris Basin sites from the remainder, the second eigenvector seems to distinguish all sites intra-regionally.

Table 12 shows the Mahalanobis distance measures derived from the R-matrix analysis. Those sites that are significantly different from each other are highlighted in bold and indicated with an asterisk. Frénouville is distinct from nearly all other sites with the exception of those from the Normandy region, as well as from Précy-sur-Oise. Interestingly, the biological distances between Frénouville and Mareuil-sur-Ourcq, and those of Frénouville and Verson approach significance ($p \leq 0.10$), possibly indicating a more complex relationship within and between the Normandy and Paris Basin regions. In

fact, the sites from the Paris Basin (with the exception of Précy-sur-Oise and Mareuil-sur-Ourcq) are significantly different from the Norman sites, as well as the sites from further south (i.e., Granède and Larina). In contrast, Précy-sur-Oise and Mareuil-sur-Ourcq do not share the same level of biological distinction as the other sites located in the Paris Basin, which perhaps coincides with their closer spatial proximity as seen in the principal coordinates analysis (Figure 15).

Since geographic distance could be a factor in these results, a Mantel Test for isolation-by-distance compared the biological and geographic distance matrices (Figure 16). The results were significant ($R^2 = 0.340$, $p = 0.011$), suggesting that isolation-by-distance may account for significant distances among sites. However, the unique patterning exhibited in the scatterplot of the two matrices suggests that there are a number of sites that are both geographically proximate and biologically similar (sites from Normandy), as well as a number of sites that are geographically distant and yet biologically similar (sites from Normandy and those from the Midi-Pyrénées and Rhône-Alps Regions). The cloud of points in the middle of the figure primarily represents those sites from the Paris Basin, which are overall biologically distinct from the others (see Figure 15). Thus, the scatterplot does not reveal a linear geographic relationship that would be expected given the significant Mantel results. It is possible that the greater number of individual sites from the Normandy Region promote a more linear response than might be the case should this same test be performed on a regional level.

The estimate of between-site variance (F_{ST}) was significantly different from zero, having a value of 0.056 ($p \leq 0.05$). Likewise, Relethford-Blangero residuals (Table 13) reveal that some sites had significantly less than expected external gene flow

(Frénouville, Réville, Giberville, Mareuil-sur-Ourcq), while others had significantly greater than expected extra-local gene flow (Granède, Larina, Champlieu, Chelles). These results are mirrored graphically in Figure 17, with sites like Frénouville and Giberville being well below the line and Larina being well above the line.

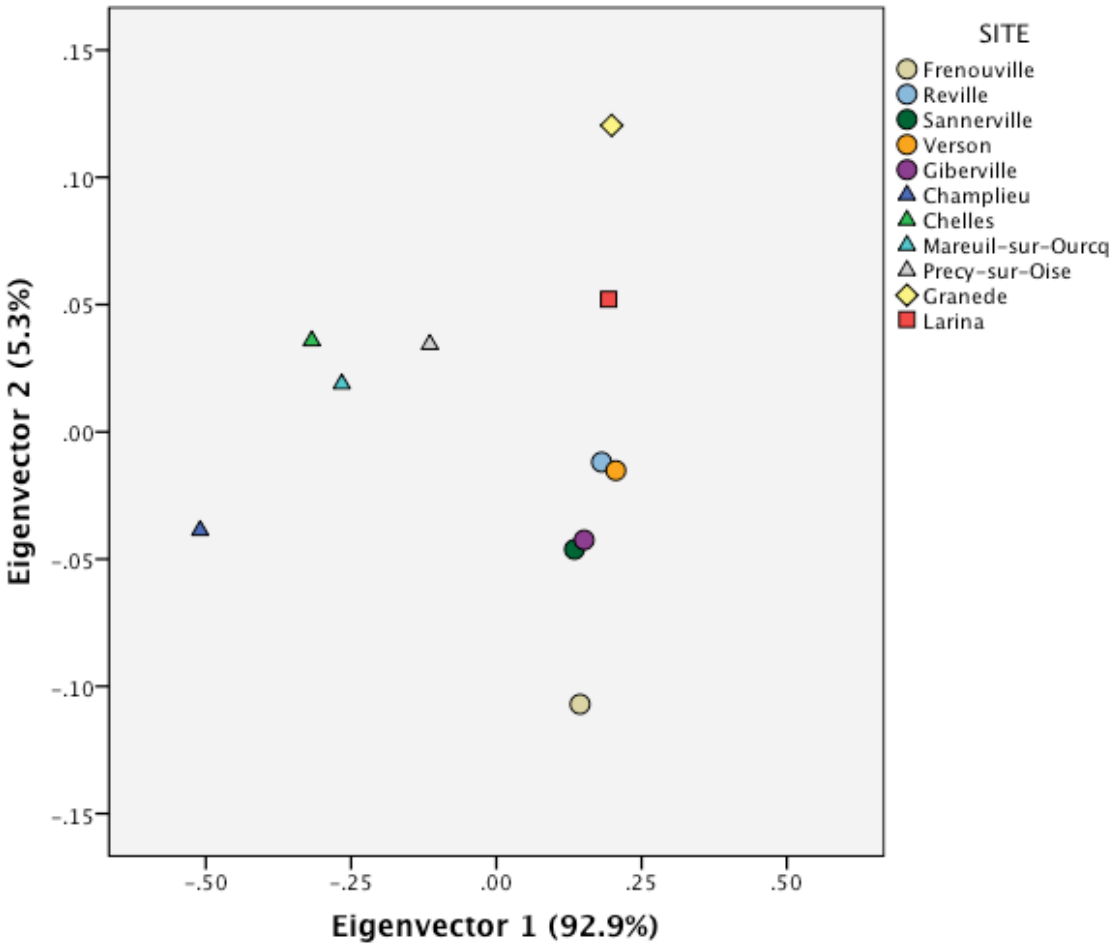

Figure 15. Scatterplot of Principal Coordinate 1 (PCO 1) vs. PCO 2 (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 1).

Table 12

Biological Distance (d^2) Matrix (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 1).

	Frén	Granède	Larina	Champ	Chelles	Mareuil	Précy	Réville	Sanner	Verson	Giber
Frénouville	-										
Granède	0.049**	-									
Larina	0.035**	0.004	-								
Champlieu	0.423**	0.525**	0.495**	-							
Chelles	0.221**	0.256**	0.255**	0.022	-						
Mareuil-sur-Ourcq	0.165*	0.197*	0.189*	0.018	0.000	-					
Précy-sur-Oise	0.075	0.084	0.105	0.149	0.016	0.000	-				
Réville	0.003	0.010	0.006	0.474**	0.234**	0.167*	0.072	-			
Sannerville	0.000	0.027	0.009	0.406**	0.198**	0.124	0.058	0.000	-		
Verson	0.012*	0.015	0.014	0.507**	0.268**	0.204**	0.082	0.000	0.000	-	
Giberville	0.002	0.024	0.007	0.425**	0.214**	0.151	0.066	0.000	0.000	0.000	-

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

Table 13

Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 1).

Site	Residual
Frénouville	-0.055**
Granède	0.159**
Larina	0.442**
Champlieu	0.154**
Chelles	0.101**
Mareuil-sur-Ourcq	-0.351**
Précy-sur-Oise	0.054
Réville	-0.152**
Sannerville	-0.017
Verson	0.005
Giberville	-0.340**

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

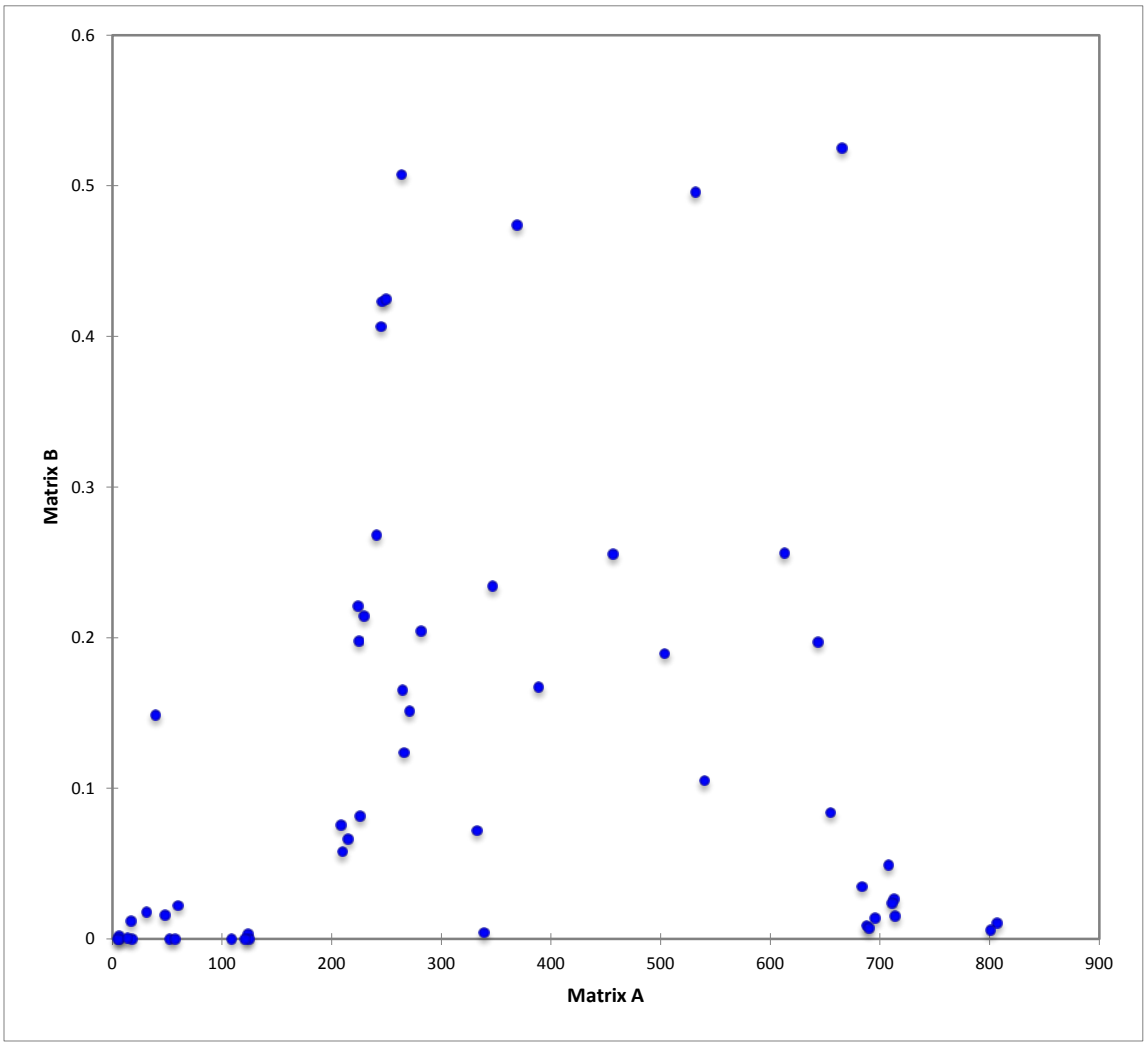

Figure 16. Scatterplot of the Mantel Test (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 1).

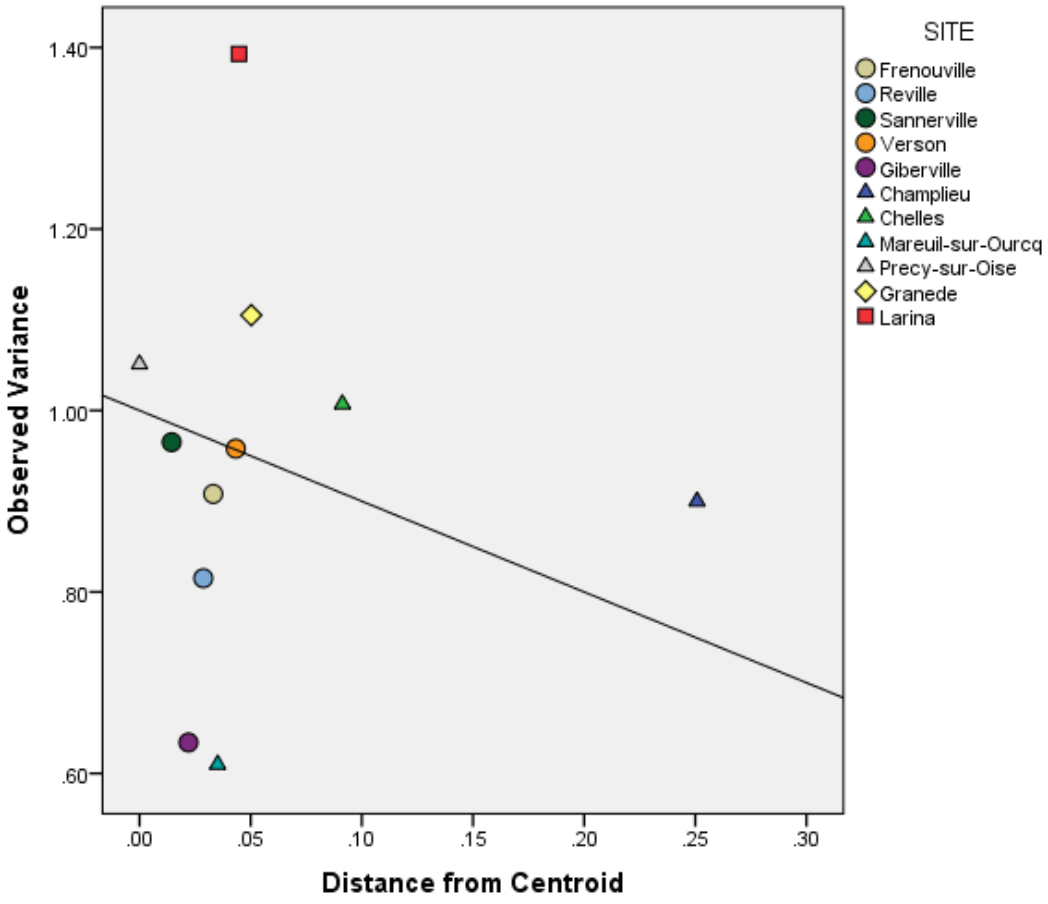

Figure 17. Scatterplot of Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 1).

9.1.2 Demographic Scenario 2

Under the second demographic scenario (equal population weights, $h^2 = 0.55$), the overall patterns remain the same. The first two eigenvectors account for 97.1% of the variability from the sample of 11 sites (Figure 18). Likewise, the groupings for sites in the Normandy Region (Frénouville, Réville, Sannerville, Verson, Giberville) and the Paris Basin (Champlieu, Chelles, Mareuil-sur-Ourcq, Précy-sur-Oise) remain the same. The north-south gradient along the second eigenvector that was evident in the first demographic scenario is also present here: Sites further north have values less than 0.0, while sites further south have values greater than 0.0. An exception to this trend in both scenarios is Champlieu.

Mahalanobis distances are found in Table 14. The strength of the distance relationships noted or suggested by Table 12 are greater in this demographic scenario. Those sites from the Normandy region (Frénouville, Réville, Sannerville, Verson, Giberville) remain overall more distinct from the remaining sites, but with exceptions (Précy-sur-Oise, Granède). Adjusting the narrow-sense heritability (h^2) from 1.0 to 0.55 results in a significant biological distance between Frénouville and Verson, two sites located within the same region (Normandy). Both Granède and Larina, sites representing the Midi-Pyrénées and Rhone Alps, respectively, are overall differentiated from the remaining sites. However, they are not significantly different from each other, despite their apparent dispersion seen on Figure 18. Additionally, they vary in significance from many of the Norman sites (c.f., Frénouville and Réville), which is not clearly indicated by the principal coordinates analysis (Figure 18).

A Mantel Test for isolation-by-distance yielded significant results ($R^2 = 0.336$, $p = 0.015$) (Figure 19). Again, much of this pattern seems to stem from biological similarities held between sites in the same region (e.g., Normandy), and those of sites further away (Granède, Larina) bearing greater biological similarity with those from Normandy. However, the former observation is not entirely comprehensive, since Table 14 revealed that there are some distinctions between sites in the Normandy region (i.e., Frénouville and Verson).

Regional heterogeneity ($F_{ST} = 0.106$) was significantly different from zero, indicating that between-site variability was high. As noted in Table 15, all sites from the Normandy region (Frénouville, Réville, Sannerville, Verson, Giberville) have significantly less than expected extra-local gene flow. Likewise, a single site from the Paris Basin (Mareuil-sur-Ourcq) has significantly less than expected extra-local gene flow. In contrast, two sites from the Paris Basin (Champlieu, Chelles), Granède and Larina exhibit significantly greater than expected extra-local gene flow. As seen in Figure 20, those sites above the line have significantly greater than expected extra-local gene flow, while those below the line have significantly less than expected extra-local gene flow.

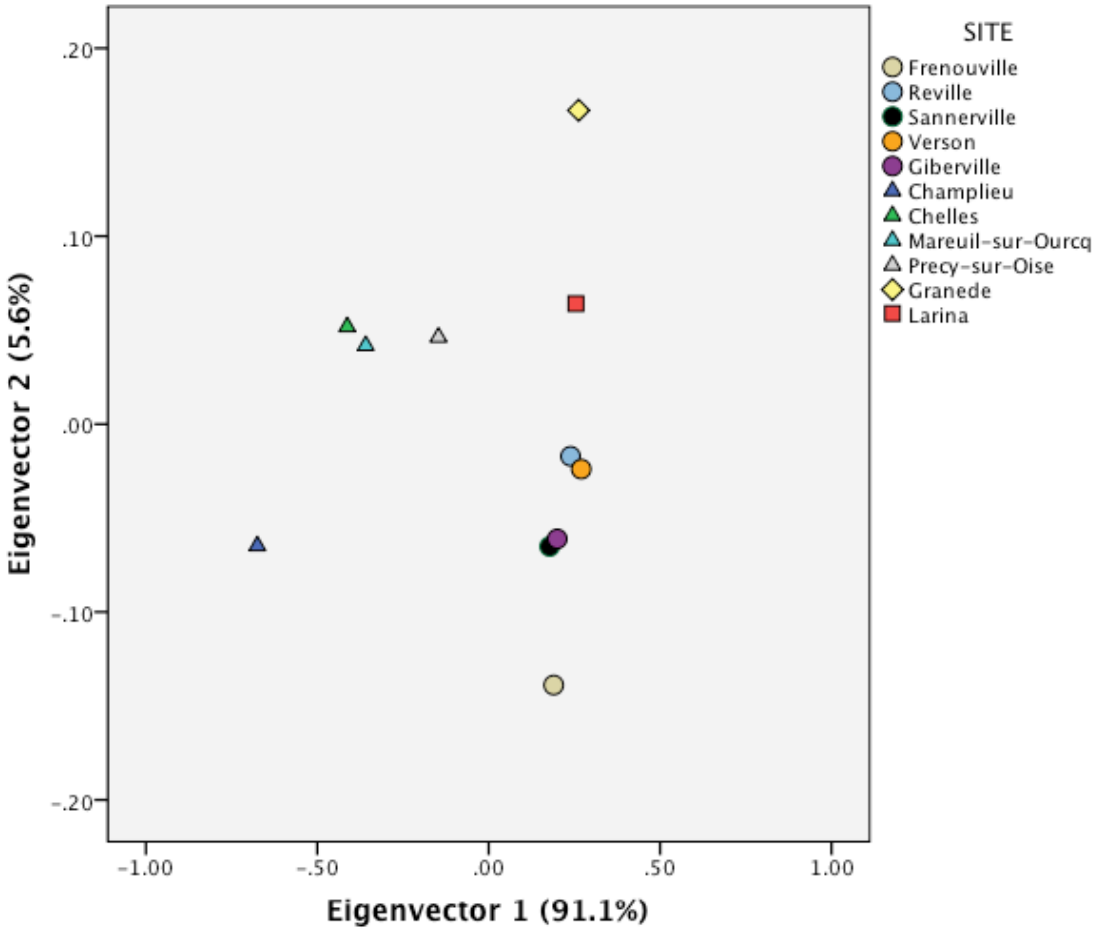

Figure 18. Scatterplot of PCO 1 vs. PCO 2 (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 2).

Table 14

Biological Distance (d^2) Matrix (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 2).

	Frén	Granède	Larina	Champ	Chelles	Mareuil	Précy	Réville	Sanner	Verson	Giber
Frénouville	-										
Granède	0.094**	-									
Larina	0.065**	0.020	-								
Champlieu	0.752**	0.934**	0.880**	-							
Chelles	0.386**	0.454**	0.449**	0.070*	-						
Mareuil-sur-Ourcq	0.335**	0.398**	0.380**	0.107	0.000	-					
Précy-sur-Oise	0.130	0.152*	0.184*	0.280**	0.033	0.010	-				
Réville	0.012	0.032	0.020	0.844**	0.413**	0.343**	0.128	-			
Sannerville	0.003	0.062**	0.027	0.730**	0.353**	0.271**	0.107	0.000	-		
Verson	0.024**	0.037*	0.031**	0.898**	0.469**	0.404**	0.143*	0.004	0.009	-	
Giberville	0.009	0.054**	0.022	0.759**	0.378**	0.315**	0.118	0.000	0.000	0.008	-

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

Table 15

Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 2).

Site	Residual
Frénouville	-0.055**
Granède	0.159**
Larina	0.442**
Champlieu	0.154**
Chelles	0.101**
Mareuil-sur-Ourcq	-0.351**
Précy-sur-Oise	0.054
Réville	-0.152**
Sannerville	-0.017
Verson	0.005
Giberville	-0.340**

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

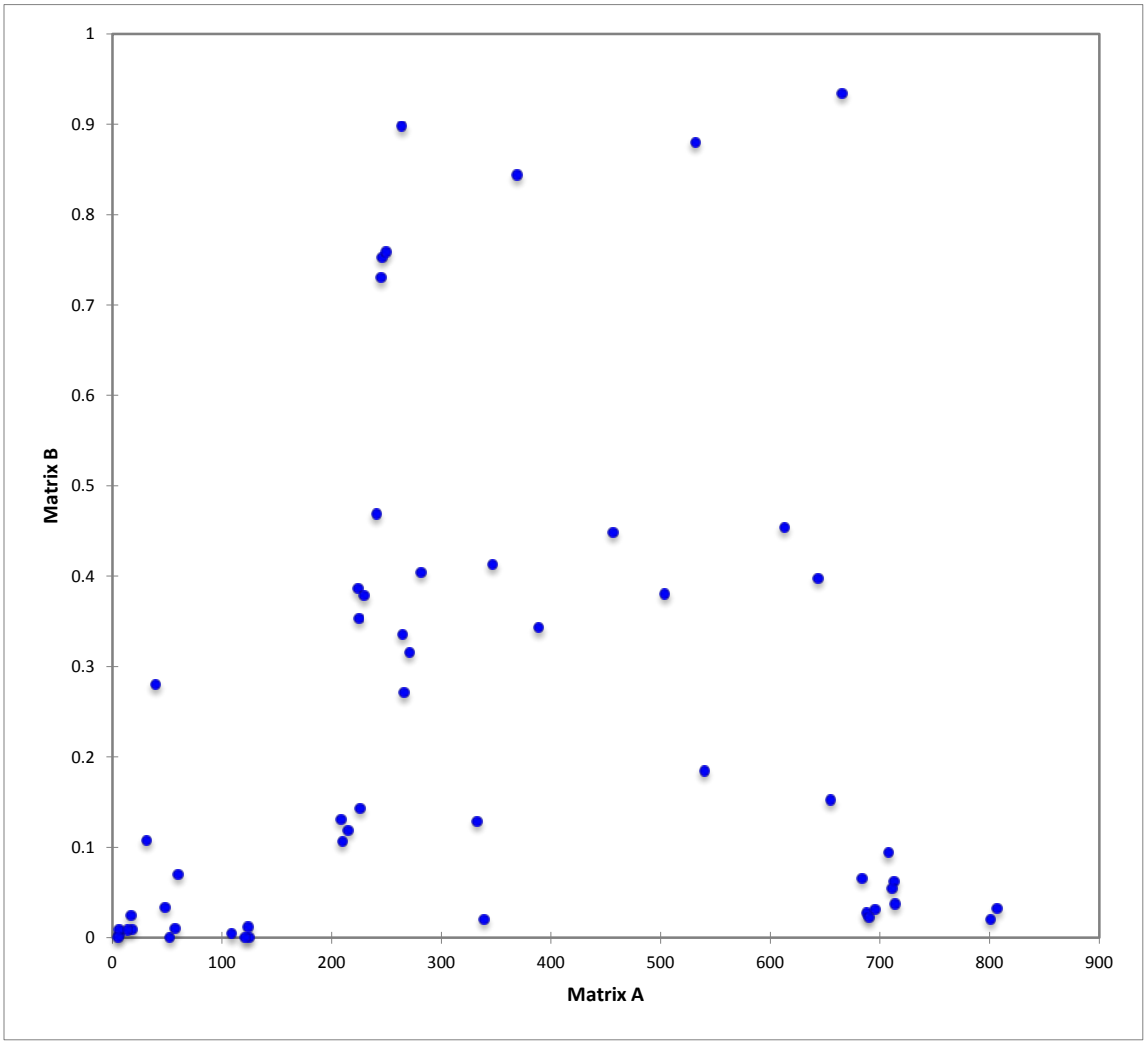

Figure 19. Scatterplot of the Mantel Test (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 2).

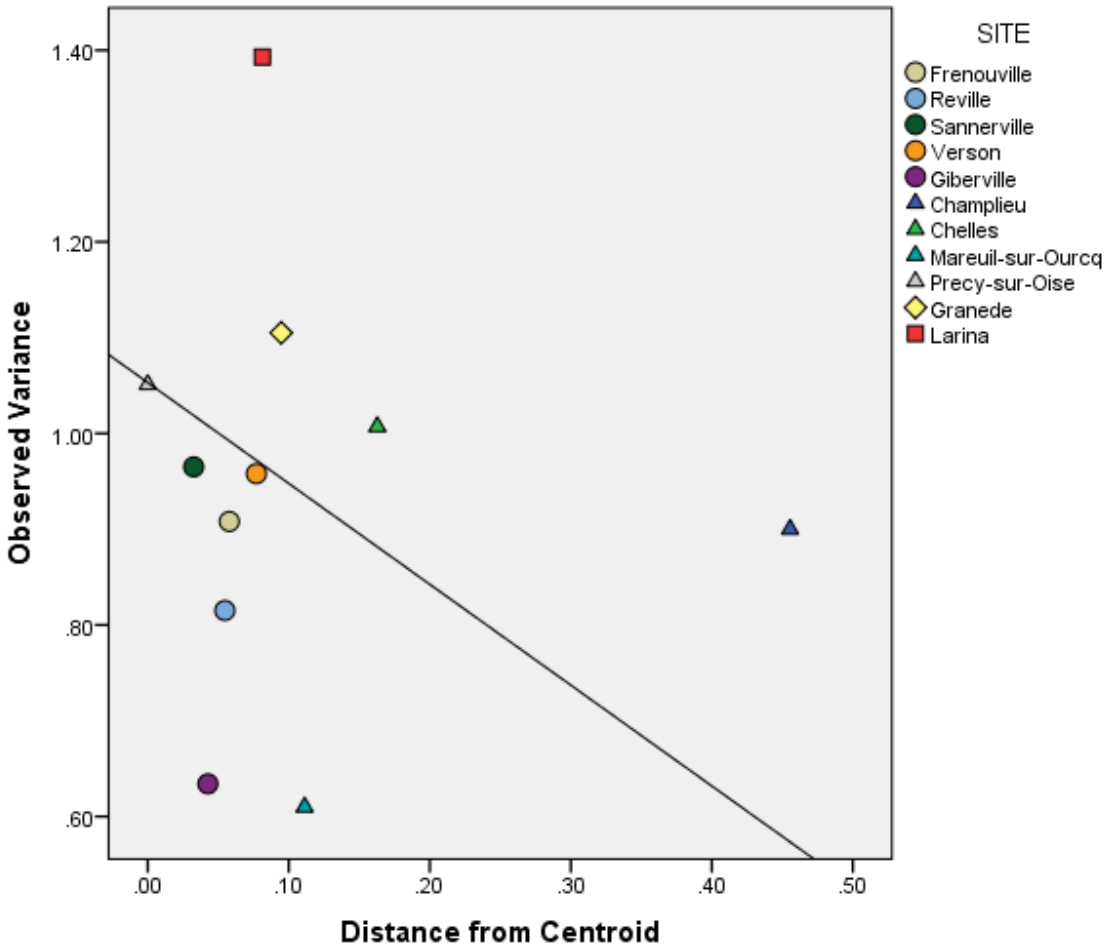

Figure 20. Scatterplot of Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 2).

9.1.3 Demographic Scenario 3

Since small(er) populations are subject to greater effects of genetic drift, this scenario included relative population size as a factor. As seen in Figure 21, the first two principal coordinates still account for a large amount (98.3%) of the variation amongst the 11 sites. The majority of the variance is explained by the first principal component, where the sites from the Paris Basin (Champlieu, Chelles, Mareuil-sur-Ourcq, Précy-sur-Oise) are distinct from the remaining sites. A rough north-south gradient can still be observed, with those sites from the Normandy region (Frénouville, Réville, Sannerville, Verson, Giberville) in the north exhibiting a distinction from sites further south (Chelles, Mareuil-sur-Ourcq, Précy-sur-Oise, Granède, Larina). The exception to this pattern is Champlieu from the Paris Basin, which plots similarly to sites from the Normandy region.

Mahalanobis distances (Table 16) reveal certain trends. Most of the sites from the Normandy Region are again distinct from the other sites/regions. Likewise, the Paris Basin sites are generally distinct from the others. However, there are some interesting exceptions. Firstly, Frénouville is significantly different from Verson, an unexpected result given their extremely close geographic proximity. Additionally, Précy-sur-Oise, a site located in the Paris Basin, is not significantly different from any of the other 10 sites. Précy-sur-Oise is located near the centroid on the scatterplot for the principal coordinates (Figure 21), which may be why it retains a low biological distance from the remaining sites in this analysis. Granède and Larina, while not significantly different from each other (Table 16), are significantly distant from most of the Paris Basin sites (Champlieu, Chelles, Mareuil-sur-Ourcq), as well as from Frénouville alone. As Figure 21 shows,

Frénouville plots far from Granède and Larina, much farther in fact than the other Norman sites (Réville, Sannerville, Verson, Giberville), so a significant biological distance is not wholly unexpected.

A Mantel Test for isolation-by-distance reveals a significant relationship between biological distances and geographic distances ($R^2 = 0.280$, $p = 0.034$) (Figure 22). This pattern again appears to stem from those Normandy sites that are both remarkably similar and geographically proximate (except for Frénouville and Verson) and from those more southerly sites (Larina, Granède) that are biologically similar to sites from the Normandy Region (except for Frénouville).

Regional heterogeneity was significantly different from zero ($F_{ST} = 0.055$), suggesting that between site variability was elevated. Meanwhile, the Relethford-Blangero residuals (Table 17) yielded mixed results. Granède and Larina have significantly greater than expected extra-local gene flow, much as in demographic scenarios one and two (Tables 13 and 15). Likewise, Champlieu and Chelles – sites from the Paris Basin – have significantly greater than expected extra-local gene flow. However, Précy-sur-Oise also has significantly greater than expected extra-local gene flow, which is a change from demographic scenarios one and two (Tables 13 and 15). Similarly, Verson, which was previously non-significant (Table 15) or had significantly less than expected extra-local gene flow (Table 13), now has significantly greater than expected extra-local gene flow. Interestingly, sites from the Normandy region (Frénouville, Réville, Sannerville, Verson, Giberville) show mixed results, with some having significantly less than expected extra-local gene flow (Réville, Giberville), some having significantly greater than expected extra-local gene flow (Verson), and some with

no significance whatsoever (Frénouville, Sannerville). This is in contrast to demographic scenarios one and two in which all or nearly all of the sites from the Normandy region exhibited significantly less than expected extra-local gene flow. These patterns are reflected graphically in Figure 23 as well. Sites like Larina, Granède, Champlieu, Chelles, Précy-sur-Oise, and Verson all plot significantly above the line, while sites like Mareuil-sur-Ourcq, Réville, and Giberville all plot below the line.

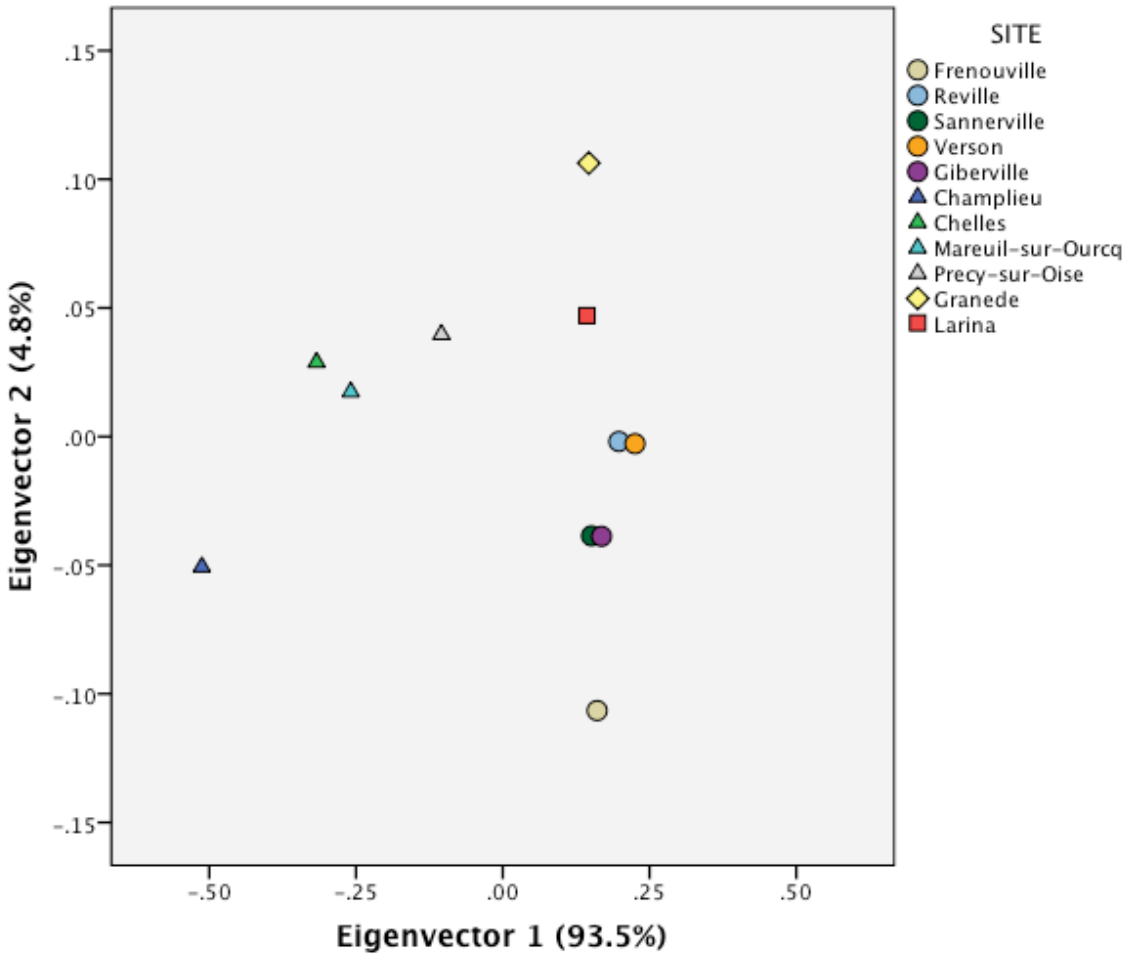

Figure 21. Scatterplot of PCO 1 vs. PCO 2 (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 3).

Table 16

Biological Distance (d^2) Matrix (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 3).

	Frén	Granède	Larina	Champ	Chelles	Mareuil	Précy	Réville	Sanner	Verson	Giber
Frénouville	-										
Granède	0.040**	-									
Larina	0.030**	0.003	-								
Champlieu	0.447**	0.456**	0.435**	-							
Chelles	0.234**	0.204**	0.206**	0.024	-						
Mareuil-sur-Ourcq	0.172**	0.142*	0.138*	0.023	0.000	-					
Précy-sur-Oise	0.083	0.053	0.072	0.166*	0.023	0.000	-				
Réville	0.004	0.007	0.005	0.503**	0.247**	0.173**	0.079	-			
Sannerville	0.000	0.015	0.003	0.432**	0.210**	0.127*	0.065	0.000	-		
Verson	0.014**	0.016	0.016*	0.541**	0.286**	0.215**	0.090	0.000	0.000	-	
Giberville	0.002	0.016	0.005	0.452**	0.228**	0.158**	0.074	0.000	0.000	0.000	-

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

Table 17

Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 3).

Site	Residual
Frénouville	-0.019
Granède	0.203**
Larina	0.485**
Champlieu	0.152**
Chelles	0.119**
Mareuil-sur-Ourcq	-0.331**
Précy-sur-Oise	0.088**
Réville	-0.114**
Sannerville	0.020
Verson	0.044**
Giberville	-0.302**

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

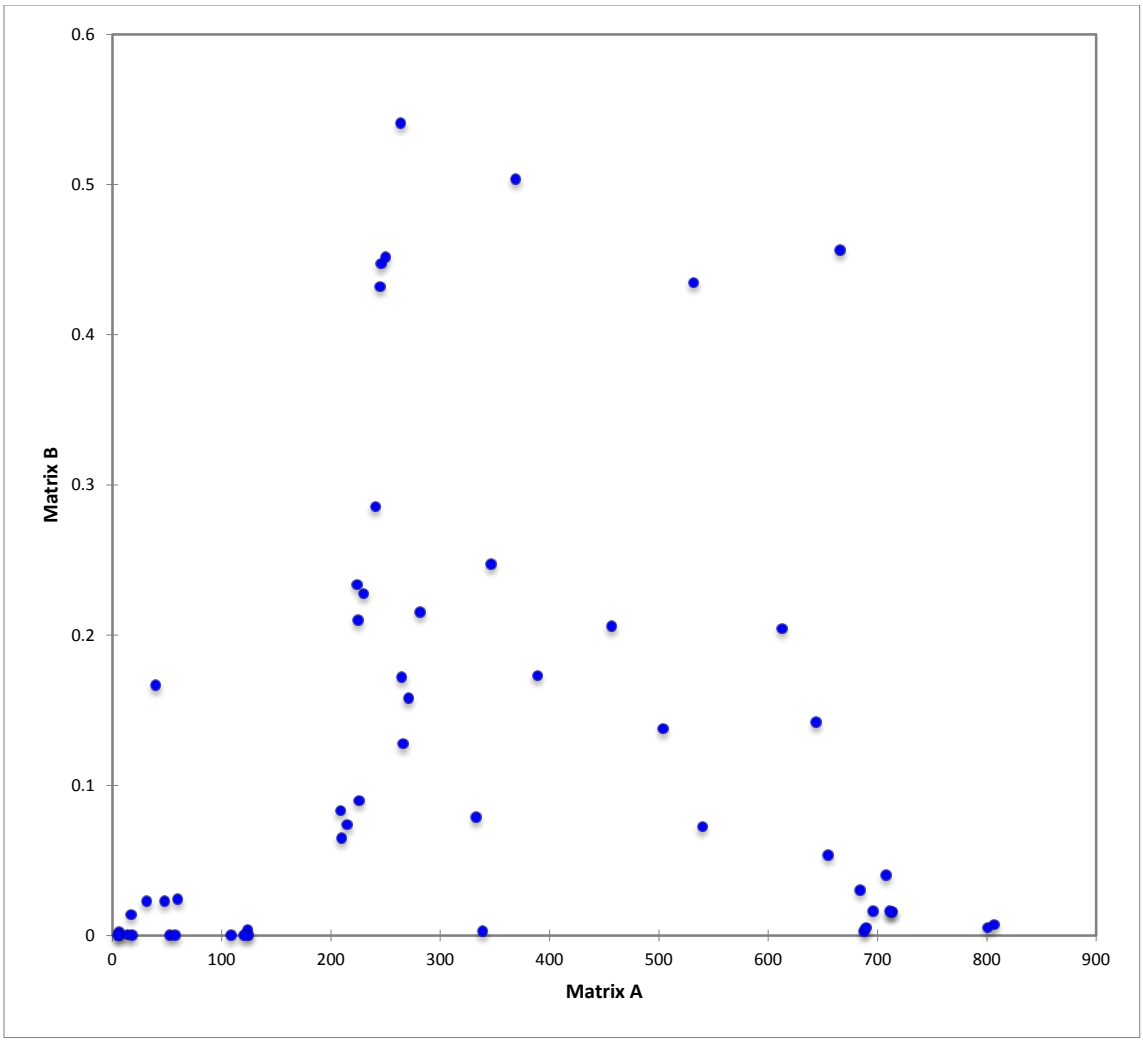

Figure 22. Scatterplot of the Mantel Test (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 3).

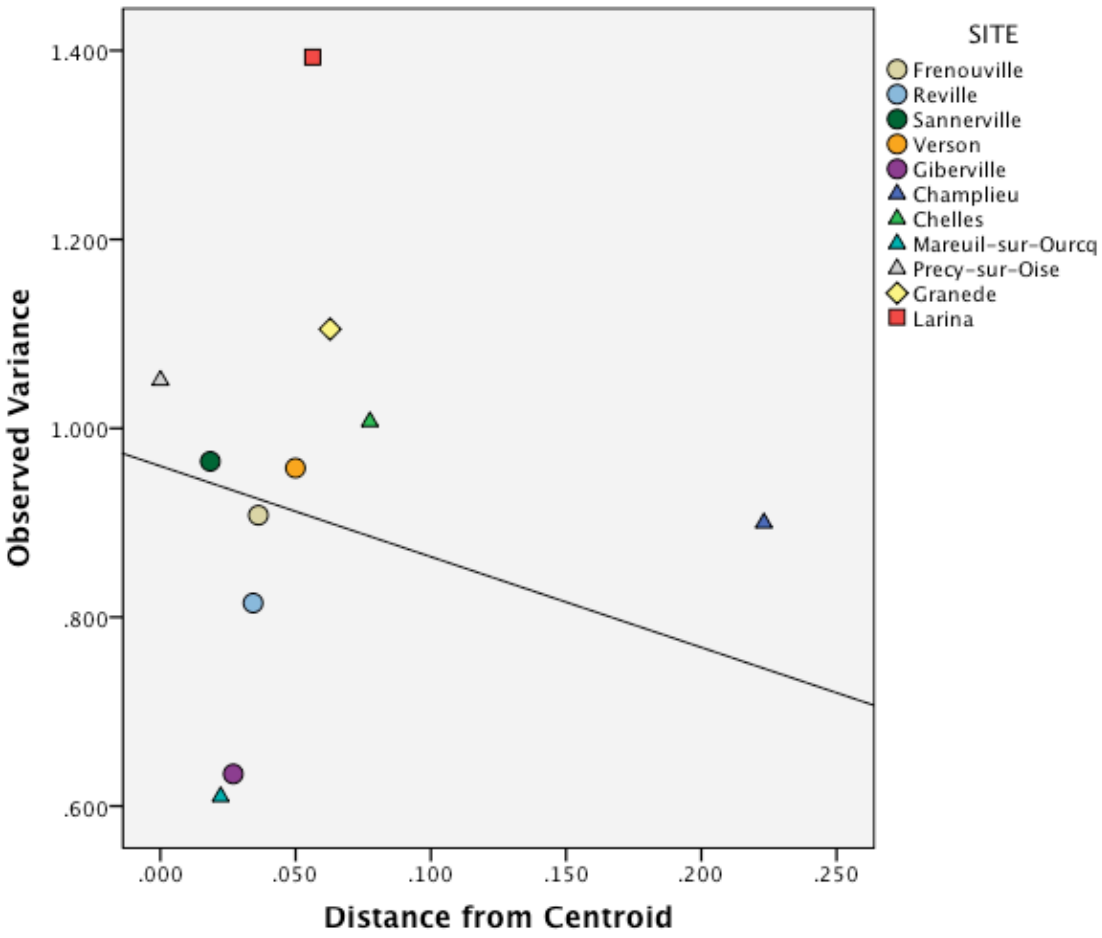

Figure 23. Scatterplot of Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 3).

9.1.4 Demographic Scenario 4

In addition to relative population size, this scenario imposed a narrow-sense heritability estimate of 0.55. As seen in Figure 24, the first two eigenvectors still account for the majority of the variation seen amongst the 11 sites (96.1%). In fact, the first eigenvector itself accounts for nearly 90% of the variation. Along the first eigenvector, the sites from the Paris Basin (Champlieu, Chelles, Mareuil-sur-Ourcq, Précy-sur-Oise) are distinct from the remaining sites, forming a loose group negatively along the first axis. In contrast, the sites from Normandy (Frénouville, Réville, Sannerville, Verson, Giberville), as well as Granède and Larina plot positively along the first axis. Along the second eigenvector, a north-south gradient is still evident. Those sites from farther north (Frénouville, Réville, Sannerville, Verson, Giberville) plot negatively along the second axis. Interestingly, a single site from the Paris Basin (Champlieu) also plots negatively along the second axis.

Mahalanobis distances are presented in Table 18. Although Champlieu plots negatively along the second axis (Figure 24), it remains significantly different from the Norman sites (Frénouville, Réville, Sannerville, Verson, Giberville). In fact, Champlieu is significantly different from all sites (c.f., Chelles, Mareuil-sur-Ourcq), including Précy-sur-Oise, which is also a site from the Paris Basin. The significant biological distance between these two sites from the same region may indicate greater heterogeneity within the Paris Basin.

Sites from the Normandy region are overall significantly different from the remaining sites, but with a few exceptions. For example, Précy-sur-Oise, a site from the Paris Basin, is *not* significantly different from three Norman sites (Réville, Sannerville,

Giberville). Interestingly, Frénouville is significantly different from Verson, both of which are sites from the Normandy region. This perhaps indicates greater variability within the Normandy region than is initially apparent.

A Mantel Test for isolation-by-distance yielded significant results ($R^2 = 0.261$, $p = 0.051$). Much as in the previous scenarios, this result stems from those relevant sites in the Normandy region, as well as those sites further south (Larina, Granède) (Figure 25). However, the greater number of sites in Normandy, as well as the increasing distinction between some sites within it, does suggest that any significant result should be understood with caution.

Regional heterogeneity ($F_{ST} = 0.105$) was significantly different from zero, indicating that heterogeneity among the sites was high. The Relethford Blangero Residuals (Table 19) show that multiple sites (Granède, Larina, Champlieu, Chelles, Verson) have greater than expected extra-local gene flow. Multiple sites also have significantly less than expected extra-local gene flow (Frénouville, Mareuil-sur-Ourcq, Réville, Giberville). Although most of the sites from the Normandy region are characterized by significantly less than expected extra-local gene flow, Verson has greater than expected extra-local gene flow. Likewise, most sites from the Paris Basin are characterized by significantly greater than expected extra-local gene flow, with the sole exception of Mareuil-sur-Ourcq, which has significantly less than expected extra-local gene flow. These results are mirrored in Figure 26. Those sites above the line have greater than expected extra-local gene flow, while those below the line have less than expected extra-local gene flow.

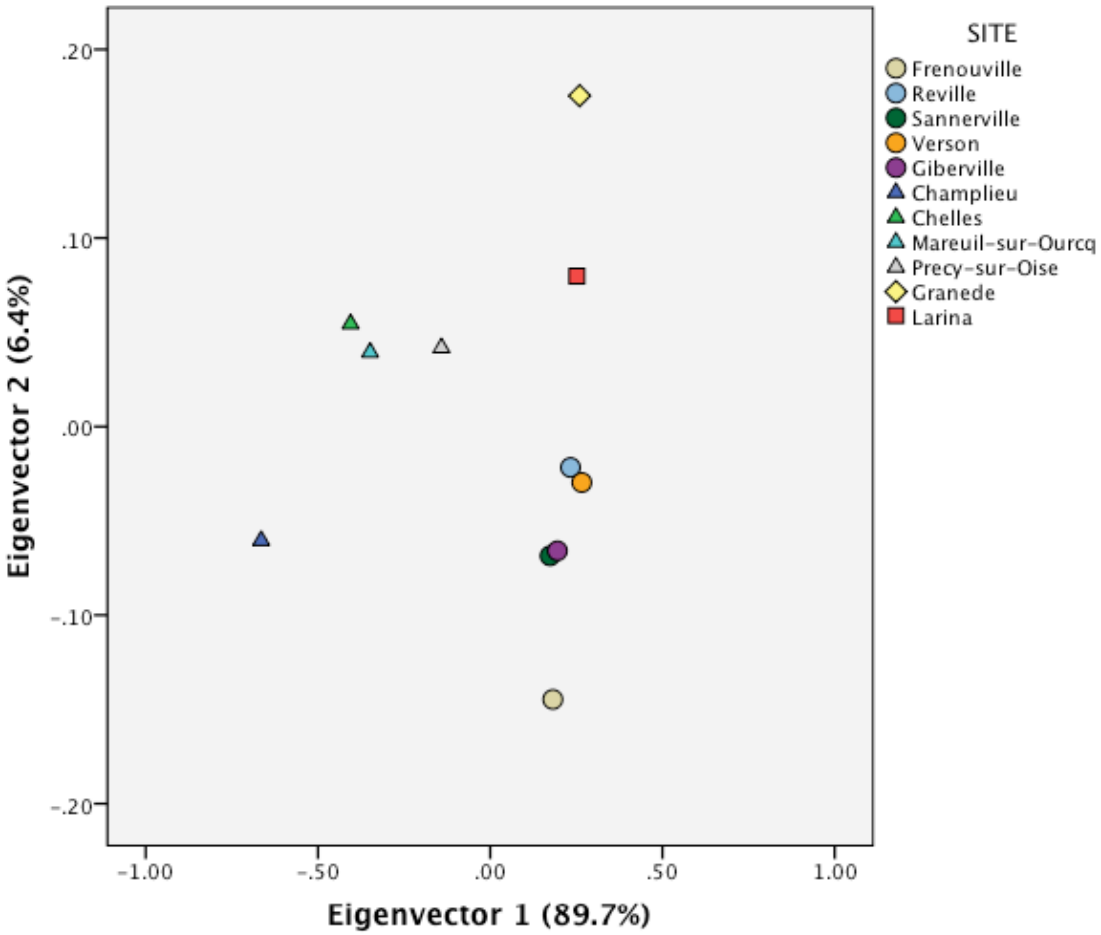

Figure 24. Scatterplot of PCO 1 vs. PCO 2 (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 4).

Table 18

Biological Distance (d^2) Matrix (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 4).

	Frén	Granède	Larina	Champ	Chelles	Mareuil	Précy	Réville	Sanner	Verson	Giber
Frénouville	-										
Granède	0.075**	-									
Larina	0.056**	0.012	-								
Champlieu	0.796**	0.815**	0.776**	-							
Chelles	0.409**	0.362**	0.362**	0.076*	-						
Mareuil-sur-Ourcq	0.352**	0.304**	0.295**	0.124	0.000	-					
Précy-sur-Oise	0.144**	0.096	0.126*	0.314**	0.046	0.023	-				
Réville	0.014*	0.023	0.017	0.898**	0.437**	0.359**	0.141*	-			
Sannerville	0.004	0.039*	0.015	0.778**	0.376**	0.283**	0.120*	0.000	-		
Verson	0.028**	0.035**	0.034**	0.958**	0.500**	0.428**	0.157**	0.005	0.010	-	
Giberville	0.010	0.038**	0.016	0.808**	0.403**	0.333**	0.132*	0.000	0.000	0.009	-

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

Table 19

Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 4).

Site	Residual
Frénouville	-0.044**
Granède	0.207**
Larina	0.480**
Champlieu	0.298**
Chelles	0.131**
Mareuil-sur-Ourcq	-0.316**
Précy-sur-Oise	0.034
Réville	-0.136**
Sannerville	-0.012
Verson	0.031**
Giberville	-0.330**

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

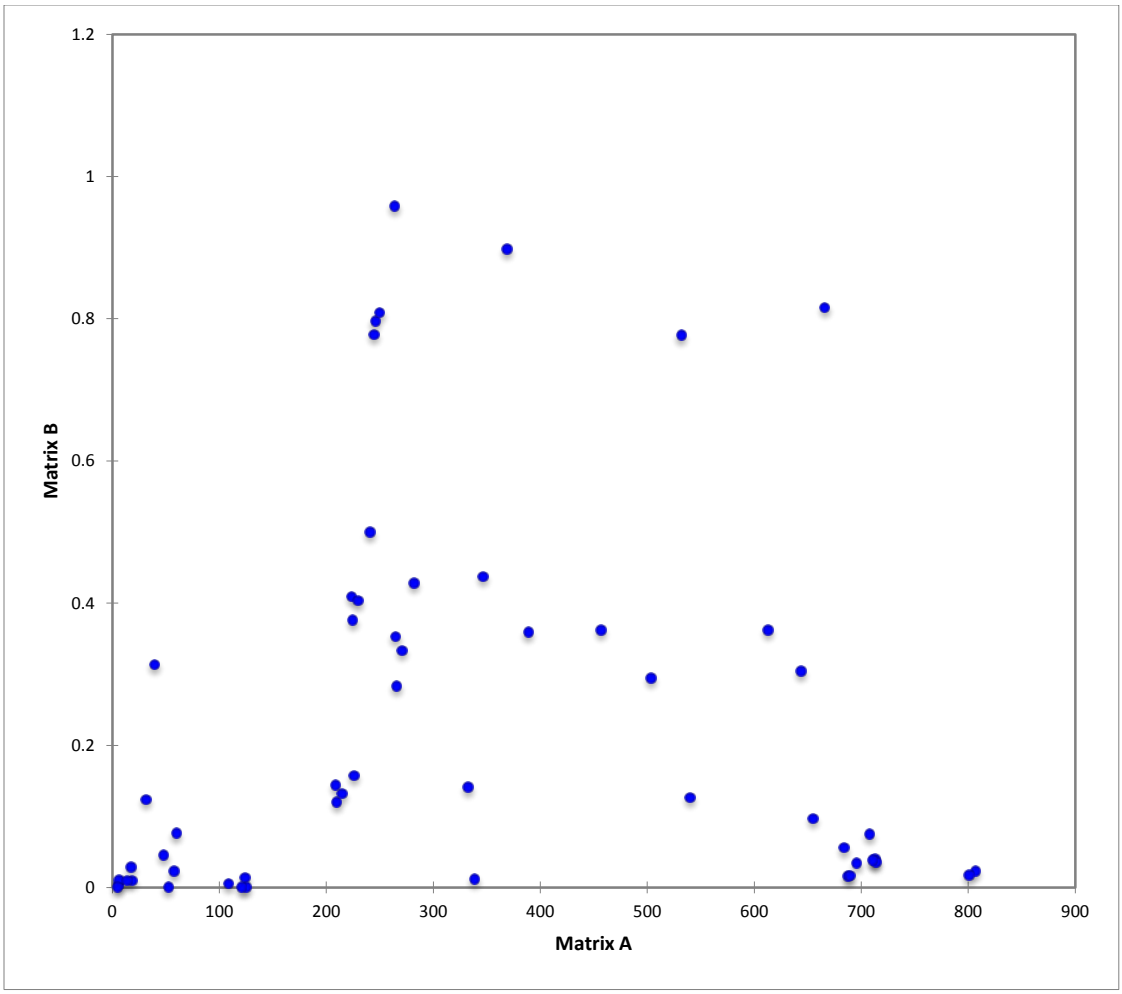

Figure 25. Scatterplot of the Mantel Test (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 4).

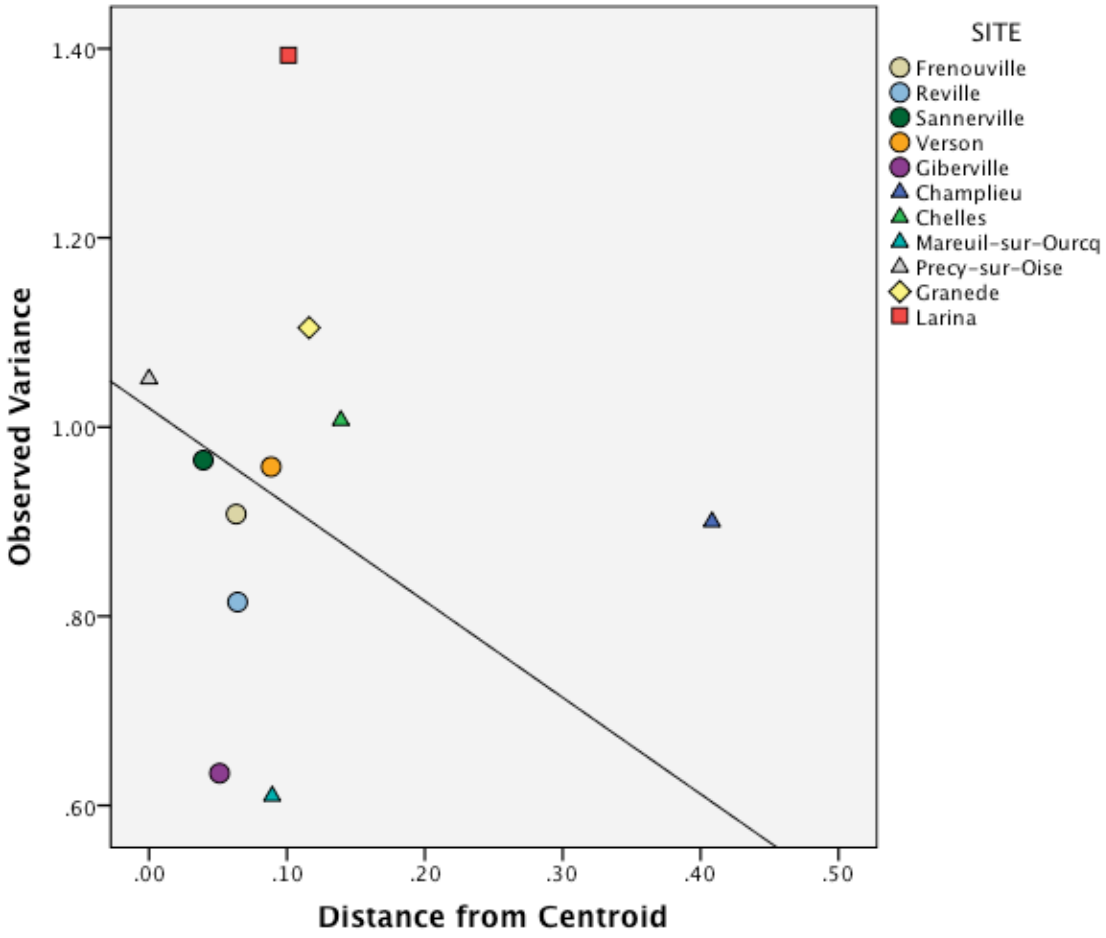

Figure 26. Scatterplot of Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Site-Level, Demographic Scenario 4).

9.1.5 Review

R-matrix analysis of individual sites yields some consistent trends. Firstly, it is clear that the majority of the underlying variation can be explained by the first eigenvector, which would suggest a significance to the overall spatial trend of biological relationships portrayed by the principal coordinates. This spatial relationship clearly differentiates sites from the Paris Basin from all other sites. Although less substantial, the second eigenvector also noticeably indicates an important aspect about sites along a north-south gradient. Sites further north plot more closely to each other than to those further south. In other words, those sites from the Normandy Region to the north cluster together, while those from the south (i.e., Larina, Granède) cluster together, and those from the Paris Basin are in between.

Mahalanobis d^2matrices assessing the strength of the biological distances between sites show that those sites from the Normandy and Paris Basin Regions are often significantly different from other sites. Furthermore, those sites from more southerly regions (Larina, Granède) are never significantly different from each other, regardless of the demographic scenario assessed. Perhaps most interesting, however, is the increasing indication of significant intra-regional biological differences. Demographic scenarios 3 and 4 clearly show that Frénouville and Verson—two sites from the northerly, Normandy Region—are significantly different from each other, despite their close geographic proximity. Similarly, sites from the Paris Basin Region begin to show more intra-regional significant differences using the parameters in Demographic Scenario 4. These results would suggest that there are some biological differences within regions.

The Mantel Tests, in contrast, yield apparently conflicting results. All tests were statistically significant, which would support the null hypothesis that geographic distance explains the biological distances obtained in the R-matrix analysis. These results might also parallel the spatial trends evident by the second eigenvector of the principal coordinates. However, the scatterplots of the relationship between geographic and biological distances are inconsistent with a valid linear relationship between geography and biology. These scatterplots suggest that there are a number of sites that are both geographically proximate and biologically proximate, and a number of sites that are both geographically distant and yet biologically proximate. A closer examination of the Mahalanobis d^2 matrices and scatterplots of the principal coordinates clearly reveals that these sites are those who all cluster linearly together along the second eigenvector. In other words, they are the sites from the northerly, Normandy Region, and those from the south (Larina, Granède), but not those from the Paris Basin. These results would suggest instead, that most of the variation depicted by the second eigenvector swamps the pattern exhibited by the Paris Basin sites, which accounts for the bell-shaped pattern of points seen on scatterplots of the Mantel Tests.

Estimates of between-site genetic heterogeneity (F_{ST}) were all significantly different from zero ($p \leq 0.05$). These results would suggest that the overall genetic variability between sites was high, which could be a result of limited gene flow between sites, as well as a result of small effective population sizes for some sites/regions. As for evidence of gene flow from outside sources, those sites from the Normandy Region typically possess significantly negative Relethford-Blangero residuals, while those from further south have significantly positive residuals. These results would also indicate that

the overall elevated genetic variability between sites might also be an effect of focused gene flow from outside sources to specific sites or regions, and/or due to a lack of abundant levels of gene flow to specific sites.

9.2.0 REGIONAL-LEVEL

9.2.1 Demographic Scenario 1

Results for the first demographic scenario (equal population weights, $h^2 = 1.0$) are shown in Figure 27. Nearly all of the variation amongst the four regions is accounted by the first two principal coordinates. Moreover, there is a striking distribution of the regions on the scatterplot from the principal coordinates analysis. Along eigenvector one, the Paris Basin region plots negatively, while the remaining regions (Normandy, Midi-Pyrénées, Rhône-Alps) plot positively along the same axis. Along eigenvector two, there are a couple of patterns. Firstly, the north-south gradient evident from the site-level analysis (Figures 15, 18, 21, and 24) are more readily apparent. Those regions from the north of France are located more positively along eigenvector two; those regions from the south of France are located more negatively. Secondly, the southerly regions (Midi-Pyrénées, Rhône-Alps) form a loose group.

Examination of Mahalanobis distances (Table 20) reveals three significantly different distances: Paris Basin and Normandy, Paris Basin and Midi-Pyrénées, and Paris Basin and Rhône-Alps. In other words, the Paris Basin region is significantly different from all other regions, which is also evident from the scatterplot of the Principal Coordinates (Figure 27).

In contrast to the site-level analysis (Figure 16), Mantel Tests for isolation-by-distance yielded no significance between biological and geographic distance ($R^2 = -0.029$, $p = 1.000$) when performed using regions as the unit of analysis (Figure 28). Although the Normandy, Midi-Pyrénées, and Rhône-Alps regions are geographically distinct from each other, they are still biologically similar to each other (see Table 20). It is solely the Paris Basin Region that exhibits such distinction from the other regions.

Regional heterogeneity ($F_{ST} = 0.055$) was significantly different from zero, which would suggest that between-region variability was high. Although the Paris Basin region is distinct as seen in the scatterplot of the principal coordinates analysis, an analysis of the Relethford-Blangero residuals shows only two regions that are significantly different from the expected variance (Table 21). Normandy has significantly less than expected extra-local gene flow, while the Rhône-Alps has significantly greater than expected extra-local gene flow. These results are perhaps most evident in Figure 29.

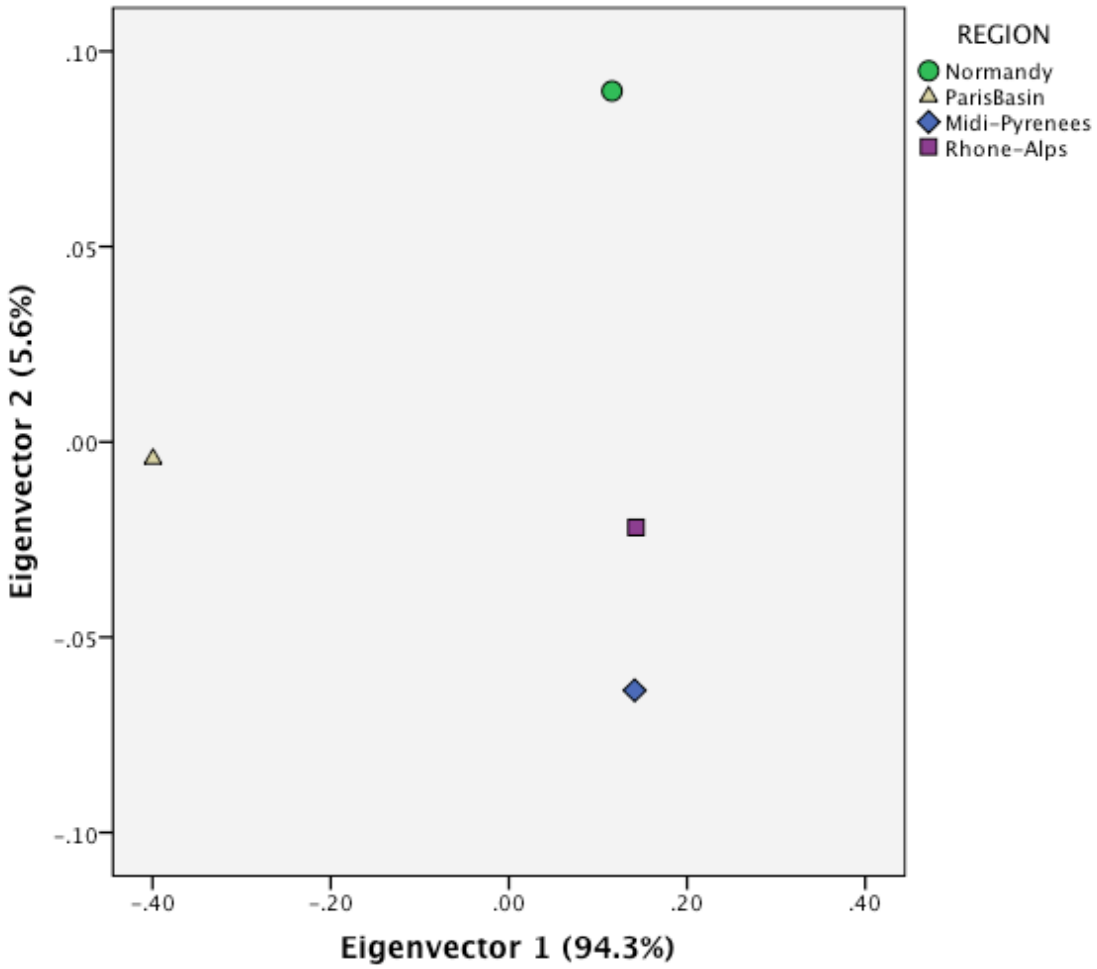

Figure 27. Scatterplot of PCO 1 vs. PCO 2 (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 1).

Table 20

Biological Distance (d^2) Matrix (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 1).

	Normandy	ParisBasin	Midi-Pyrénées	Rhône-Alps
Normandy	-			
ParisBasin	0.274**	-		
Midi-Pyrénées	0.024	0.296**	-	
Rhône-Alps	0.013	0.294**	0.002	-

Notes: $**p \leq 0.05$, $* p \leq 0.10$.

Table 21

Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 1).

Region	Residual
Normandy	-0.239**
ParisBasin	-0.005
Midi-Pyrénées	-0.022
Rhône-Alps	0.266**

Notes: $** p \leq 0.05$, $* p \leq 0.10$.

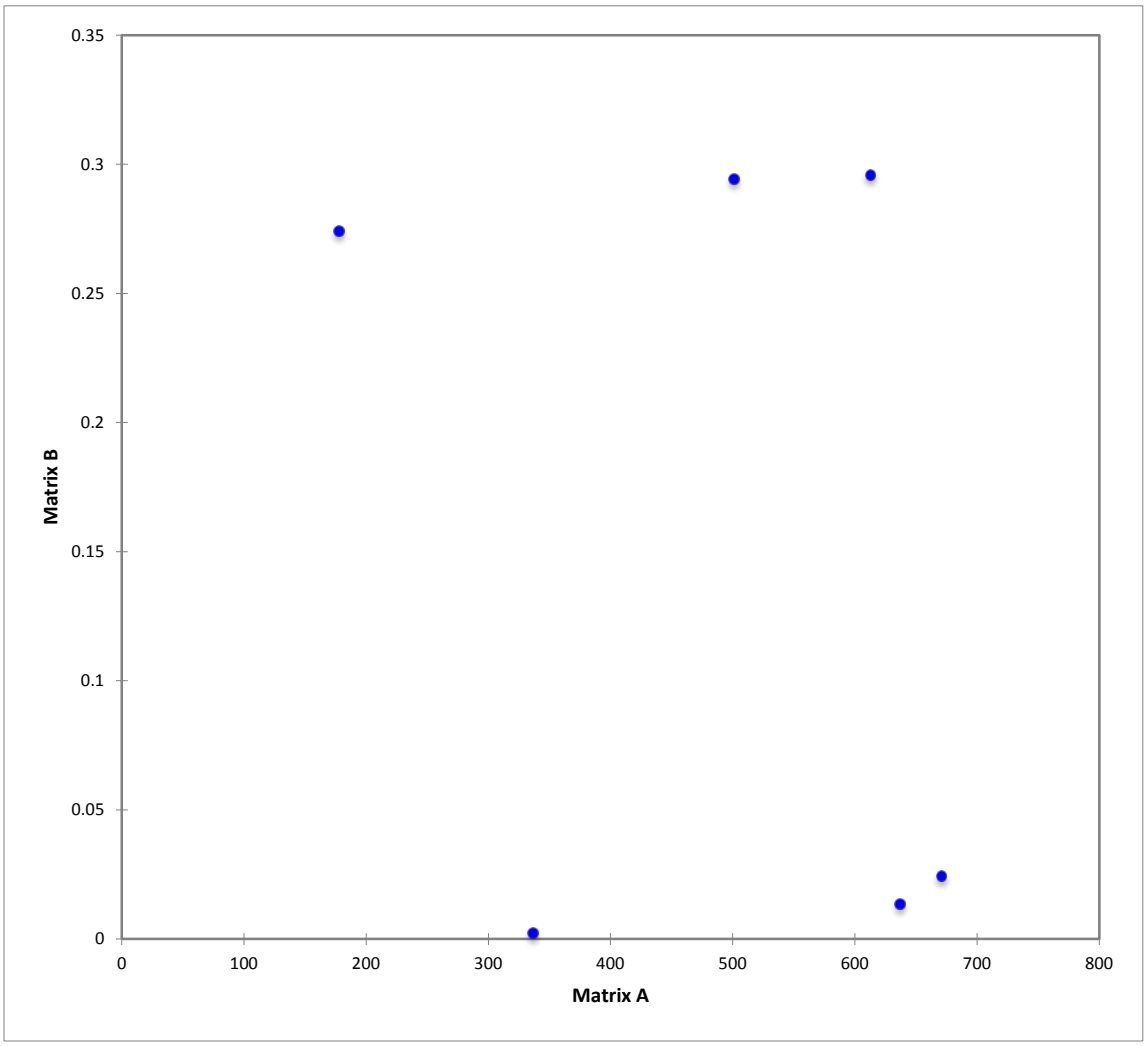

Figure 28. Scatterplot of the Mantel Test (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 1).

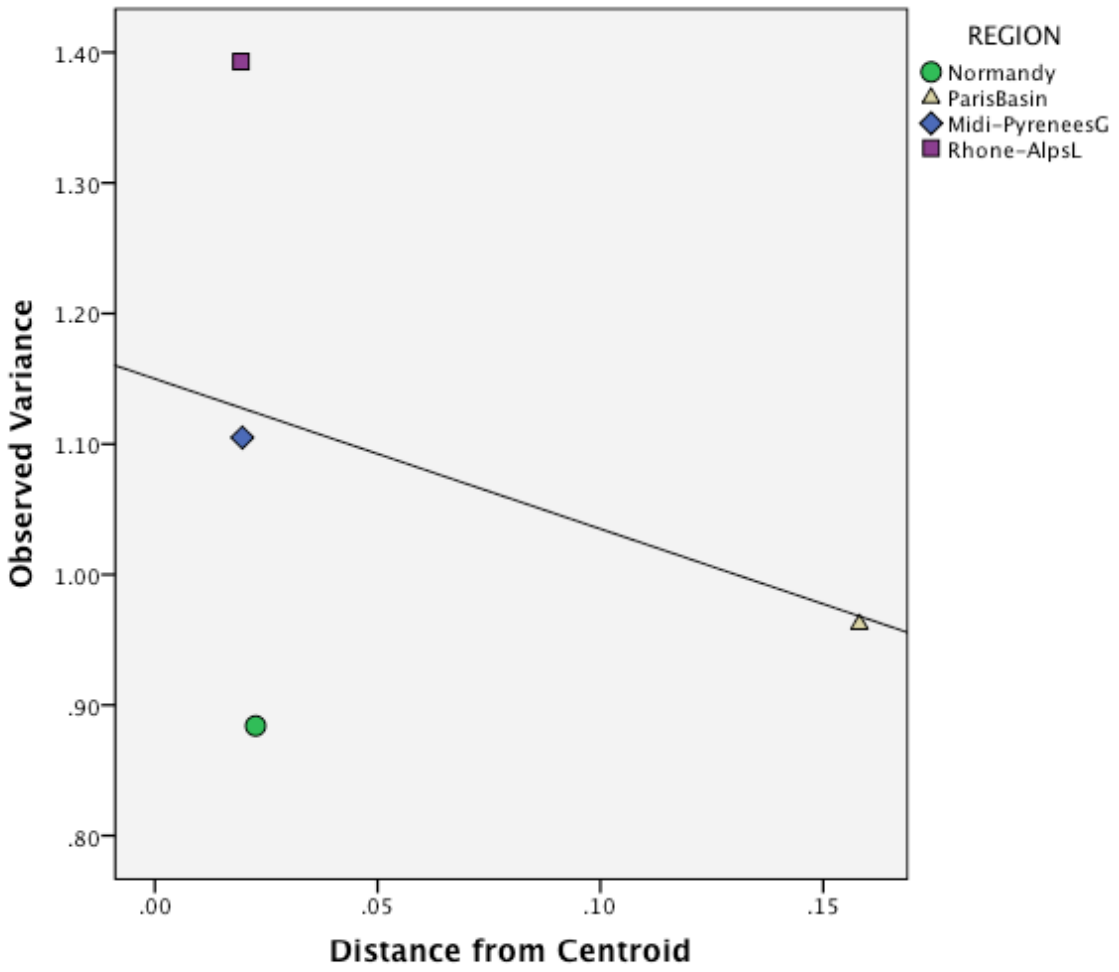

Figure 29. Scatterplot of Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 1).

9.2.2 Demographic Scenario 2

Altering the demographic parameters (equal population weights, $h^2 = 0.055$) does not change many of the underlying patterns seen in the scatterplot of the first two principal coordinates (Figure 30). Both eigenvectors account for 98.5% of the variation, although the bulk of it is from the first eigenvector. Consequently, the distinction along the first axis is clearly that of the Paris Basin from the remaining three regions (Normandy, Midi-Pyrénées, Rhône-Alps). Of minor importance is the second eigenvector. Here, the latitudinal gradient noted in Figure 27 is not as apparent, since the Paris Basin and the Rhône-Alps regions are both slightly negative along the second axis.

Examination of Mahalanobis distances (Table 22) yields the same patterns as was noted earlier (Table 20). In other words, the Paris Basin is significantly different from the remaining regions (Normandy, Midi-Pyrénées, Rhône-Alps). However, adjusting alpha from 0.05 to 0.10, the Normandy region also becomes significantly different from the remaining regions (Paris Basin, Midi-Pyrénées, Rhône-Alps).

Isolation-by-distance cannot account for these patterns, however, since the Mantel Test results were negative ($R^2 = -0.0219$, $p = 1.000$). Again, it is the Paris Basin Region that is distinct both biologically and geographically (Figure 31). Regional heterogeneity, however, was significantly different from zero ($F_{ST} = 0.099$).

Although the Mahalanobis distances were significant primarily for the Paris Basin (Table 22), it is striking to note that all of the residuals generated from the R-matrix analysis are significant (Table 23). Both the Normandy and Midi-Pyrénées regions had significantly less than expected extra-local gene flow. In contrast, both the Paris Basin and Rhône-Alps regions had significantly greater than expected extra-local gene flow.

Viewed on Figure 32, it is especially clear that the Rhône-Alps region had significantly greater than expected extra-local gene flow, and that the Normandy region had significantly less than expected extra-local gene flow.

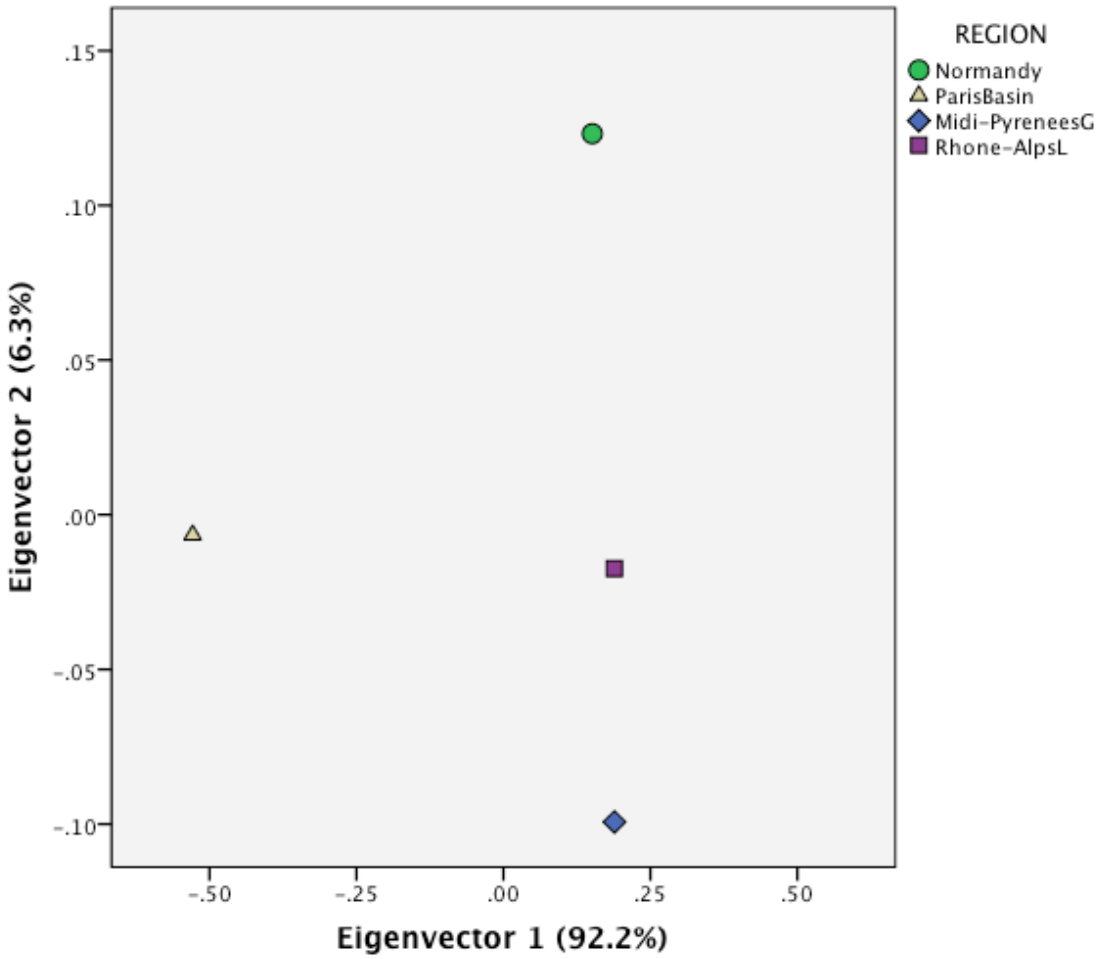

Figure 30. Scatterplot of PCO 1 vs. PCO 2 (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 2).

Table 22

Biological Distance (d^2) Matrix (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 2).

	Normandy	ParisBasin	Midi-Pyrénées	Rhône-Alps
Normandy	-			
ParisBasin	0.479**	-		
Midi-Pyrénées	0.051*	0.525**	-	
Rhône-Alps	0.028*	0.519**	0.017	-

Notes: **$p \leq 0.05$, * $p \leq 0.10$.

Table 23

Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 2).

Region	Residual
Normandy	-0.274**
ParisBasin	0.091**
Midi-Pyrénées	-0.050**
Rhône-Alps	0.233**

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

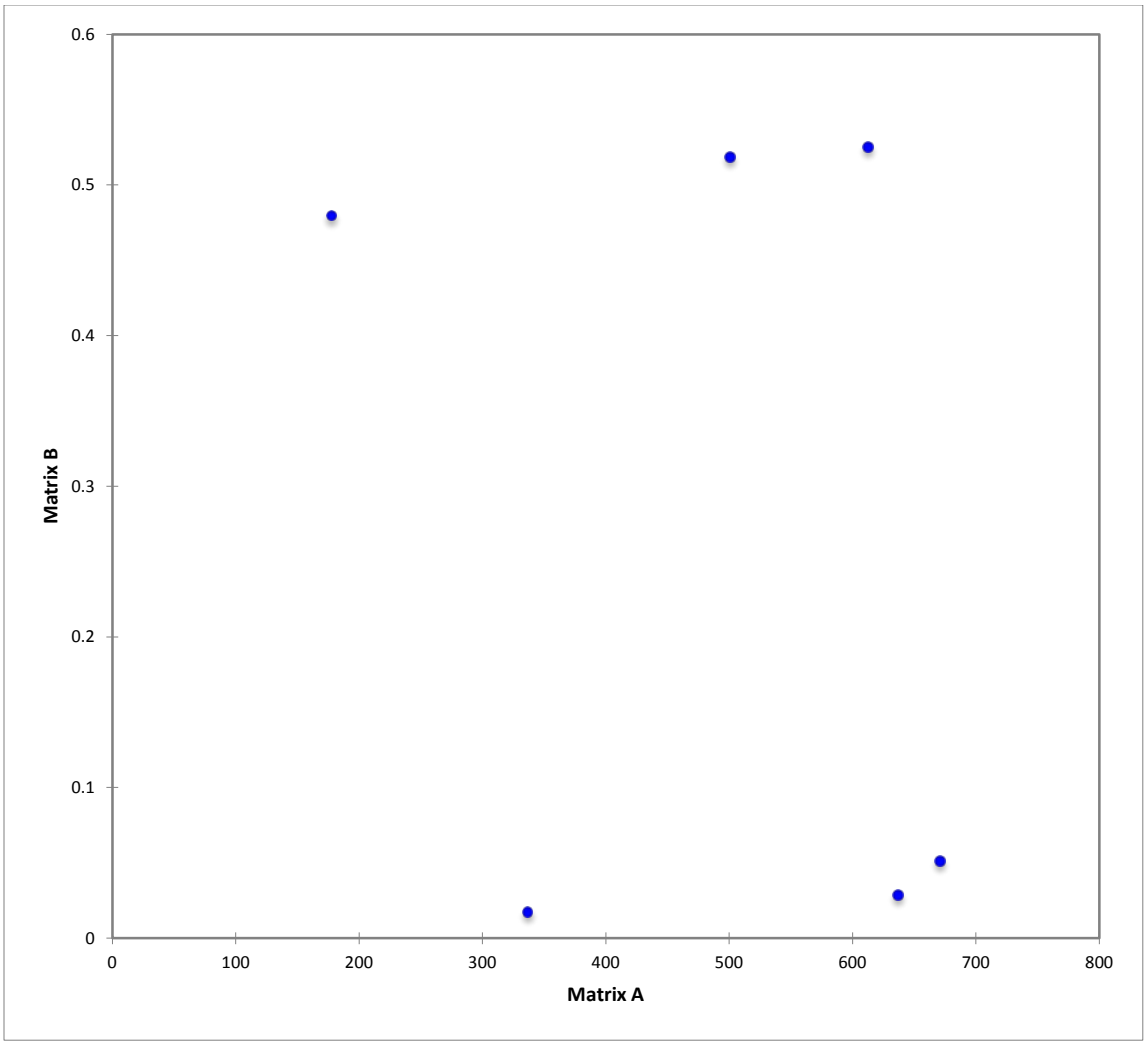

Figure 31. Scatterplot of the Mantel Test (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 2).

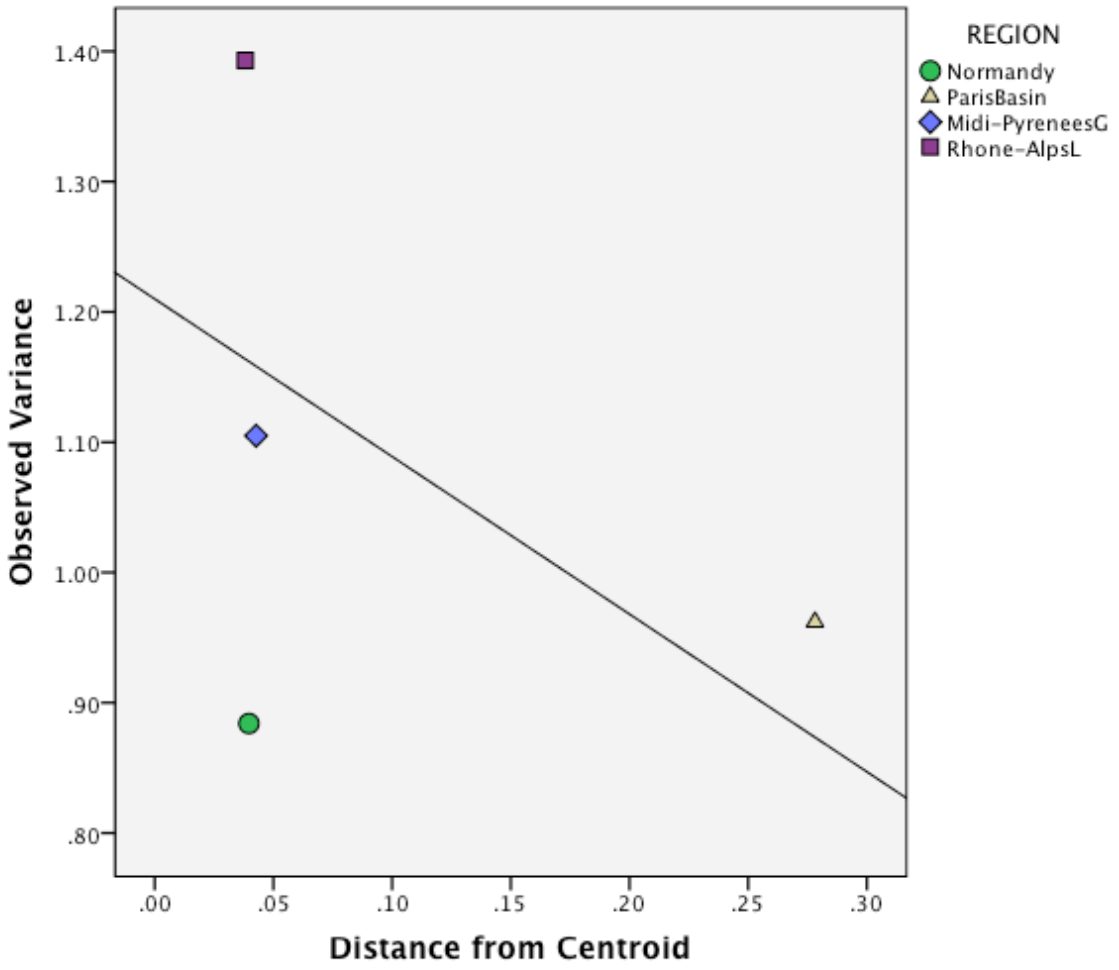

Figure 32. Scatterplot of Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 2).

9.2.3 Demographic Scenario 3

Factoring in population weights (relative population sizes, $h^2 = 1.0$) does not change the overall patterns observed in Figures 27 and 30. The total variance (98.8%) explained by the first two eigenvectors is still high, with the majority of the variance (93.3%) stemming from the first eigenvector (Figure 33). As in previous demographic scenarios, the first eigenvector clearly distinguishes the Paris Basin region from the remaining regions (Normandy, Midi-Pyrénées, Rhône-Alps). Likewise, the latitudinal gradient observed along the second eigenvector is still present here. A more significant change can be observed between the Midi-Pyrénées and Rhône-Alps regions, which are much closer to each other along the second axis than in the previous scenario (Figure 30). This trend is in striking contrast to the differences observed between Normandy and the Paris Basin along the second axis. In fact, the distinction between the Paris Basin and Normandy is large given their relatively close geographic proximity to each other.

Many of the distinctions noted from the principal coordinates analysis are also reflected by the matrix of Mahalanobis distances (Table 24). The Paris Basin region is significantly different from all other regions (Normandy, Midi-Pyrénées, Rhône-Alps), while the Normandy, Midi-Pyrénées, and Rhône-Alps regions are not significantly different from each other. This latter result is likely reflecting the patterns from eigenvector one (Figure 33) since it accounts for the bulk of the variation in the Principal Coordinates Analysis. However, when alpha is set to 0.10, the Normandy region does become significantly different from both the Midi-Pyrénées and Rhône-Alps, suggesting a greater distinction than initially apparent.

A Mantel Test for isolation-by-distance was not significant ($R^2 = -0.371$, $p = 1.000$), suggesting that geographic distance alone cannot account for the biological distances observed in Table 24 (see also Figure 34). However regional heterogeneity ($F_{ST} = 0.056$) was significantly different from zero, which indicates that between-regional variance was elevated.

An examination of Relethford-Blangero residuals (Table 25) shows that, despite its distinction, the Paris Basin region does not have significant changes in expected extra-local gene flow. In contrast, the Normandy region exhibits significantly less than expected gene flow, while the Midi-Pyrénées and Rhône-Alps regions exhibit significantly greater than expected gene flow. These changes are visible in Figure 35, where Normandy rests below the line, Midi-Pyrénées and Rhône-Alps are above the line, and the Paris Basin rests along the line for expected variance.

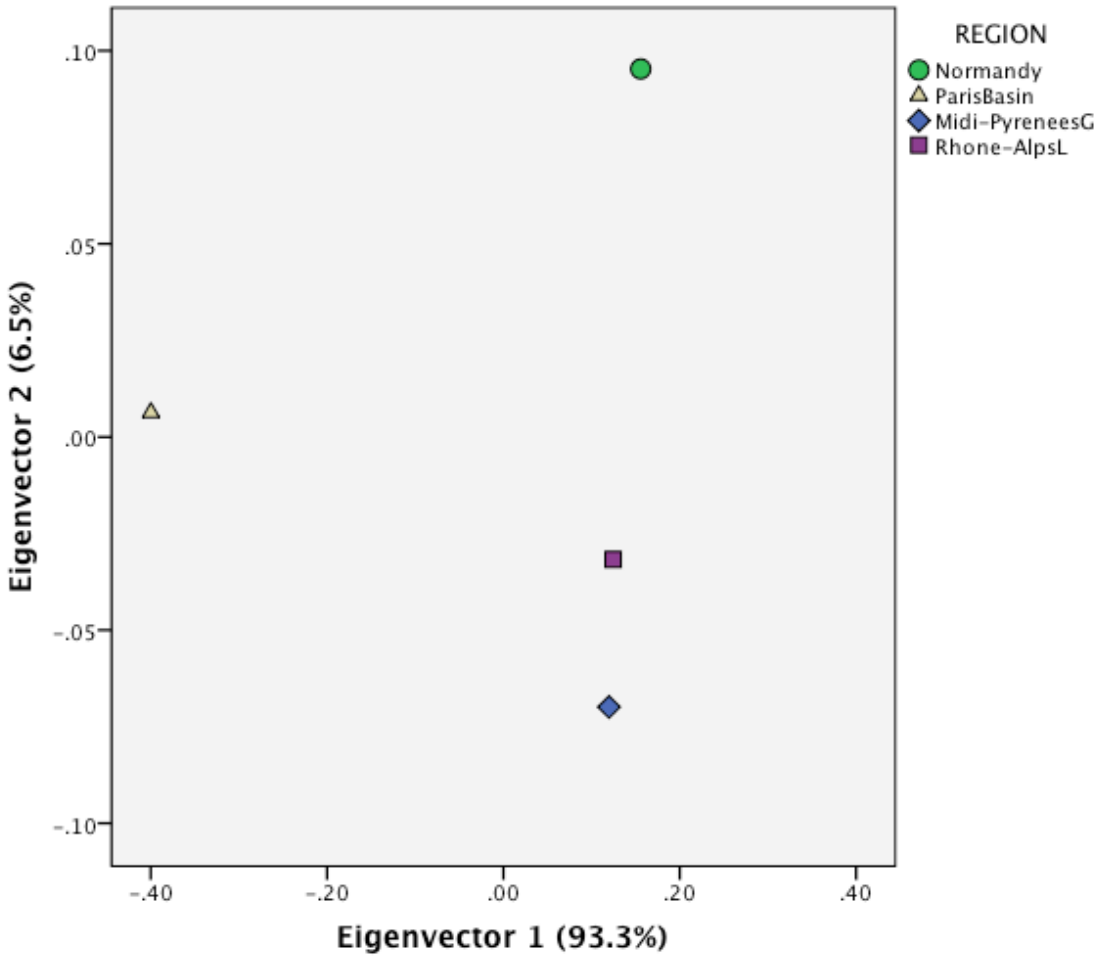

Figure 33. Scatterplot of PCO 1 vs. PCO 2 (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 3).

Table 24

Biological Distance (d^2) Matrix (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 3).

	Normandy	ParisBasin	Midi-Pyrénées	Rhône-Alps
Normandy	-			
ParisBasin	0.237**	-		
Midi-Pyrénées	0.029*	0.260**	-	
Rhône-Alps	0.016*	0.259**	0.004	-

Notes: **$p \leq 0.05$, * $p \leq 0.10$.

Table 25

Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 3).

Region	Residual
Normandy	-0.177**
ParisBasin	-0.016
Midi-Pyrénées	0.051**
Rhône-Alps	0.337**

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

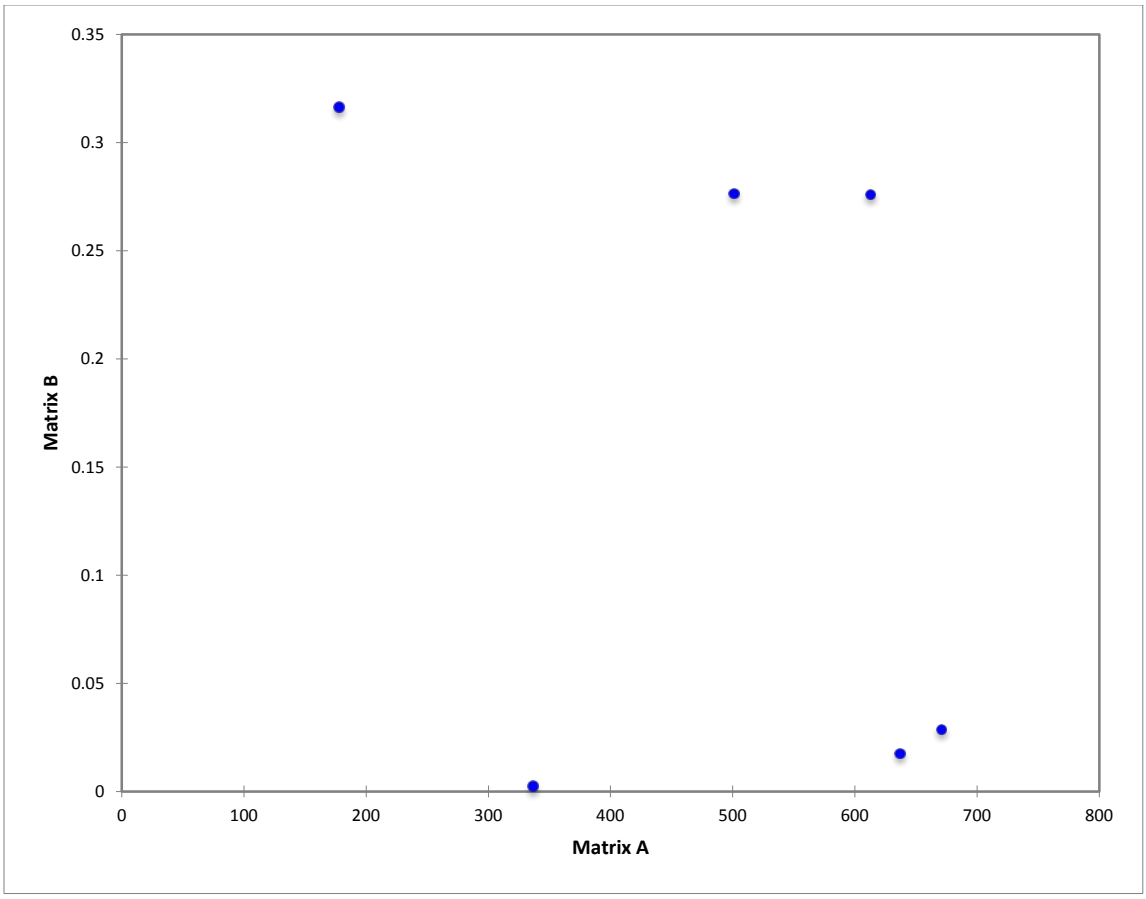

Figure 34. Scatterplot of the Mantel Test (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 3).

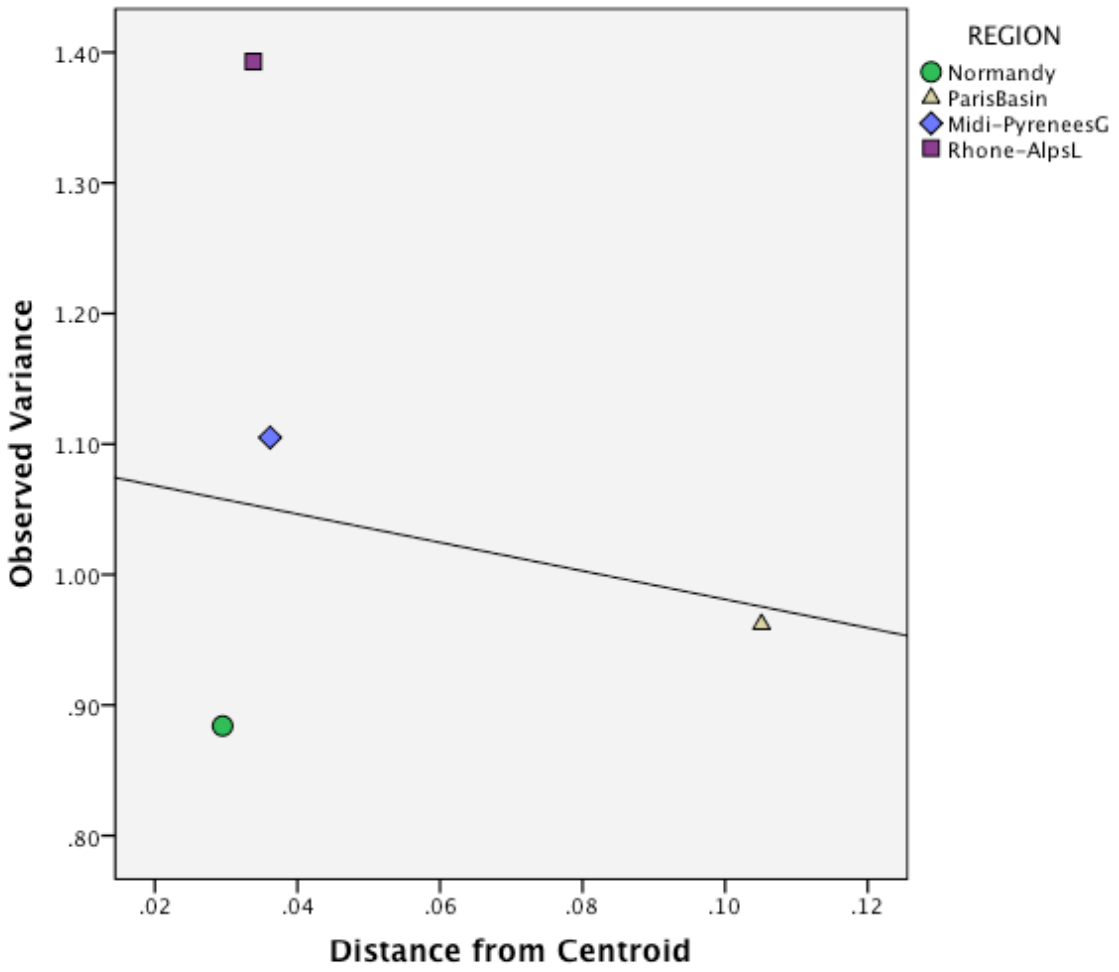

Figure 35. Scatterplot of Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 3).

9.2.4 Demographic Scenario 4

When incorporating relative population sizes and a narrow-sense heritability of 0.55, the Principal Coordinates Analysis remains remarkably similar to previous demographic scenarios (Figures 27, 30, and 33). Here, the total variance explained is nearly 98%, with the majority originating from eigenvector one (91.8%, see Figure 36). Again, the Paris Basin region is distinct from the remaining sites (Normandy, Midi-Pyrénées, Rhône-Alps), plotting negatively along the first axis. The second axis still shows a slight north-south geographic gradient, with the Normandy region plotting positively high.

Mahalanobis distances (Table 26) reflect the patterns seen in the scatterplot of the principal coordinates analysis. The Paris Basin region is significantly different than all remaining regions (Normandy, Midi-Pyrénées, Rhône-Alps). Likewise, the Normandy region is significantly different from the other three regions (Paris Basin, Midi-Pyrénées, Rhône-Alps). The only regions not significantly different from each other are the Midi-Pyrénées and the Rhône-Alps. These results clearly show that a slight alteration of the demographic parameters (narrow-sense heritability and weighted population sizes) can alter the biological distance relationships among the regions, possibly elucidating underlying patterns.

Despite the significant biological distances reflected by the Mahalanobis distances (Table 26) and the slight latitudinal gradient noted in the scatterplot of the principal coordinates (Figure 36), geographic distance does not appear to be a factor in these results. Mantel Tests for isolation-by-distance were not significant ($R^2 = -0.341$,

$p = 1.000$) (Figure 37), although regional heterogeneity ($F_{ST} = 0.102$) was significantly different from zero.

Examination of Relethford-Blangero residuals (Table 27) shows only two regions with significant changes in expected extra-local gene flow. Normandy has significantly less than expected extra-local gene flow, while the Rhône-Alps region has significantly greater than expected extra-local gene flow. These results are in contrast to demographic scenarios two and three (Tables 23 and 25, Figures 32 and 35), wherein every, or nearly every, region exhibited significant changes in expected extra-local gene flow. The scatterplot with the expected line of variance (Figure 38) again shows Normandy with less than expected extra-local gene flow, and Rhône-Alps with greater than expected extra-local gene flow. Both the Paris Basin and Midi-Pyrénées regions rest close to the line and are not significantly different from the expected variance.

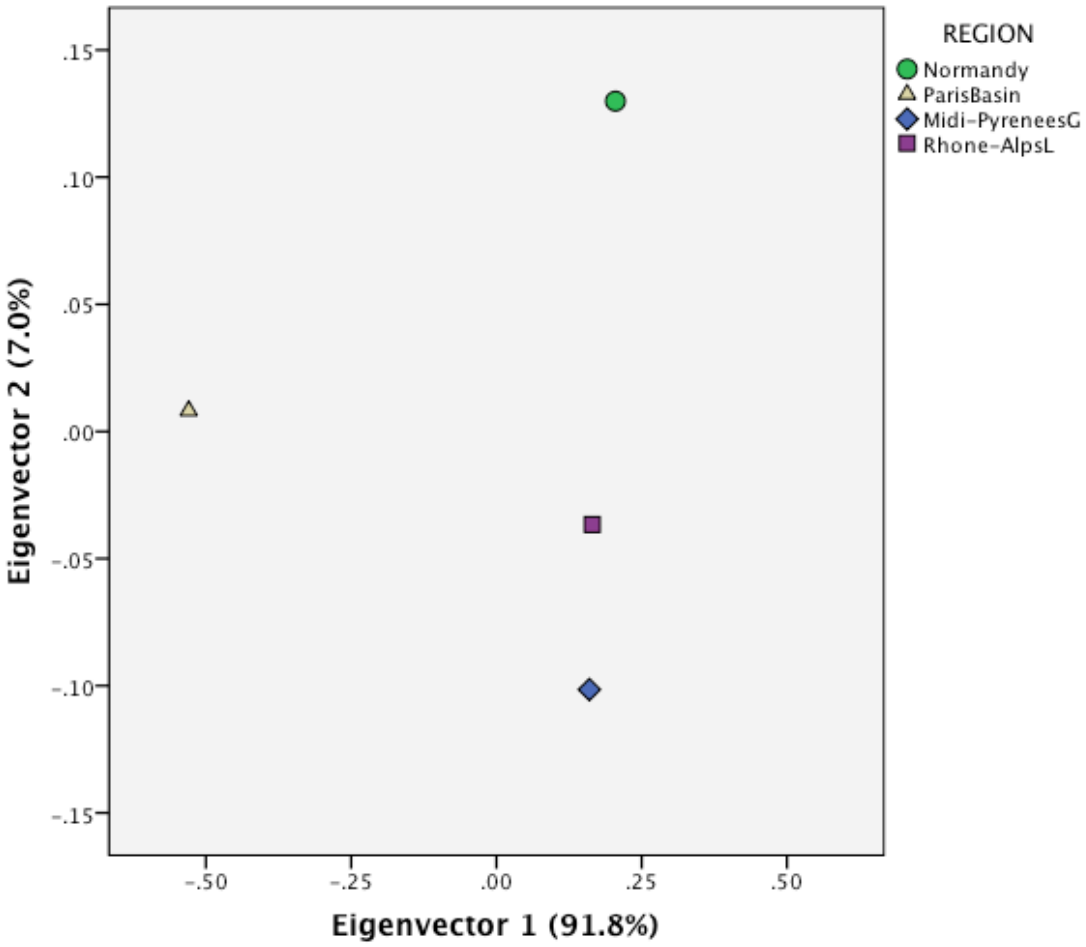

Figure 36. Scatterplot of PCO 1 vs. PCO 2 (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 4).

Table 26

Biological Distance (d^2) Matrix (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 4).

	Normandy	ParisBasin	Midi-Pyrénées	Rhône-Alps
Normandy	-			
ParisBasin	0.415**	-		
Midi-Pyrénées	0.059**	0.462**	-	
Rhône-Alps	0.033**	0.458**	0.019	-

Notes: $**p \leq 0.05$, $* p \leq 0.10$.

Table 27

Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 4).

Region	Residual
Normandy	-0.205**
ParisBasin	0.028
Midi-Pyrénées	0.038*
Rhône-Alps	0.317**

Notes: $** p \leq 0.05$, $* p \leq 0.10$.

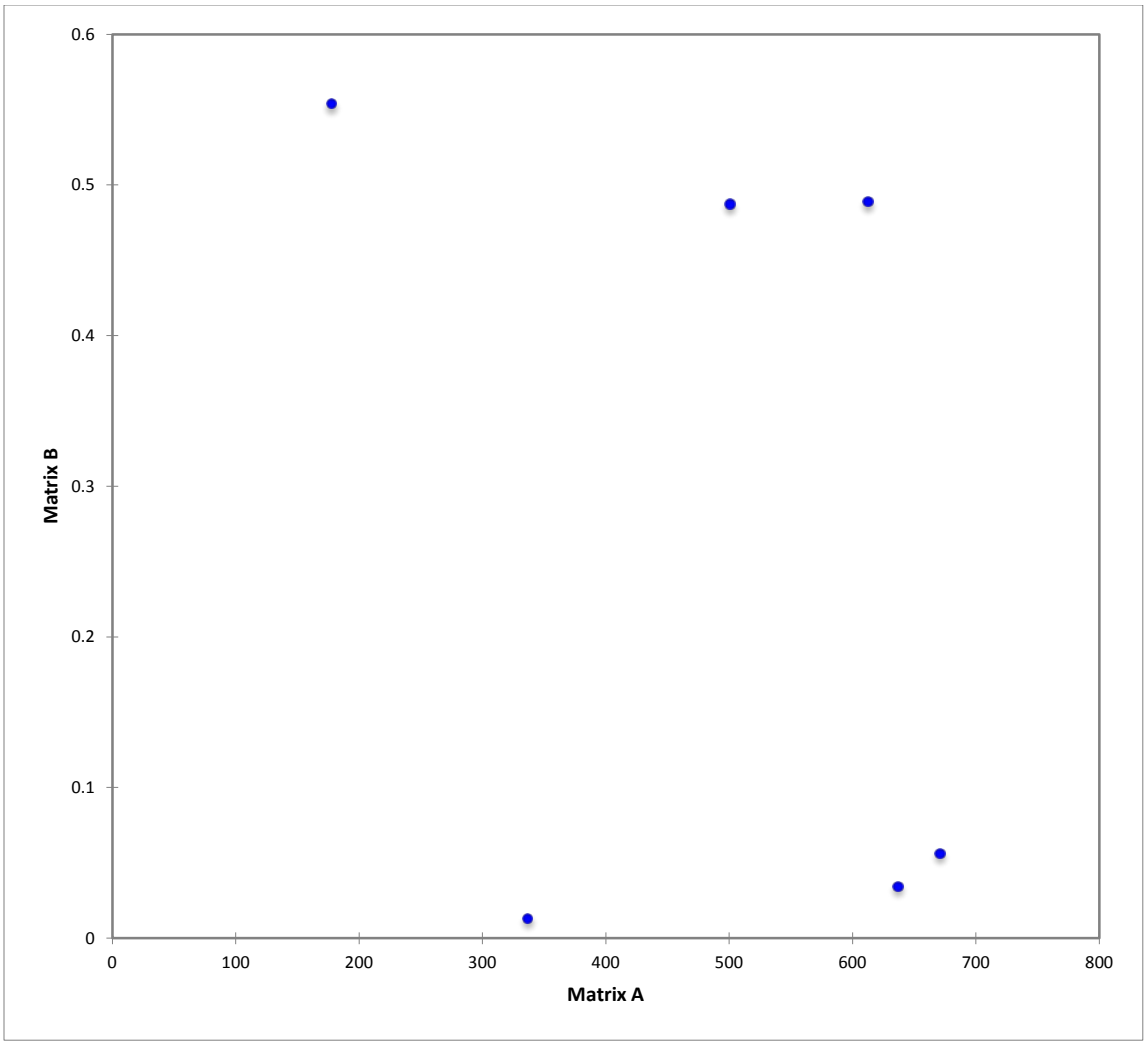

Figure 37. Scatterplot of the Mantel Test (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 4).

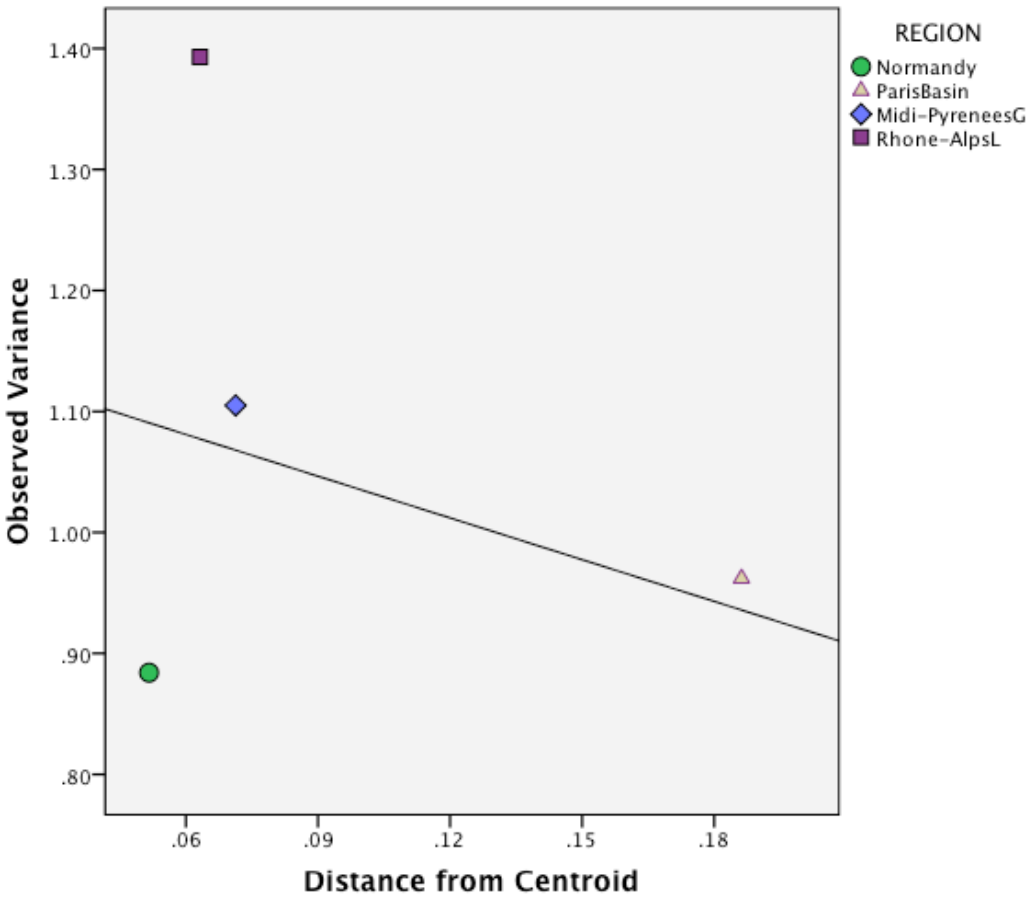

Figure 38. Scatterplot of Relethford-Blangero Residuals (Odontometric Analysis: Synchronic, Regional-Level, Demographic Scenario 4).

9.2.5 Review

Much like the site-level results, the R-matrix analyses using regions as the unit/subpopulation of analysis yield clear patterns. A large percentage of the variation present in the relationship matrix is explained by the first two eigenvectors. The first eigenvector distinctly separates the Paris Basin Region from all other regions. Furthermore, the second eigenvector appears to maintain a north-south division of regions, whereby those regions further north are more negative along the second axis and those regions further south are more positive along the second axis.

Mahalanobis d^2 matrices assessing the strength of the biological distances between regions show that the Paris Basin Region is both consistently and significantly different from all other regions. With changing demographic scenarios, however, the Normandy Region also begins to show significant differences between it and others. Only the Rhône-Alps and Midi-Pyrénées Regions fail to exhibit significant distances between them. This pattern is obvious in the scatterplots of the principal coordinates, where both the Normandy and Paris Basins are spatially distinct and the Rhône-Alps and Midi-Pyrénées Regions group close to each other.

Despite the latitudinal gradient observed by the scatterplot of the principal coordinates, not a single Mantel Test yielded a significant result. In other words, geographic distance does not account for the apparent spatial differences noted in the scatterplots. Nor does geographic distance account for the significant differences noted in the Mahalanobis d^2 matrices.

Estimates of inter-regional heterogeneity are significantly different from zero ($p \leq 0.05$) in all demographic scenarios examined. These results would suggest that at

least some regions were genetically isolated from each other, consisted of very small effective population sizes, or, at the very least, were not engaging in enough inter-regional gene flow to overcome the effects of genetic drift. Individualized gene flow from external sources also does not seem to account fully for the biological differences observed. Relethford-Blangero residuals nearly always show that the Normandy Region has significantly less than expected extra-local gene flow, and the Rhône-Alps Region has significantly greater than expected extra-local gene flow. Yet, the Paris Basin Region, which is so distinct on scatterplots and Mahalanobis d^2 matrices, does not possess any consistently significant negative or positive residuals.

9.3.0 SUMMARY

Both the site-level and regional-level analyses yield revealing trends. The first of these is the consistently high amount of variation from the R-matrix analysis explained by the first two eigenvectors. As depicted on the scatterplots of the principal coordinates, the Paris Basin is reliably distinct from other sites/regions, whether considering individual sites or the region as a whole. Another trend repeatedly shown by these results is a possible latitudinal gradient between sites/regions along the second eigenvector, regardless of the level of the analysis or the demographic scenario.

The significance of the biological distances presented in Mahalanobis d^2 matrices are variable depending on the level of the analysis. Although sites from the Normandy Region are often significantly different from other sites in other regions, the same is not true when grouping all of the sites together into their respective regions. In other words, the Normandy Region is not significantly different from other regions, until the

parameters of the demographic scenarios are altered to reflect relative population sizes and a less conservative narrow-sense heritability estimate. This intriguing comparison might be a product of the increasing evidence for intra-regional variation previously noted for the Normandy Region.

A similar pattern can be observed for sites from the Paris Basin Region. Most, though not all, of the sites from this region are significantly different from other sites, regardless of their region. Likewise, when considering the Paris Basin Region as a whole, it is always significantly different from the other regions. However, to state that the Paris Basin Region represents a homogeneous subpopulation would be misleading. As revealed by changing demographic scenarios, sites from within the Paris Basin Region exhibit increasing intra-regional variation, much like sites from the Normandy Region.

The most striking differences between the site- and regional-level analyses are the results of the Mantel Tests. For the site-level, all Mantel Test results were significant; for the regional-level, no results were significant. Given the greater number of sites within the Normandy Region that are both biologically proximate *and* geographically proximate, it is not surprising that significant results for Mantel Tests would be generated. Indeed, by combining these sites into a single region, it becomes obvious that the significant results were an artifact of the relative numbers of sites within specific regions, rather than a reflection of isolation-by-distance.

Estimates of both inter-site and inter-regional heterogeneity (F_{ST}) were all significantly different from zero. These consistent results would suggest that communities were overall highly diverse. However, the lack of significant biological distances between sites from the same region also suggests a certain degree of

homogeneity within regions. Thus, the significant estimates of (F_{ST}) are more than likely operating at the regional scale. These patterns could result from limited gene flow between regions, differences in relative effective population sizes, and differences in relative reception of external gene flow.

Indeed, the latter point may be observed for the Normandy Region, for which the Relethford-Blangero residuals are significantly negative. In contrast, the Rhône-Alps Region has significantly greater than expected extra-local gene flow. Consequently, some of the heterogeneity observed among these sites and regions could be a product of directed gene flow from sources not included in these analyses. Regardless, the possible lack of external sources of gene flow does not appear to explain the striking differentiation held by sites and the region of the Paris Basin. Perhaps the sites and the region were subject to a smaller effective population size, or some other factors—such as limited intra-regional gene flow—resulted in greater phenotypic diversity for the region overall.

CHAPTER 10

RESULTS: ODONTOMETRIC DIACHRONIC ANALYSIS

10.0.0 INTRODUCTION

This chapter introduces the results for the diachronic biodistance analysis. These results stem from 63 odontometric variables from four regions (Table 11). The goal of this portion of the analysis was to assess 1) how each region changes over time, and 2) how contemporaneous regions relate to each other. However, not all regions were represented in each time period. For example, the Paris Basin region is only represented in the Merovingian and Carolingian Periods, and the Rhône-Alps region is only represented in the Merovingian Period. Likewise, the sample size for some time periods is low (see Table 28).

R-matrix analyses used the region as the unit/subpopulation of analysis. In other words, the scale of analysis and the results presented are for the region. Furthermore, all results are sub-divided by different demographic scenarios. These scenarios are based on varying permutations of population sizes (equal or relative) and of narrow-sense heritability estimates ($h^2 = 1.0$ or $h^2 = 0.55$). Each report includes details on the following: 1) the percentage of variation accounted for by the relationship matrix; 2) the spatial relationship among the analytical units/subpopulations depicted by a scatterplot of principal coordinates; 3) the results of the Mahalanobis d^2 matrix; 4) the results of the Mantel Test; 5) the estimate of between-unit variance (i.e., the estimate of genetic diversity; F_{ST}); 6) the average within-region phenotypic variance; and 7) the Relethford-Blangero residuals (i.e., estimate of gene flow).

Table 28

Odontometric Sample Sizes: Regions and Time Periods

Region and Time Period	Relative Population Size	Sample Size (n)
Gallo-Roman:		
Normandy	1	74
Midi-Pyrénées	0.5	2
Merovingian:		
Normandy	1	563
Paris Basin	1	78
Rhône-Alps	0.5	78
Midi-Pyrénées	0.5	13
Carolingian:		
Paris Basin	1	7
Midi-Pyrénées	0.75	7
Total		822

10.1.0 REGIONAL-LEVEL

10.1.1 Demographic Scenario 1

Results for the first demographic scenario (equal population sizes, $h^2 = 1.0$) are shown in Figure 39. The first two eigenvectors account for 96.3% of the variance, with the majority stemming from the first eigenvector (85.8%) itself. Much like in Figure 33, the Paris Basin Region is distinct from the remaining regions (Normandy, Midi-Pyrénées, Rhône-Alps) along eigenvector 1, regardless of time period. Moreover, it does not appear to change over time, as evidenced by the very slight shift from the Merovingian to Carolingian Periods. Interestingly, the latitudinal gradient observed in previous analyses disappears when factoring time periods. The Paris Basin Region is now similarly placed along eigenvector 2 as the Rhône-Alps region (Merovingian Period) and the Midi-Pyrénées region (Carolingian Period). Regardless, there appear to be some interesting trends, although not all regions are represented in each time period. From the Gallo-Roman to Merovingian Periods, regions become more distinct from each other. From the Merovingian to Carolingian Periods, regions become more similar to each other.

Examination of Mahalanobis d^2 matrices (Table 29) seems to confirm the trends noted in the scatterplot of the principal coordinates (Figure 39). Because these proxy subpopulations lived in different time periods, they could not logically interbreed. Thus, the biological distance matrix is split; the lower matrix shows d^2 values regardless of time period, while the upper matrix shows d^2 values by time period. Although of limited interpretive value, the lower half of the d^2 matrix is still useful for considering how a region changes over time when compared to *itself*. For example, the Normandy Region during the Gallo-Roman Period is *not* significantly different from the Normandy Region

during the Merovingian Period (lower matrix, Table 29). Likewise, the Midi-Pyrénées and Paris Basin Regions are biologically indistinct from themselves over time. These results would suggest a degree of intra-regional homogeneity over time.

When factoring in temporal constraints (upper matrix, Table 29), the Normandy Region during the Gallo-Roman Period is *not* significantly different from the Midi-Pyrénées Region from the same time period. Yet, this overall pattern changes during the Merovingian Period during which the Paris Basin Region is distinct from the remaining regions from the same time period. By the Carolingian Period, regions are not significantly different from each other.

Considering measures of heterogeneity (Table 30), inter-region heterogeneity (F_{ST}) is significantly different from zero for only the Merovingian Period. However, it is also clear that inter-region heterogeneity increases over time. This would suggest that 1) gene flow between regions decreased over time; 2) some regions were subject to greater amounts of extra-local gene flow than others; and/or 3) effective population sizes of some or all regions decreased over time. Despite these results, the changes in F_{ST} over time are not significantly different from each other, as based on Z tests (Table 31). In contrast to F_{ST}, average within-region phenotypic variance decreases over time. Interestingly, these results would suggest that, despite increasing differentiation between regions, intra-regional variance was actually decreasing, perhaps through gene flow within specific regions.

Due to obvious data constraints, it is not prudent to perform a test for isolation-by-distance using the lower d^2 matrix. Given that an analysis for each region filtered by time period is most useful, the sole Mantel Test performed was for the Merovingian

Period. This time period also possessed the requisite minimum number of regions in order to successfully perform the analysis. As seen in Figure 40, there is very little linear arrangement between the biological and geographic distances. Furthermore, the results are negative ($R^2 = -0.029$, $p = 0.979$).

Relethford-Blangero residuals also reveal some interesting trends (Table 32 and Figure 41). Firstly, the Normandy Region always exhibits significantly less than expected extra-local gene flow. In contrast, the Midi-Pyrénées Region always exhibits significantly greater than expected extra-local gene flow. The Paris Basin, however, shows no significant deviation from the expected levels of extra-local gene flow during the Merovingian Period, but shows a drastic reduction during the Carolingian Period with significantly less than expected extra-local gene flow. No single time period is characterized by all regions having a greater than expected extra-local gene flow, nor by all regions having a less than expected extra-local gene flow. For example, regions from the Merovingian Period possess significantly positive or negative residuals, but not all positive or all negative. Rather, a mixture is presented, which perhaps contributes to the varied results for estimates of F_{ST}, average phenotypic variance, and significant Mahalanobis d^2 distances.

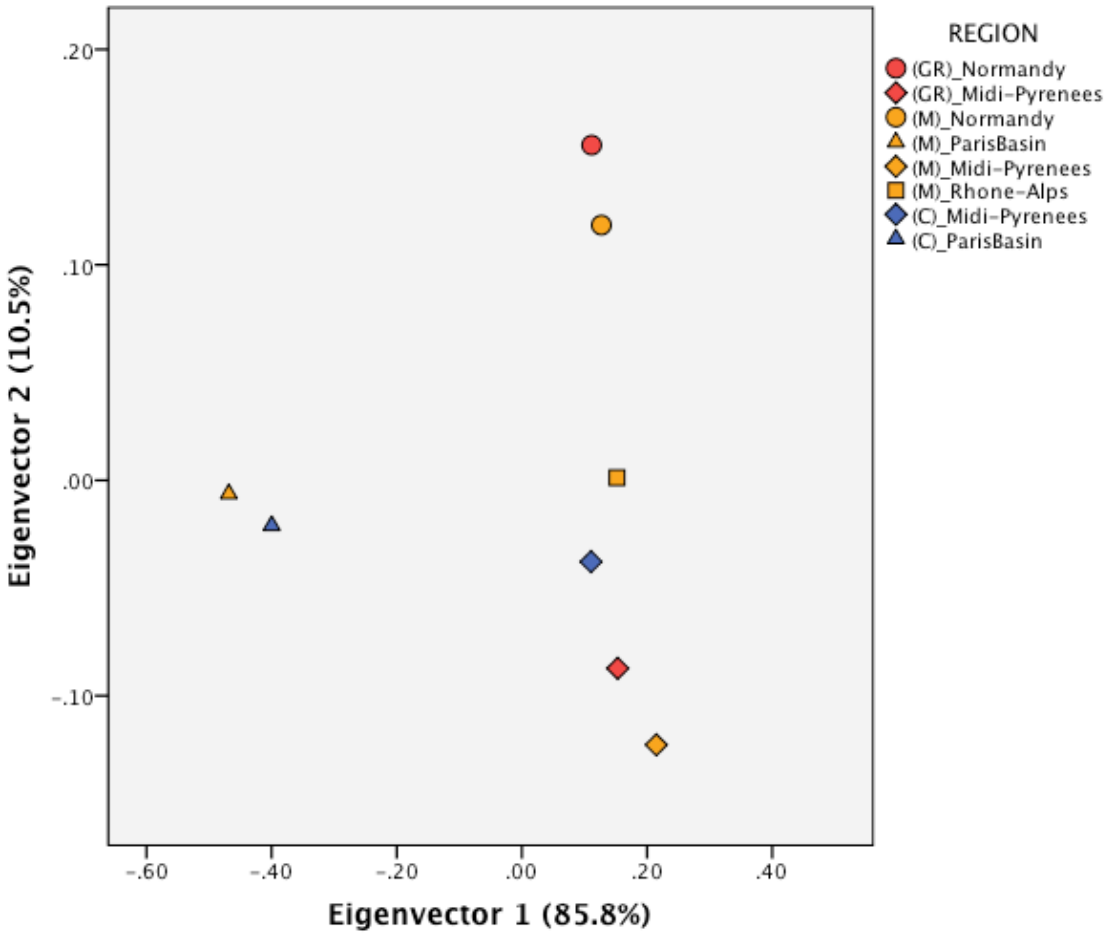

Figure 39. Scatterplot of PCO 1 vs. PCO 2 (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 1).

Table 29

Biological Distance (d^2) Matrix (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 1).

	(GR)_Norm	(GR)_Midi	(M)_Norm	(M)_ParisB	(M)_Midi	(M)_Rhone	(C)_ParisB	(C)_Midi
(GR)_Normandy	-	0.310	-	-	-	-	-	-
(GR)_Midi-Pyrénées	0.050	-	-	-	-	-	-	-
(M)_Normandy	0.000	0.026	-	0.265**	0.042	0.013	-	-
(M)_ParisBasin	0.356**	0.372	0.359**	-	0.344**	0.290**	-	-
(M)_Midi-Pyrénées	0.083	0.000	0.064	0.481**	-	0.000	-	-
(M)_Rhône-Alps	0.026	0.005	0.014	0.381**	0.010	-	-	-
(C)_ParisBasin	0.279**	0.288	0.287**	0.00	0.360**	0.291**	-	0.629
(C)_Midi-Pyrénées	0.037	0.000	0.026	0.302**	0.028	0.0121	0.283	-

Notes: Lower matrix represents biological distances regardless of time period; upper matrix represents biological distances only for contemporaneous regions. $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 30

Estimates of Inter-Regional Heterogeneity and Average Within-Region Phenotypic Variance (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 1).

Period	F_{ST}	Average Within-Region Phenotypic Variance
Gallo-Roman	0.049	1.608
Merovingian	0.056**	1.141
Carolingian	0.122	0.911

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 31

Z-Test Results (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 1).

Change in F_{ST}	Z
Gallo-Roman to Merovingian (GR-M)	-0.146
Merovingian to Carolingian (M-C)	-1.591
Gallo-Roman to Carolingian (GR-C)	-1.179

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 32

Relethford-Blangero Residuals (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 1).

Region and Time Period	Residual
Gallo-Roman:	
Normandy	-0.418**
Midi-Pyrénées	0.669**
Merovingian:	
Normandy	-0.345**
ParisBasin	0.033
Midi-Pyrénées	0.074**
Rhône-Alps	0.221**
Carolingian:	
ParisBasin	-0.468**
Midi-Pyrénées	0.235**

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

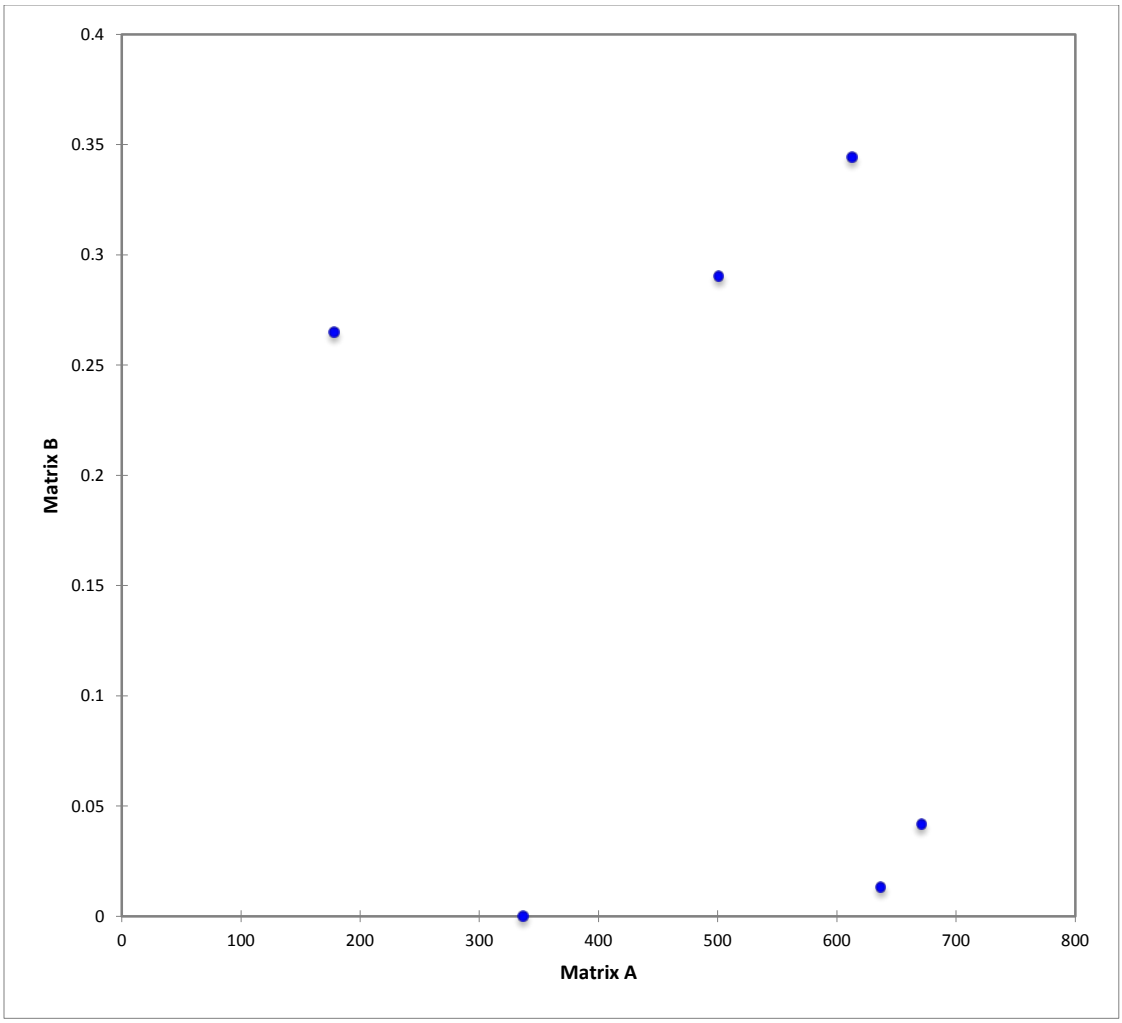

Figure 40. Scatterplot of the Mantel Test (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 1).

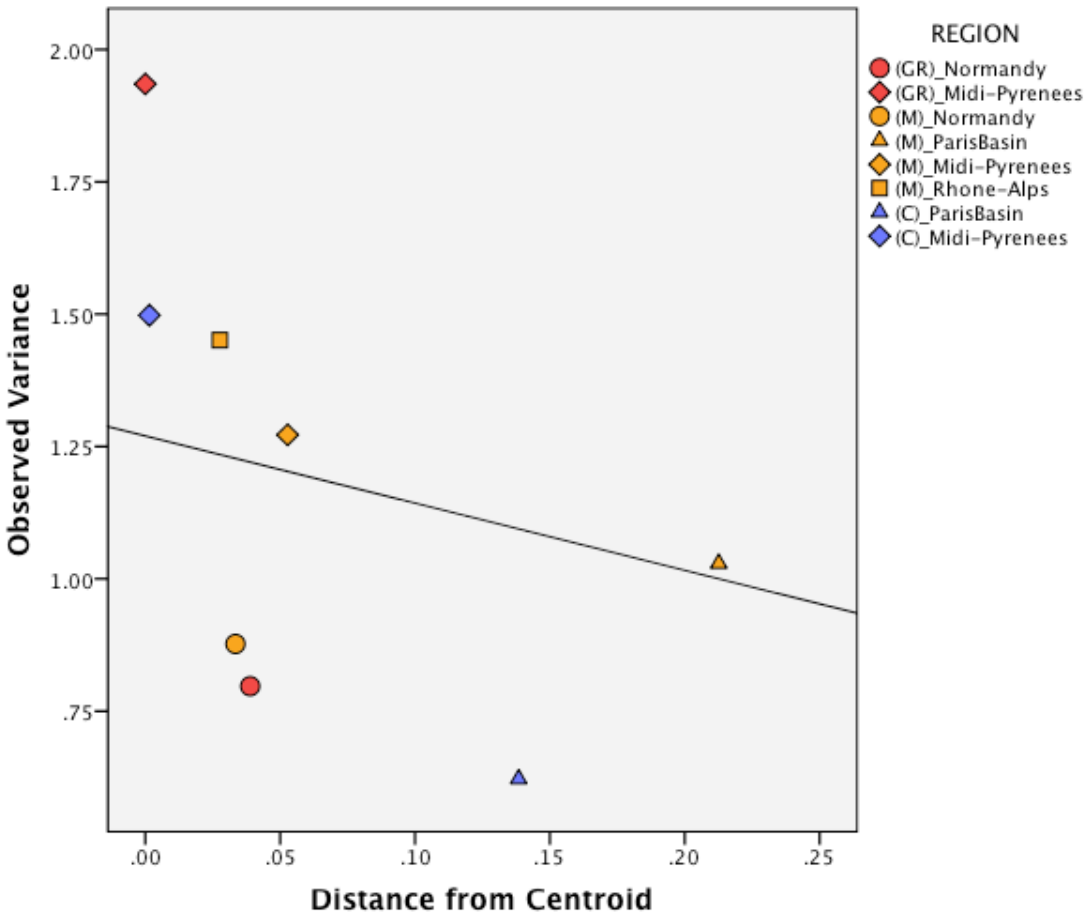

Figure 41. Scatterplot of Relethford-Blangero Residuals (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 1).

10.1.2 Demographic Scenario 2

When narrow-sense heritability is changed to 0.55, a scatterplot (Figure 42) of the principal coordinates shows similar patterns as in Figure 39. In this demographic scenario, over 90% of the variance is explained by the first two eigenvectors, of which 81.7% is explained by eigenvector 1 alone. The Paris Basin Region is distinct from the other three regions along eigenvector 1. This difference disappears along eigenvector 2, where the Paris Basin Region (Merovingian and Carolingian Periods) is similar to Merovingian Rhône-Alps and Carolingian Midi-Pyrénées. Consequently, the Normandy Region becomes quite distinct from the remaining regions along the second axis. Overall, though, it appears that regions become more distinct from the Gallo-Roman to Merovingian Periods. This pattern is reversed from the Merovingian to Carolingian Periods when regions become more similar to each other.

Mahalanobis d^2 distances (Table 33) seem to confirm some of the relationships seen in Figure 42. First, the lower d^2 matrix shows that, of the regions with diachronic representation, there is *no* intra-regional significant difference. This would again suggest biological continuity over time. Based on the upper d^2 matrix, the Normandy and Paris Basin Regions from the Gallo-Roman Period are not significantly different from each other. Likewise, the Carolingian Period Paris Basin and Midi-Pyrénées Regions are not significantly different from each other. It is only during the Merovingian Period that inter-regional differences become significant. Specifically, the Merovingian Period Paris Basin Region is significantly different from all other regions during the same time period. The Normandy and Rhône-Alps Regions approach significance during the Merovingian Period, but only attain it when $\alpha = 0.10$.

These results would suggest that inter-region heterogeneity would be higher during the Merovingian Period, which may not be fully supported (Table 34). For example, while F_{ST} is significantly different from zero during the Merovingian Period, it is part of a trend of increasing inter-regional heterogeneity over time. In fact, the change in F_{ST} from the Merovingian to Carolingian Periods is significant as based on *Z* tests (Table 35). Likewise, the overall change in heterogeneity from the Gallo-Roman to Carolingian Periods is significant. This could indicate that 1) gene flow between regions decreased over time, 2) overall population size decreased over time, 3) a combination of decreased inter-regional gene flow and decreasing population size occurred, 4) some regions, but not all, were subject to extra-local gene flow; or 5) as yet unknown processes occurred. However, the Merovingian Period does not exhibit significant results using the Mantel Test ($R^2 = -0.200$, $p = 0.771$; Figure 43). Thus, whatever patterning may be present during this time period, it is not a result of isolation-by-distance since there is no correlation between the geographic and biological distance matrices.

If increased extra-local gene flow were a factor for specific regions or time periods, then the Relethford-Blangero residuals should reflect this possibility. As seen in Table 36 and Figure 44, there is a mixture of significantly greater or less than expected extra-local gene flow by time period. In other words, no time period exclusively exhibits significantly positive residuals or significantly negative residuals. By region, however, the Normandy Region shows less than expected extra-local gene flow regardless of time period. Likewise, the Midi-Pyrénées Region exhibits greater than expected extra-local gene flow during the Gallo-Roman and Carolingian Periods.

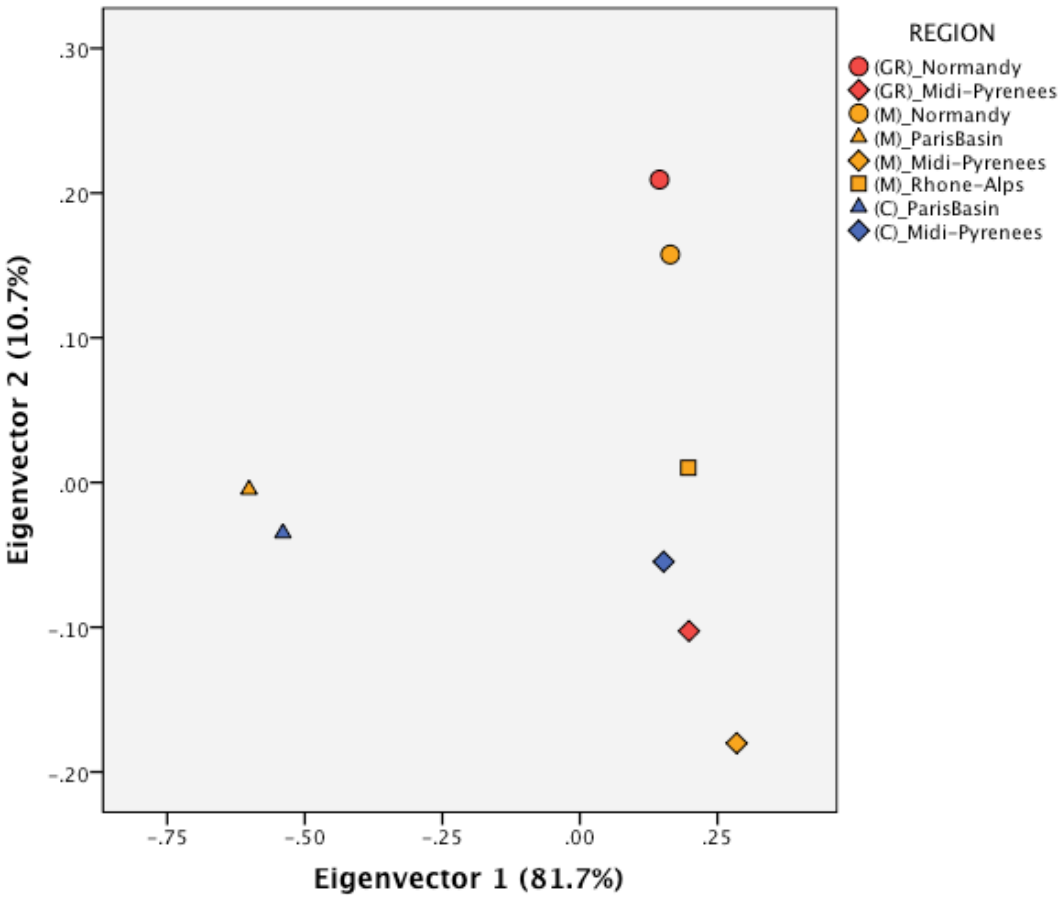

Figure 42. Scatterplot of PCO 1 vs. PCO 2 (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 2).

Table 33

Biological Distance (d^2) Matrix (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 2).

	(GR)_Norm	(GR)_Midi	(M)_Norm	(M)_ParisB	(M)_Midi	(M)_Rhone	(C)_ParisB	(C)_Midi
(GR)_Normandy	-	0.523	-	-	-	-	-	-
(GR)_Midi-Pyrénées	0.089	-	-	-	-	-	-	-
(M)_Normandy	0.003	0.045	-	0.461**	0.100	0.028*	-	-
(M)_ParisBasin	0.607	0.629*	0.609**	-	0.625**	0.509**	-	-
(M)_Midi-Pyrénées	0.171	0.000	0.134**	0.840**	-	0.028	-	-
(M)_Rhône-Alps	0.053*	0.013	0.029**	0.649**	0.047	-	-	-
(C)_ParisBasin	0.522**	0.533	0.531**	0.000	0.679**	0.543**	-	1.070
(C)_Midi-Pyrénées	0.116	0.001	0.092	0.560**	0.122	0.073	0.573**	-

Notes: Lower matrix represents biological distances regardless of time period; upper matrix represents biological distances only for contemporaneous regions. $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 34

Estimates of Inter-Regional Heterogeneity and Average Within-Region Phenotypic Variance (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 2).

Period	F_{ST}	Average Within-Region Phenotypic Variance
Gallo-Roman	0.085	1.608
Merovingian	0.106**	1.141
Carolingian	0.232	0.911

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 35

Z-Test Results (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 2).

Change in F_{ST}	Z
Gallo-Roman to Merovingian (GR-M)	-0.394
Merovingian to Carolingian (M-C)	-3.007**
Gallo-Roman to Carolingian (GR-C)	-2.204**

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 36

Relethford-Blangero Residuals (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 2).

Region and Time Period	Residual
Gallo-Roman:	
Normandy	-0.460**
Midi-Pyrénées	0.583**
Merovingian:	
Normandy	-0.398**
ParisBasin	0.166**
Midi-Pyrénées	0.076
Rhône-Alps	0.168**
Carolingian:	
ParisBasin	-0.350**
Midi-Pyrénées	0.215**

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

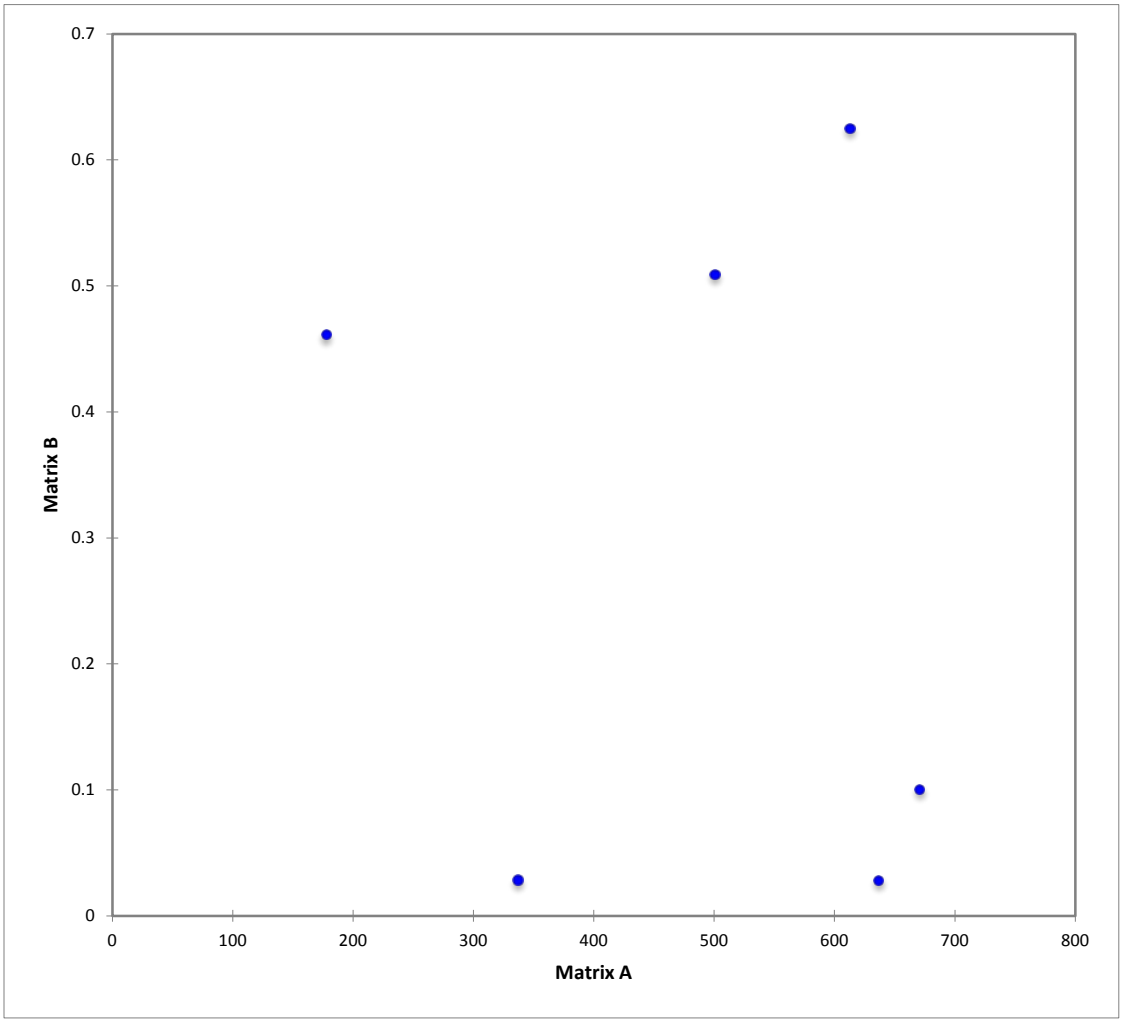

Figure 43. Scatterplot of the Mantel Test (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 2).

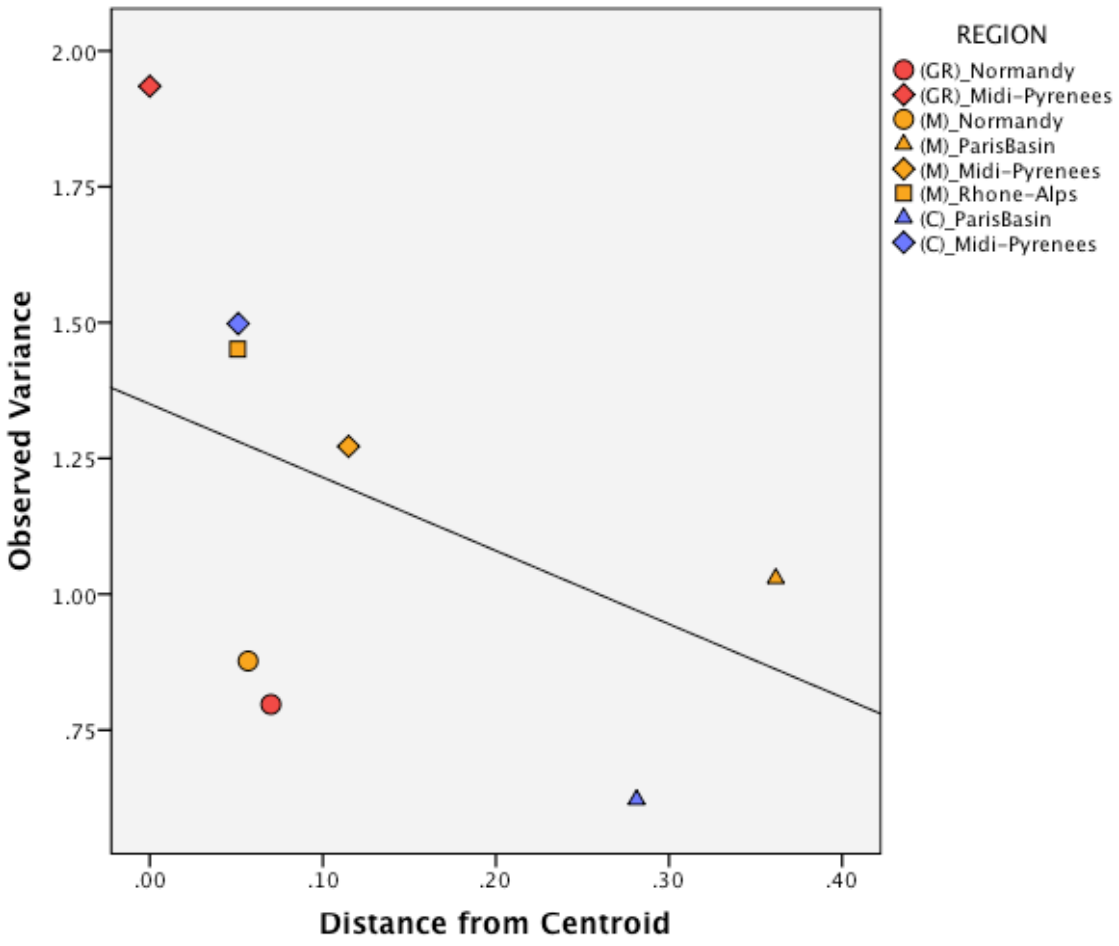

Figure 44. Scatterplot of Relethford-Blangero Residuals (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 2).

10.1.3 Demographic Scenario 3

Considering weighted population sizes, the pattern presented in the scatterplot of principal coordinates (Figure 45) remains similar to those in the previous demographic scenarios (Figures 39 and 42). However, the regional differences are better defined. For example, the Midi-Pyrénées Region represents a tight cluster of time periods along eigenvector 2. The Normandy Region also forms a cluster of time periods along eigenvector 2. Although the bulk of the variation (83.6%) is accounted by eigenvector 1, eigenvector 2 also accounts for 11.9% of the variation and appears to reflect a slight latitudinal gradient mentioned in previous analyses (for example, see Figure 33). Although not all regions are represented in each time period, it appears that regions become more distinct from each other when passing from the Gallo-Roman to Merovingian Periods, but that this trend appears possibly to reverse from the Merovingian to Carolingian Periods. In other words, regions expand from the centroid during the Merovingian Period, then contract toward the centroid during the Carolingian Period.

Mahalanobis d^2 distances (Table 37) seem to confirm the overall pattern noted in Figure 45. The lower d^2 matrix shows that each of the regions having diachronic representation do not differ significantly from themselves. In contrast, the upper d^2 matrix shows that the two regions from the Gallo-Roman Period (Normandy, Midi-Pyrénées) are not significantly different from each other. Likewise, the two regions from the Carolingian Period (Paris Basin, Midi-Pyrénées) are not significantly different from each other. It is only during the Merovingian Period in which regions become

significantly different from each other, specifically the Paris Basin Region from the other regions (Normandy, Rhône-Alps, Midi-Pyrénées).

While regional heterogeneity during the Merovingian Period is significantly different from zero (Table 38), there is a trend of increasing inter-regional heterogeneity over time (Table 39). This would suggest that 1) inter-regional gene flow decreased over time; 2) some regions may have been subject to extra-local gene flow; and/or 3) that population size decreased. However, none of the changes for F_{ST} over time are significant based on *Z*-tests, even considering the global change from the Gallo-Roman to Carolingian Periods. Regardless, averaged phenotypic variance decreases over time, which suggests that intra-region heterogeneity was decreasing at the same time that inter-region heterogeneity was decreasing.

Examination of Relethford-Blangero residuals (Table 40 and Figure 46) confirms that a large number of regions from each time period exhibited significantly greater than expected extra-local gene flow. The Midi-Pyrénées Region is characterized by greater than expected extra-local gene flow regardless of time period. Inversely, the Normandy Region is characterized by less than expected extra-local gene flow for the two periods in which it is represented (Gallo-Roman, Merovingian). Interestingly, it is during the Merovingian Period that regions come closer to the expected levels of extra-local gene flow, a pattern noted in the closer position of those points to the regression line in Figure 46. It is this same region that was subjected to a test for isolation-by-distance (Figure 47). Much like the previous scenarios, results were not significant ($R^2 = -0.143$, $p = 0.817$), and thus the null hypothesis for a correlation between geographic and biological distances cannot be supported.

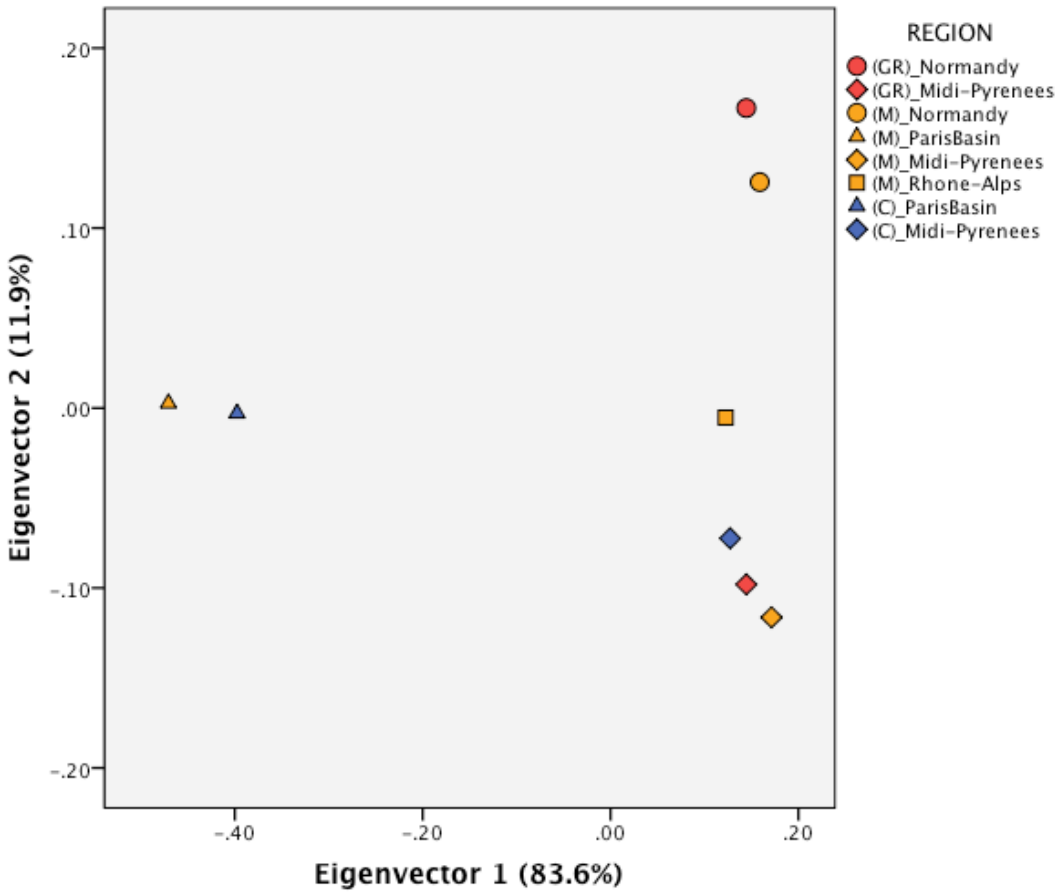

Figure 45. Scatterplot of PCO 1 vs. PCO 2 (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 3).

Table 37

Biological Distance (d^2) Matrix (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 3).

	(GR)_Norm	(GR)_Midi	(M)_Norm	(M)_ParisB	(M)_Midi	(M)_Rhone	(C)_ParisB	(C)_Midi
(GR)_Normandy	-	0.246	-	-	-	-	-	-
(GR)_Midi-Pyrénées	0.045	-	-	-	-	-	-	-
(M)_Normandy	0.000	0.019	-	0.229**	0.052	0.015	-	-
(M)_ParisBasin	0.323**	0.318	0.325**	-	0.311**	0.254**	-	-
(M)_Midi-Pyrénées	0.093	0.000	0.073	0.453**	-	0.004	-	-
(M)_Rhône-Alps	0.027	0.000	0.016*	0.348**	0.015	-	-	-
(C)_ParisBasin	0.250**	0.238	0.256**	0.000	0.332**	0.261**	-	0.641
(C)_Midi-Pyrénées	0.051	0.000	0.039	0.285**	0.041	0.023	0.279	-

Notes: Lower matrix represents biological distances regardless of time period; upper matrix represents biological distances only for contemporaneous regions. $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 38

Estimates of Inter-Regional Heterogeneity and Average Within-Region Phenotypic Variance (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 3).

Period	F_{ST}	Average Within-Region Phenotypic Variance
Gallo-Roman	0.036	1.519
Merovingian	0.059**	1.074
Carolingian	0.121	0.862

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 39

Z-Test Results (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 3).

Change in F_{ST}	Z
Gallo-Roman to Merovingian (GR-M)	-0.519
Merovingian to Carolingian (M-C)	-1.530
Gallo-Roman to Carolingian (GR-C)	-1.439

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 40

Relethford-Blangero Residuals (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 3).

Region and Time Period	Residual
Gallo-Roman:	
Normandy	-0.344**
Midi-Pyrénées	0.742**
Merovingian:	
Normandy	-0.269**
ParisBasin	0.028
Midi-Pyrénées	0.174**
Rhône-Alps	0.305**
Carolingian:	
ParisBasin	-0.460**
Midi-Pyrénées	0.332**

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

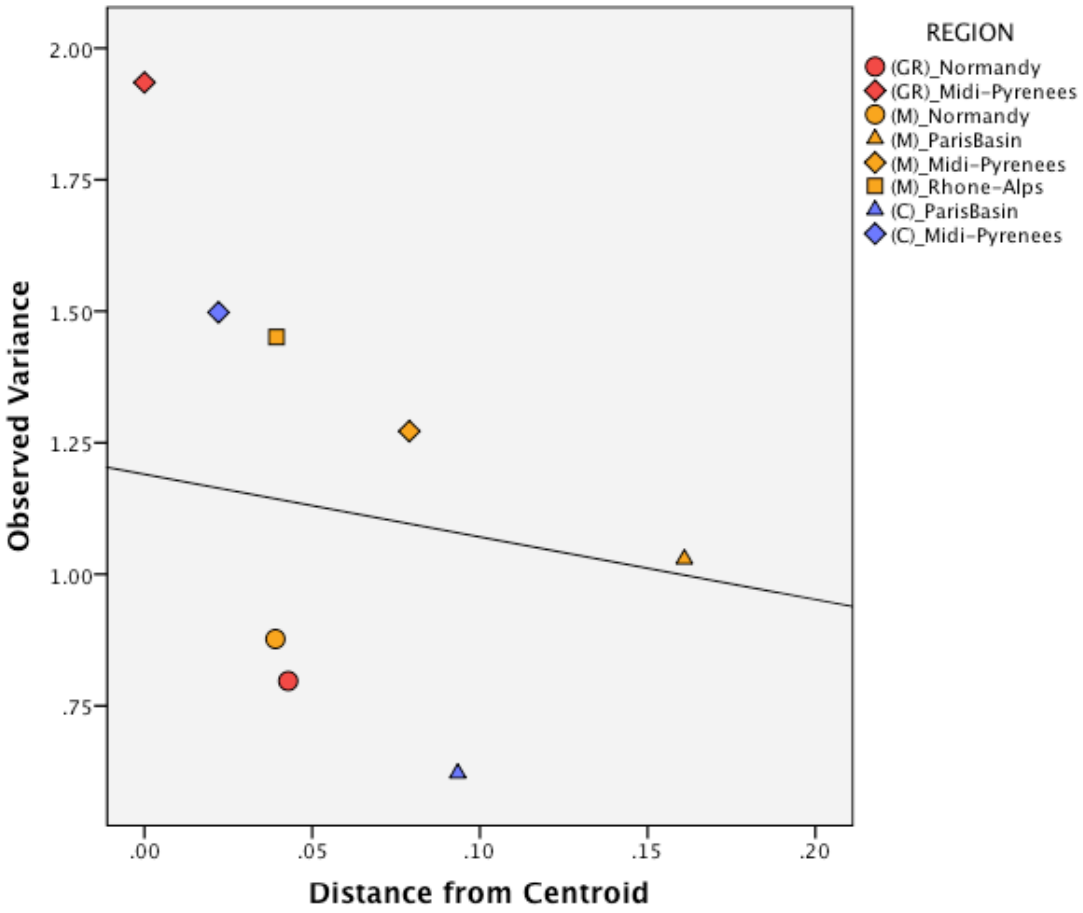

Figure 46. Scatterplot of Relethford-Blangero Residuals (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 3).

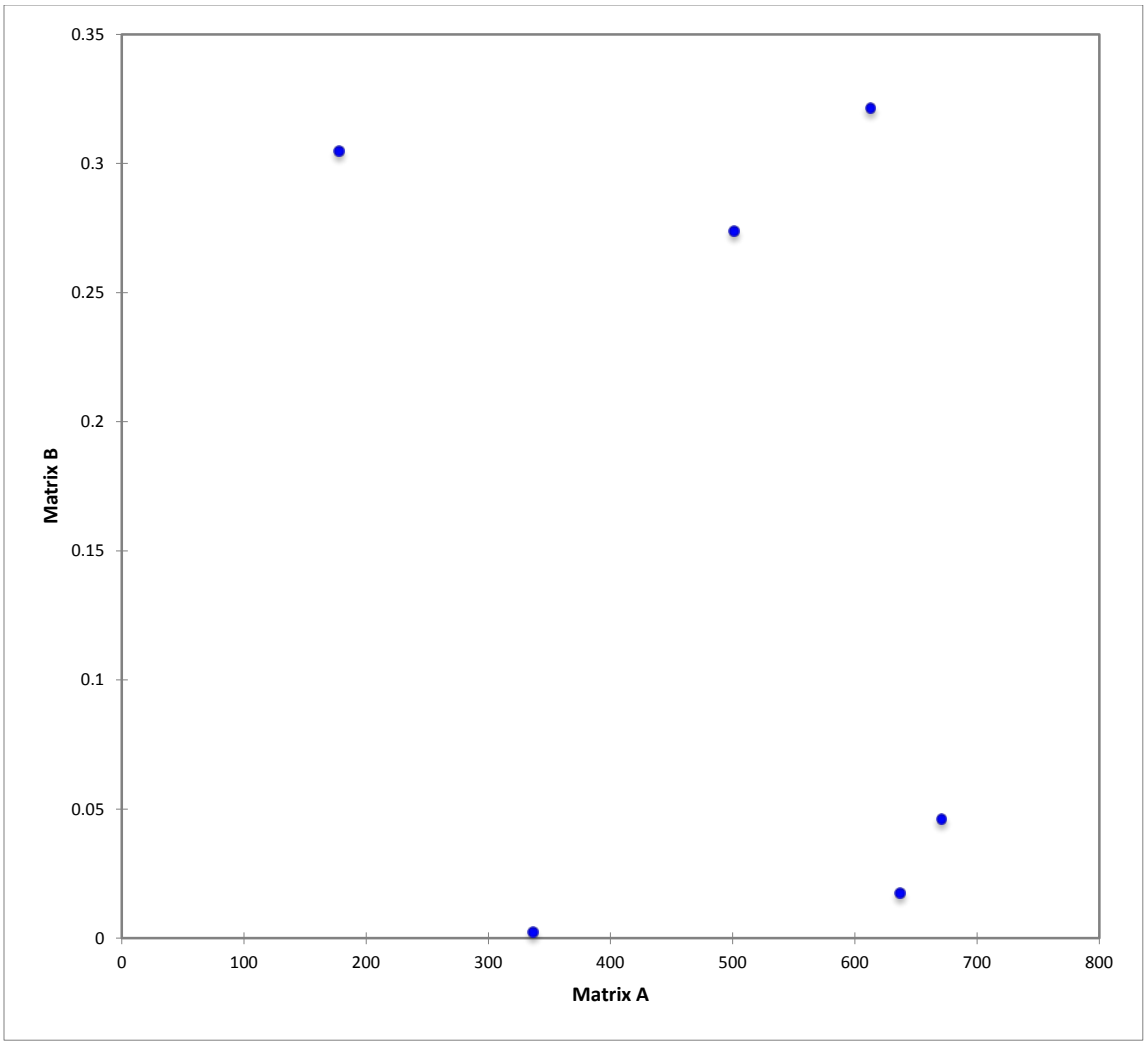

Figure 47. Scatterplot of the Mantel Test (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 3).

10.1.4 Demographic Scenario 4

Altering the parameters to consider both weighted population sizes as well as a less conservative narrow-sense heritability reveals even clearer patterns than noted under the previous demographic scenarios. As seen in Figure 48, each region remains closely internally grouped on the principal coordinates scatterplot for the R-matrix analysis, regardless of time period. Given that over 80% of the variance is represented by the first eigenvector, the separation of the Paris Basin Region for each time period in which it is represented (Merovingian, Carolingian) from the other regions is striking. Likewise, the overall changes in time for the Normandy Region from the more southerly regions (Paris Basin, Rhône-Alps, Midi-Pyrénées) is also of note. However, it is less apparent that there are patterned temporal changes. Although it is still likely that the Merovingian Period exhibits the greatest amount of regional differentiation, it is less clear whether the exhibited change from the Gallo-Roman to Merovingian Periods or the change from the Merovingian to Carolingian Periods is meaningful.

Mahalanobis d^2 distances (Table 41) clarify these issues, but cannot resolve all of them. For example, in the upper d^2 matrix, the two regions from the Gallo-Roman Period (Normandy, Midi-Pyrénées) are not significantly different from each other, but the two regions from the Carolingian Period (Paris Basin and Midi-Pyrénées) are significantly different from each other, which contrasts with previous demographic scenarios (Tables 29, 33, and 37). The Merovingian Period still bears significant differences among many of the regions, primarily for the Paris Basin Region, with the Normandy Region approaching significance when $\alpha = 0.10$. However, geographic distances are not sufficient to explain these biological differences (Figure 49). Indeed, tests for isolation-

by-distance show no correlation between geographic and biological matrices ($R^2 = -0.143$, $p = 0.817$). In the lower d^2 matrix, none of the regions having diachronic representation are significantly different from themselves over time. In other words, each region appears to exhibit some kind of biological continuity.

Despite the suggested intra-regional temporal homogeneity (Table 41), measures of inter-regional heterogeneity increase over time (Table 42). These results are consistent with 1) a decrease in inter-region gene flow; 2) a significant influx of externally originating gene flow to some regions over others; and/or 3) a decrease in population size for some regions relative to others. While the Merovingian Period is the sole time period in which F_{ST} is significant, the overall change in F_{ST} from the Merovingian to Carolingian Periods is also significant (Table 43), as based on *Z*-tests. Likewise, the overall change in F_{ST} from Gallo-Roman to Carolingian Periods is significant, again suggesting that inter-regional gene flow was decreasing over time. In contrast, average phenotypic variance decreases over time, which suggests that intra-regional variance was decreasing over time.

The Relethford-Blangero residuals are all significant (Table 44 and Figure 50). Overall, the Merovingian Period is characterized by greater than expected extra-local gene flow. The sole exception is the Normandy Region, which consistently has less than expected extra-local gene flow. Regardless, every region from the Merovingian Period appears to close in on the expected level of variance depicted by the regression line. The Midi-Pyrénées Region has consistently greater than expected extra-local gene flow. A region such as the Paris Basin, however, has mixed results, going from significantly greater than expected during the Merovingian Period, to significantly less than expected

during the Carolingian Period. This last result hints at a possible change occurring during the Carolingian Period for the Paris Basin region.

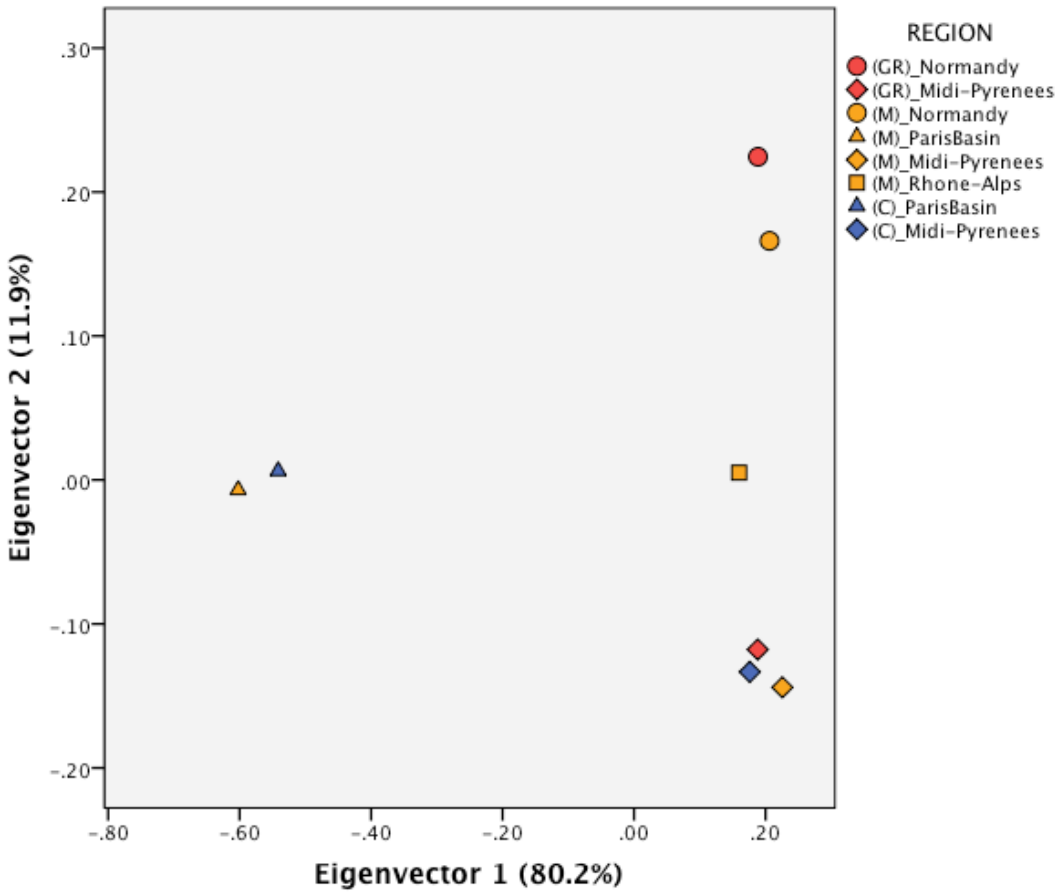

Figure 48. Scatterplot of PCO 1 vs. PCO 2 (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 4).

Table 41

Biological Distance (d^2) Matrix (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 4).

	(GR)_Norm	(GR)_Midi	(M)_Norm	(M)_ParisB	(M)_Midi	(M)_Rhone	(C)_ParisB	(C)_Midi
(GR)_Normandy	-	0.420	-	-	-	-	-	-
(GR)_Midi-Pyrénées	0.000	-	-	-	-	-	-	-
(M)_Normandy	0.000	0.101	-	0.532**	0.099*	0.034	-	-
(M)_ParisBasin	0.099*	0.150**	0.149*	-	0.578**	0.480**	-	-
(M)_Midi-Pyrénées	0.046	0.113	0.122	0.003*	-	0.026	-	-
(M)_Rhône-Alps	0.619	0.747	0.601	0.678**	0.677	-	-	-
(C)_ParisBasin	0.511**	0.585**	0.625**	0.583	0.590*	0.005**	-	1.089**
(C)_Midi-Pyrénées	0.000	0.034	0.074	0.057**	0.034	0.597	0.484**	-

Notes: Lower matrix represents biological distances regardless of time period; upper matrix represents biological distances only for contemporaneous regions. $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 42

Estimates of Inter-Regional Heterogeneity and Average Within-Region Phenotypic Variance (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 4).

Period	F_{ST}	Average Within-Region Phenotypic Variance
Gallo-Roman	0.063	1.519
Merovingian	0.108**	1.074
Carolingian	0.230	0.862

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 43

Z-Test Results (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 4).

Change in F_{ST}	Z
Gallo-Roman to Merovingian (GR-M)	-0.871
Merovingian to Carolingian (M-C)	-2.970**
Gallo-Roman to Carolingian (GR-C)	-2.583**

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 44

Relethford-Blangero Residuals (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 4).

Region and Time Period	Residual
Gallo-Roman:	
Normandy	-0.379**
Midi-Pyrénées	0.660**
Merovingian:	
Normandy	-0.313**
ParisBasin	0.104**
Midi-Pyrénées	0.200**
Rhône-Alps	0.266**
Carolingian:	
ParisBasin	-0.391**
Midi-Pyrénées	0.333**

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

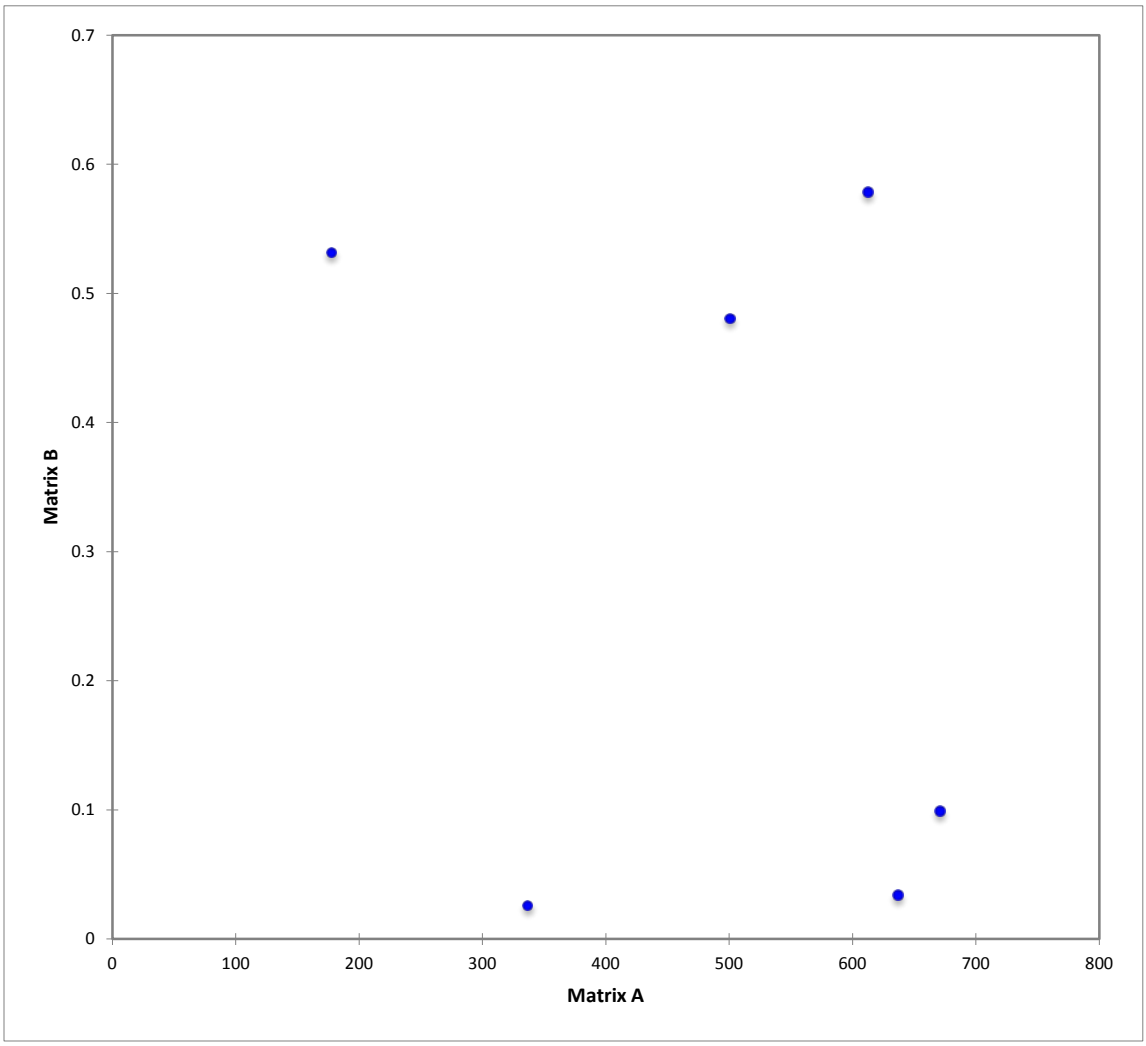

Figure 49. Scatterplot of the Mantel Test (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 4).

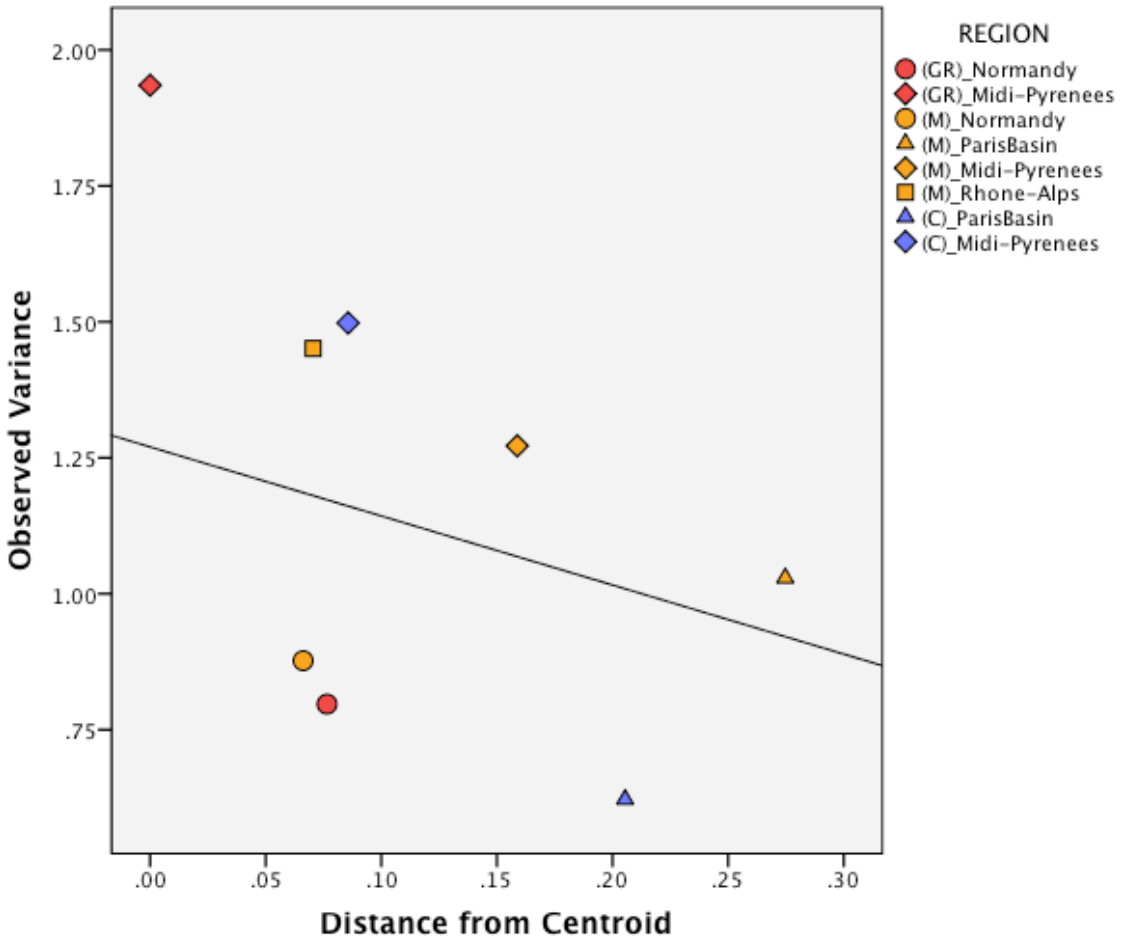

Figure 50. Scatterplot of Relethford-Blangero Residuals (Odontometric Analysis: Diachronic, Regional-Level, Demographic Scenario 4).

10.2.0 SUMMARY

Much like the synchronic analyses, the first two eigenvectors of the diachronic analyses also include most of the variation inherent in the R-matrix. Moreover, the two temporal components of the Paris Basin Region are again distinct from all others along eigenvector 1. In other words, the consistent pattern of dissimilarity for the Paris Basin Region is repeated diachronically as well. Unlike the synchronic analyses, though, eigenvector 2 only exhibits a latitudinal gradient under demographic scenarios that consider relative population sizes.

Most striking, however, is an apparent diachronic shift in spatial patterning for the most conservative demographic scenarios. From the Gallo-Roman to Merovingian Periods, regions become more distinct from each other, as reflected by a greater dispersal of points on the scatterplots. This pattern reverses from the Merovingian to Carolingian Periods, when regions become more similar to each other, as reflected by more closely clustered points on the scatterplots. However, this possible diachronic shift disappears when using less conservative estimates of demographic parameters. Specifically, when relative population sizes are included, the diachronic shift disappears entirely and regions exhibit continuity over time with little obvious structure.

The Mahalanobis d^2 matrices also reveal some clear trends. Because subpopulations from different time periods could not interbreed, each matrix was visually and analytically divided into halves. The lower halves represented tests on the significance of biological distances between all regions regardless of time period and are best used to assess how a region compares to itself over time. The upper halves reflected tests on the significance of biological distances between regions from contemporary time

periods. When considering the lower halves of the matrices, it is apparent that regions exhibit a certain degree of homogeneity over time. In other words, for all regions represented diachronically, there is evidence for biological continuity.

The upper halves of the d^2 matrices reveal that there are no significant biological distances for regions from the Gallo-Roman or Carolingian Periods. In other words, subpopulations from these two time periods are indistinct from each other, although the smaller number of regions being compared likely impact these results. In contrast, regions from the Merovingian Period do exhibit some significant biological differences. Specifically, the Paris Basin Region during the Merovingian Period is significantly different from all other regions from the same time period. The distinction noted for the Paris Basin Region, however, cannot be attributed to differences in geographic distances. All Mantel Tests for isolation-by-distance were insignificant, which would suggest that any of the patterns previously noted are not due to geographic distances between regions.

Estimates for inter-regional heterogeneity (F_{ST}) and average intra-regional phenotypic variation were generated for each time period. The Merovingian Period was the sole time period to exhibit estimates of F_{ST} that were significantly different from zero. However, assessing the actual changes in F_{ST} over time produced some interesting results. Under every demographic scenario, F_{ST} increases from the Gallo-Roman to Carolingian Periods, in some cases up to a three- or four-fold increase. However, only under demographic scenarios 2 and 4 (i.e., when $h^2 = 0.55$) were the actual changes in F_{ST} from the Merovingian to Carolingian Periods and from the Gallo-Roman to Carolingian Periods statistically significant based on *Z*-tests. Changes in F_{ST} from the

Gallo-Roman to Merovingian Periods were never significant, suggesting that the greatest effect on inter-regional heterogeneity occurred during the Carolingian Period.

Finally, at the same time that inter-regional heterogeneity was increasing over time, average intra-regional phenotypic variation was decreasing over time. These results would imply regions were becoming more homogeneous within themselves. In other words, regions became more distinct from each other over time, while communities *within each region* became more similar to each other over time. There are a number of micro-evolutionary factors that could contribute to these results. A decrease in inter-regional gene flow, whether due to social or ecological factors, would prevent the sharing of alleles between regions. Likewise, a decrease in effective population sizes, perhaps through demographic collapse, could also serve to increase stochastic effects like genetic drift. Another possibility stems from the introduction of novel alleles to some regions, but not all.

This latter prospect can be assessed using Relethford-Blangero residuals. The Normandy Region almost always exhibits significantly less than expected extra-local gene flow, regardless of time period. In contrast, the Midi-Pyrénées Region almost always has significantly greater than expected extra-local gene flow, regardless of time period. The Paris Basin Region, for which much distinction is noted on scatterplots and the upper halves of the d^2 matrices, presents mixed results over time. Often bearing significantly positive residuals during the Merovingian Period, patterns of extra-local gene flow reverse during the Carolingian Period when the Paris Basin Region always exhibits significantly negative residuals.

CHAPTER 11

RESULTS: CRANIOMETRIC SYNCHRONIC ANALYSIS

11.0.0 INTRODUCTION

This chapter presents the results for synchronic biodistance analyses performed on the craniometric dataset. Relevant pre-analytical data treatments were performed (see Chapter 8), resulting in 16 craniometric variables (see Table 6) for three regions comprised of 20 sites (Table 45). Given the large number of sites grouped into regions, no attempt was made to assess these data at a site level. The goal of this portion of the analysis was 1) to establish overall "snapshots" of the relationships between regions, much like in the odontometric analysis; and 2) to elucidate any additional trends by comparing these results with those obtained by the regional-level odontometric analysis. Unfortunately, contemporaneous craniometric data for the Midi-Pyrénées Region were not available. Consequently, these results reflect three of the four geographic regions (Normandy, Paris Basin, and Rhône-Alps). All time periods (Gallo-Roman, Merovingian, and Carolingian) are represented.

Results are presented using four demographic scenarios based on different permutations of population sizes (equal or relative) and of narrow-sense heritability estimates ($h^2 = 1.0$ or $h^2 = 0.55$). Each report includes details on the following: 1) the percentage of variation accounted for by the relationship matrix; 2) the spatial relationship among the regions depicted by a scatterplot of principal coordinates; 3) the results of the Mahalanobis d^2 matrix; 4) the results of the Mantel Test; 5) the estimate of

between-unit variance (i.e., the estimate of genetic diversity; F_{ST}); and 6) the Relethford-Blangero residuals (i.e., estimate of gene flow).

Table 45

Craniometric Sample Sizes: Regions

Region	Relative Population Size	Sample Size (n)	Sites in Region (n)
Normandy	1	1106	13
Paris Basin	1	59	4
Rhône-Alps	0.5	61	3
Midi-Pyrénées	-	0	0
Total		1226	20

11.1.0 Regional-Level

11.1.1 Demographic Scenario 1

Under this scenario, population sizes were considered equal, and narrow-sense heritability (h^2) was set to 1.0. As shown in the scatterplot of the principal coordinates (Figure 51), all of the variation in the data is accounted by the first two eigenvectors. The three regions (Normandy, Paris Basin, Rhône-Alps) appear to be roughly equidistant from each other and to have very little structure. An overall geographic pattern also does not appear to be evident, although the Rhône-Alps and the Normandy Regions are closer to each other along eigenvector 1, than to the Paris Basin Region.

It is not clear why the Normandy and Rhône-Alps Regions would be more similar to each other in this scenario. Indeed, the Mahalanobis d^2 matrix (Table 46) yields no significant difference between any of the regions, which may suggest that the distinctions noted in Figure 51 are trivial. Furthermore, the Mantel Test for isolation-by-distance suggests that there is no correlation between geographic and biological distances ($R^2 = -0.500$, $p = 0.667$; Figure 52). Thus, it is not surprising that inter-regional heterogeneity ($F_{ST} = 0.006$) is also not significantly different from zero. Such a low value implies that gene flow between regions was high.

However, the Relethford-Blangero residuals (Table 47 and Figure 53) show that the Paris Basin Region has significantly less than expected extra-local gene flow, while the Rhône-Alps Region exhibits significantly greater than expected extra-local gene flow. Although the results for the Rhône-Alps Region are consistent with those from the Odontometric Analysis (for example, see Table 27), here the Normandy Region demonstrates a positive residual (albeit not significant), rather than a significantly

negative one (Table 47). It is possible, then, that the Normandy Region did receive some measure of extra-local gene flow, but not more than might be expected on average. Regardless, the Normandy and Rhône-Alps Regions did not appear to be recipients of gene flow from the same external source given the lack of genetic structure evident in the scatterplot.

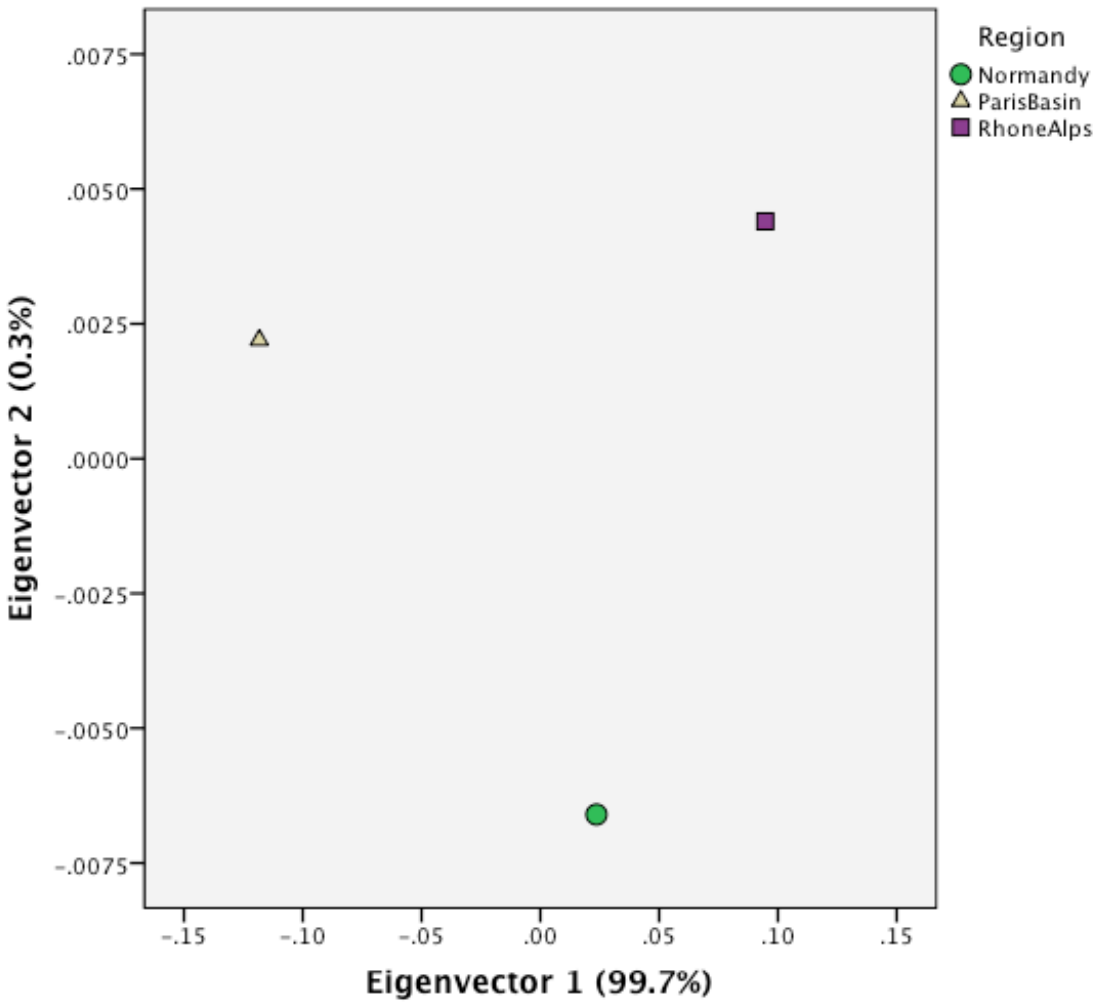

Figure 51. Scatterplot of PCO 1 vs. PCO 2 (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 1).

Table 46

Biological Distance (d^2) Matrix (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 1).

	Normandy	ParisBasin	Rhône-Alps
Normandy	-		
ParisBasin	0.020	-	
Rhône-Alps	0.005	0.045	-

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

Table 47

Relethford-Blangero Residuals (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 1).

Region	Residual
Normandy	0.028
ParisBasin	-0.083**
Rhône-Alps	0.056**

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

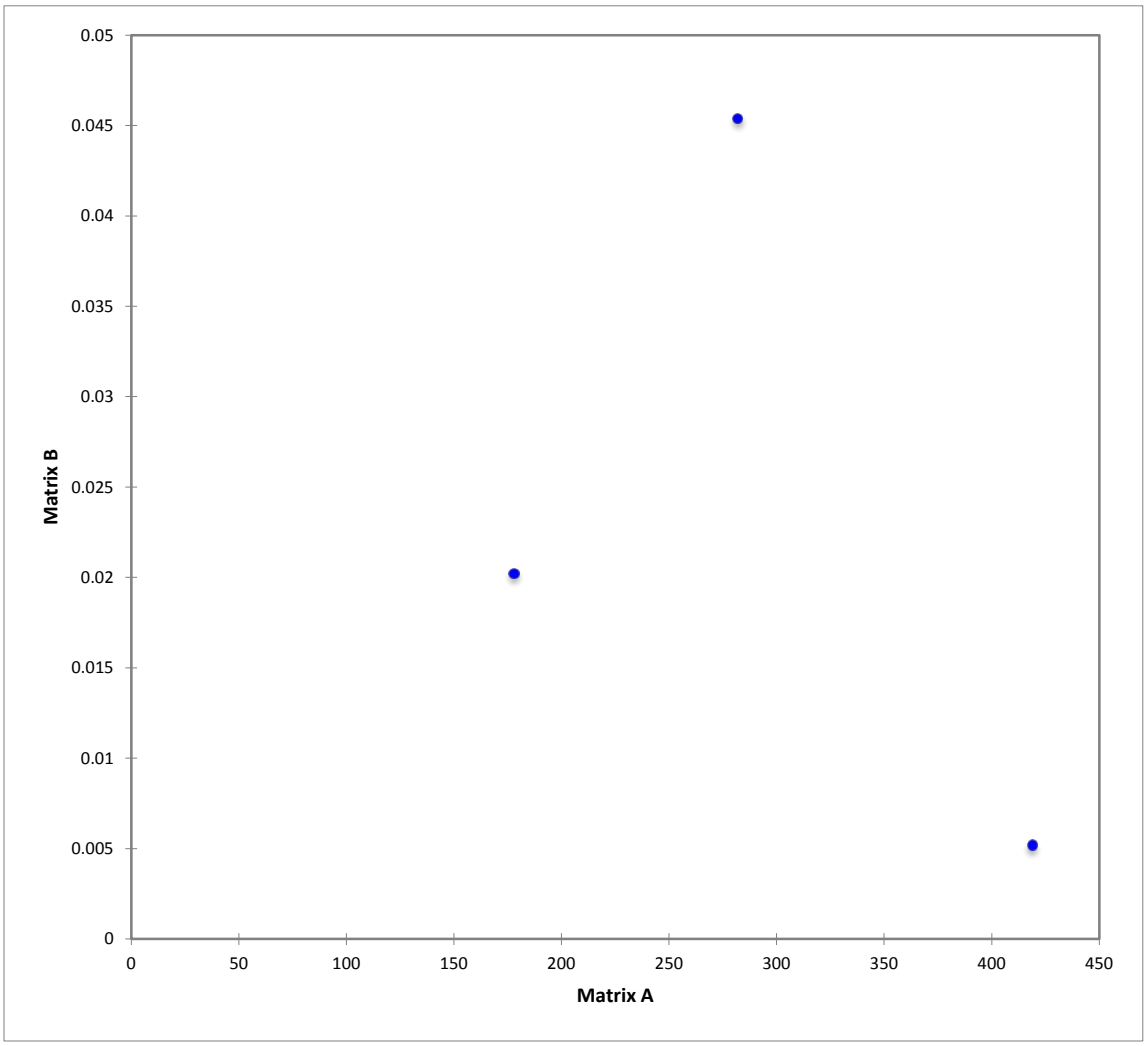

Figure 52. Scatterplot of the Mantel Test (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 1).

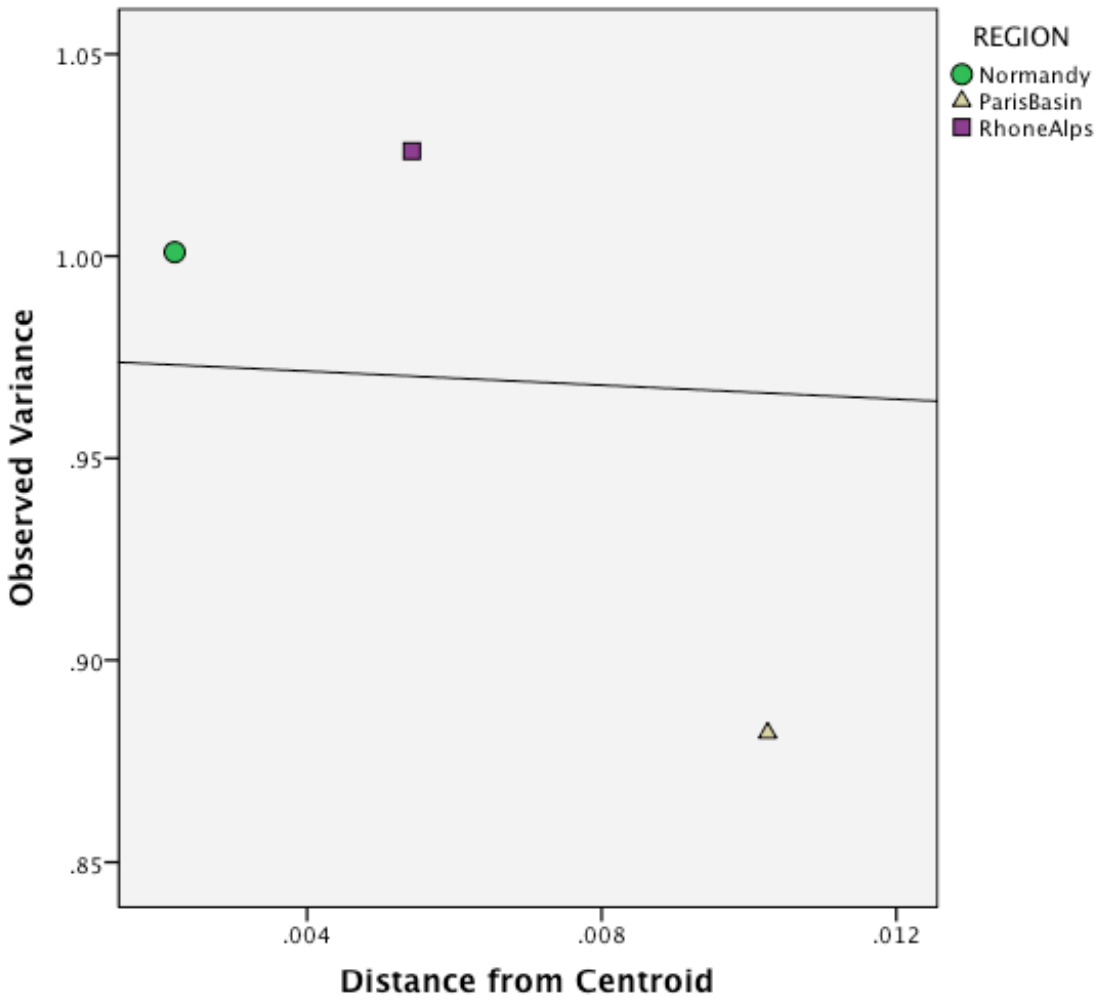

Figure 53. Scatterplot of Relethford-Blangero Residuals (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 1).

11.1.2 Demographic Scenario 2

Upon changing the narrow-sense heritability estimate from 1.0 to 0.55, the overall patterns noted previously do not change (Figure 54). The three regions are still roughly equidistant from each other when examined as a whole, and 100% of the variation can be explained by the first two eigenvectors. However, if assessing each eigenvector by itself, there are subtle differences. For example, the Paris Basin Region is more distinct from the Normandy and Rhône-Alps Regions along the first axis, while the Normandy region is more distinct from the Paris Basin and Rhône-Alps Regions along the second axis.

Much like in the previous scenario (Table 46), the Mahalanobis d^2 matrix (Table 48) does not show any significant differences between the regions, despite a possible distinction in the scatterplot of principal coordinates (see Figure 54). These results are quite different than those from the synonymous Odontometric Analysis (Chapter 9), wherein the biological distances between the Paris Basin Region and both the Normandy and Rhône-Alps Regions were significantly different (see Table 22). Thus, it is not surprising that there is no significant correlation between geographic and biological distances ($R^2 = -0.500$, $p = 0.667$; Figure 55). Even regional heterogeneity (F_{ST}=0.015) is fairly low and insignificant. This result implies that gene flow may have been high, which might explain the lack of significant biological differences between regions.

A consideration of the Relethford-Blangero residuals (Table 49 and Figure 56) confirms the general lack of significant differences from the expected levels of extra-local gene flow. Only the Paris Basin Region exhibits a significantly less than expected extra-local gene flow. This result is in contrast to the Relethford-Blangero residuals from

the Odontometric Analysis where the Paris Basin Region has a significantly positive residual (see Table 23 and Figure 32).

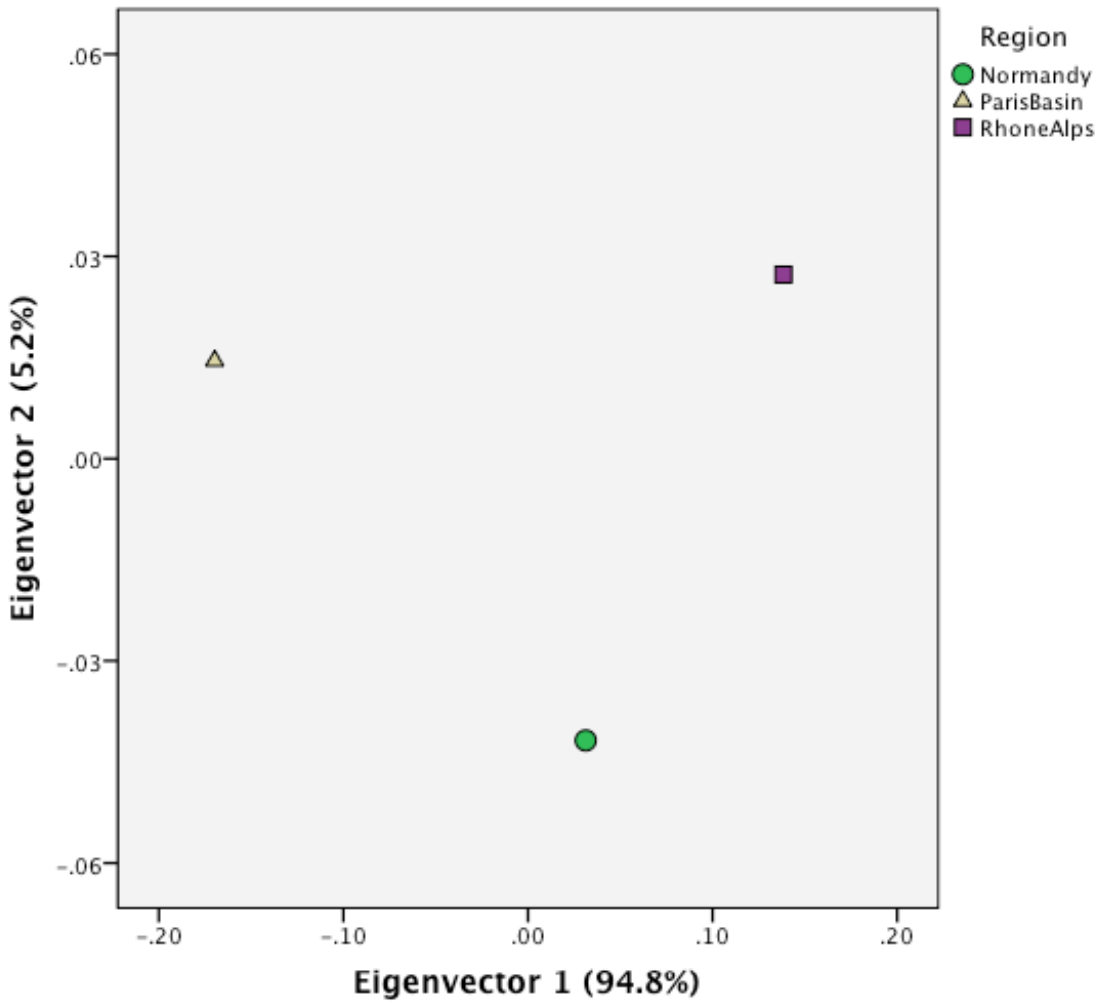

Figure 54. Scatterplot of PCO 1 vs. PCO 2 (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 2).

Table 48

Biological Distance (d^2) Matrix (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 2).

	Normandy	ParisBasin	Rhône-Alps
Normandy	-		
ParisBasin	0.044	-	
Rhône-Alps	0.016	0.095	-

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

Table 49

Relethford-Blangero Residuals (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 2).

Region	Residual
Normandy	0.020
ParisBasin	-0.078**
Rhône-Alps	0.057*

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

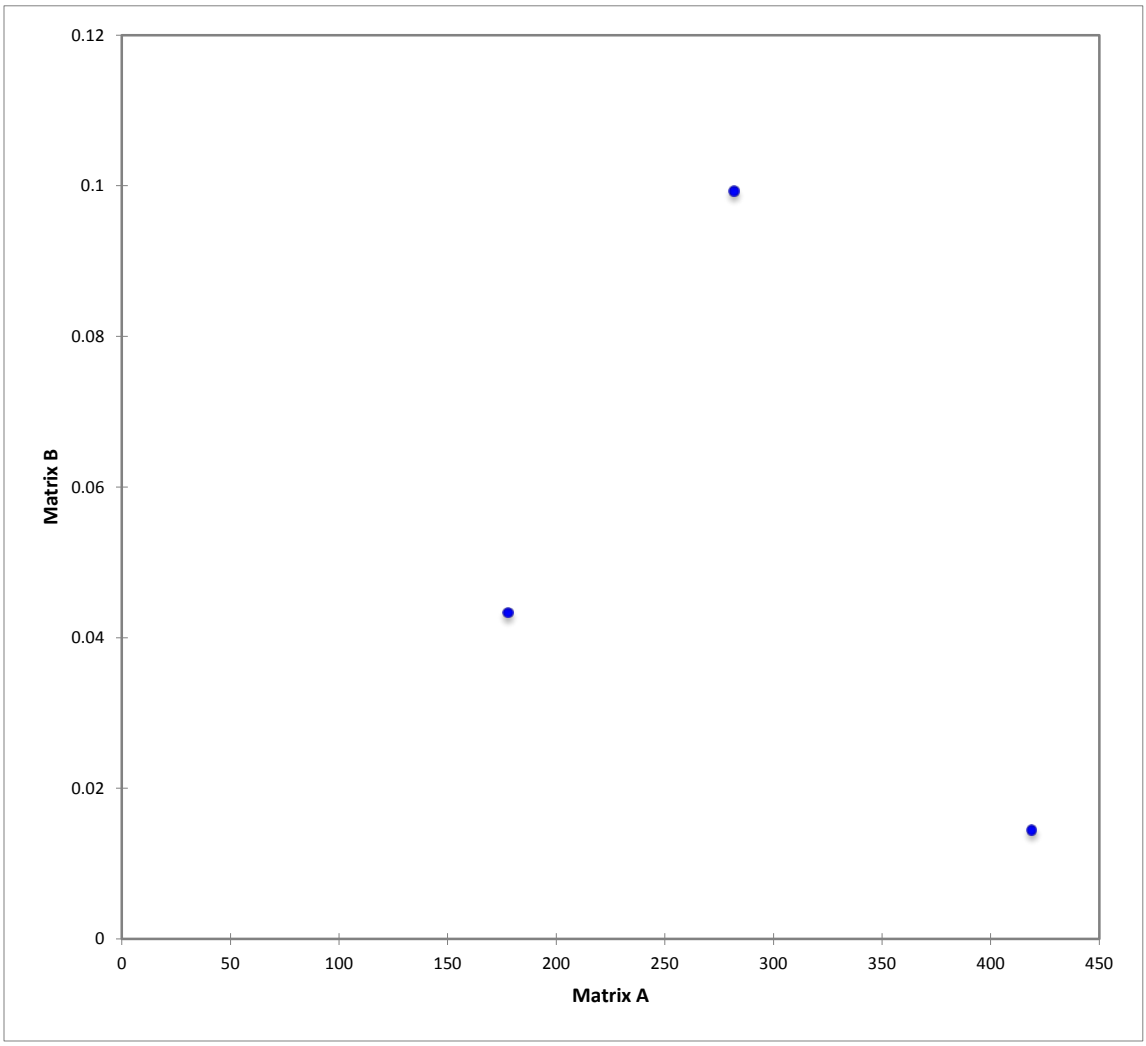

Figure 55. Scatterplot of the Mantel Test (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 2).

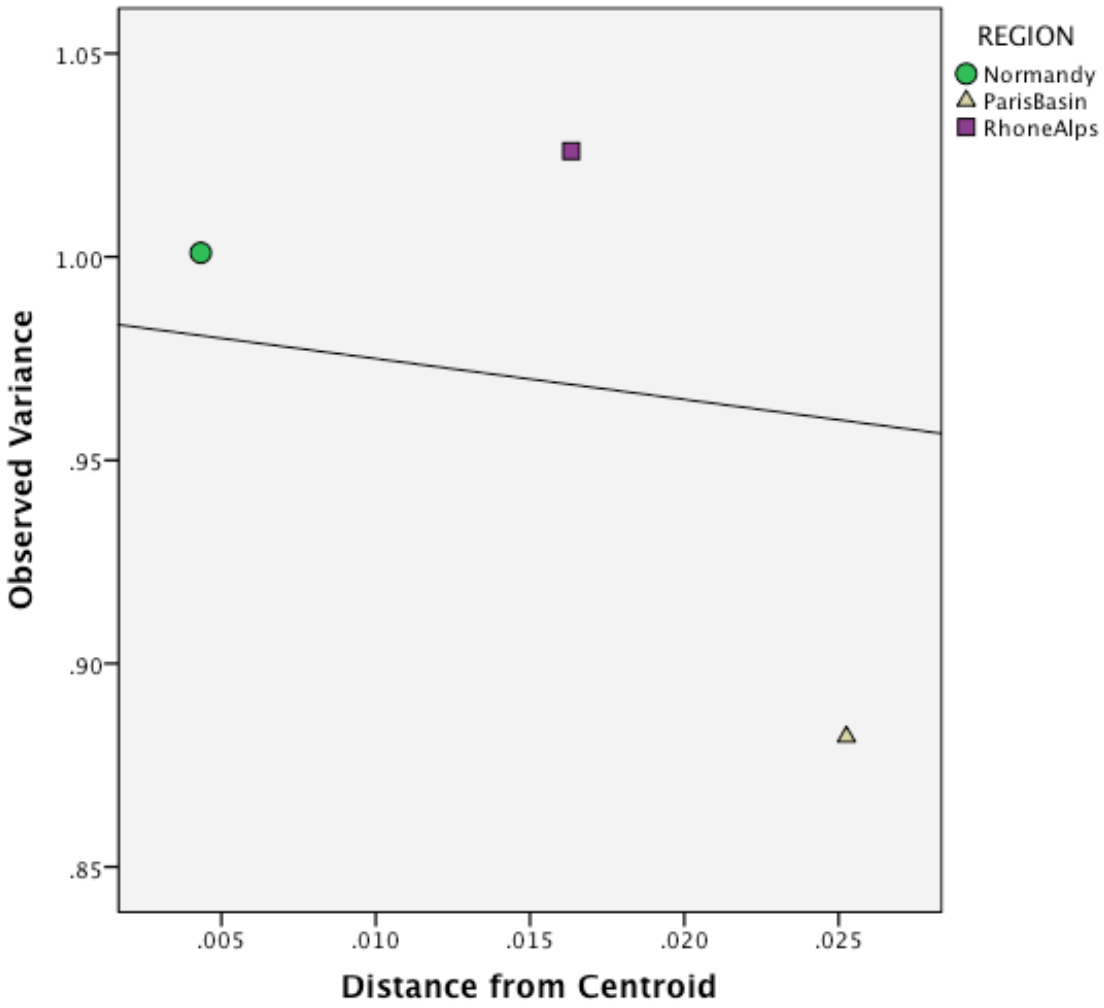

Figure 56. Scatterplot of Relethford-Blangero Residuals (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 2).

11.1.3 Demographic Scenario 3

The inclusion of relative population sizes does not change the overall patterns exhibited in the scatterplot of principal coordinates (Figure 57). However, the Rhône-Alps Region does shift further away along eigenvector 2 from the Paris Basin Region than in the previous analyses (Figures 51 and 54).

However, the biological distances do not reflect any of these spatial differences (Table 50). In fact, no region exhibited a significant biological distance from another, perhaps indicating an overall level of homogeneity. Furthermore, the Mantel Tests results were not significant ($R^2 = -0.500, p = 0.667$), suggesting that geographic distance was not a structuring agent in the biological distances that were obtained (Figure 58).

The measure of regional heterogeneity (F_{ST}) is only 0.005 and is not significant, lending further support to an interpretation of widespread gene flow and homogeneity. On the other hand, the Relethford-Blangero residuals show mixed results (Table 51 and Figure 59). The Paris Basin Region again shows significantly less than expected extra-local gene flow. But, unlike the previous scenario (see Table 49 and Figure 56), the Rhône-Alps Region exhibits significantly greater than expected extra-local gene flow. Interestingly, the Normandy Region does not deviate from the expected level of variance, which contrasts with the significantly negative residuals obtained in similar analyses for the odontometric data (Chapter 9).

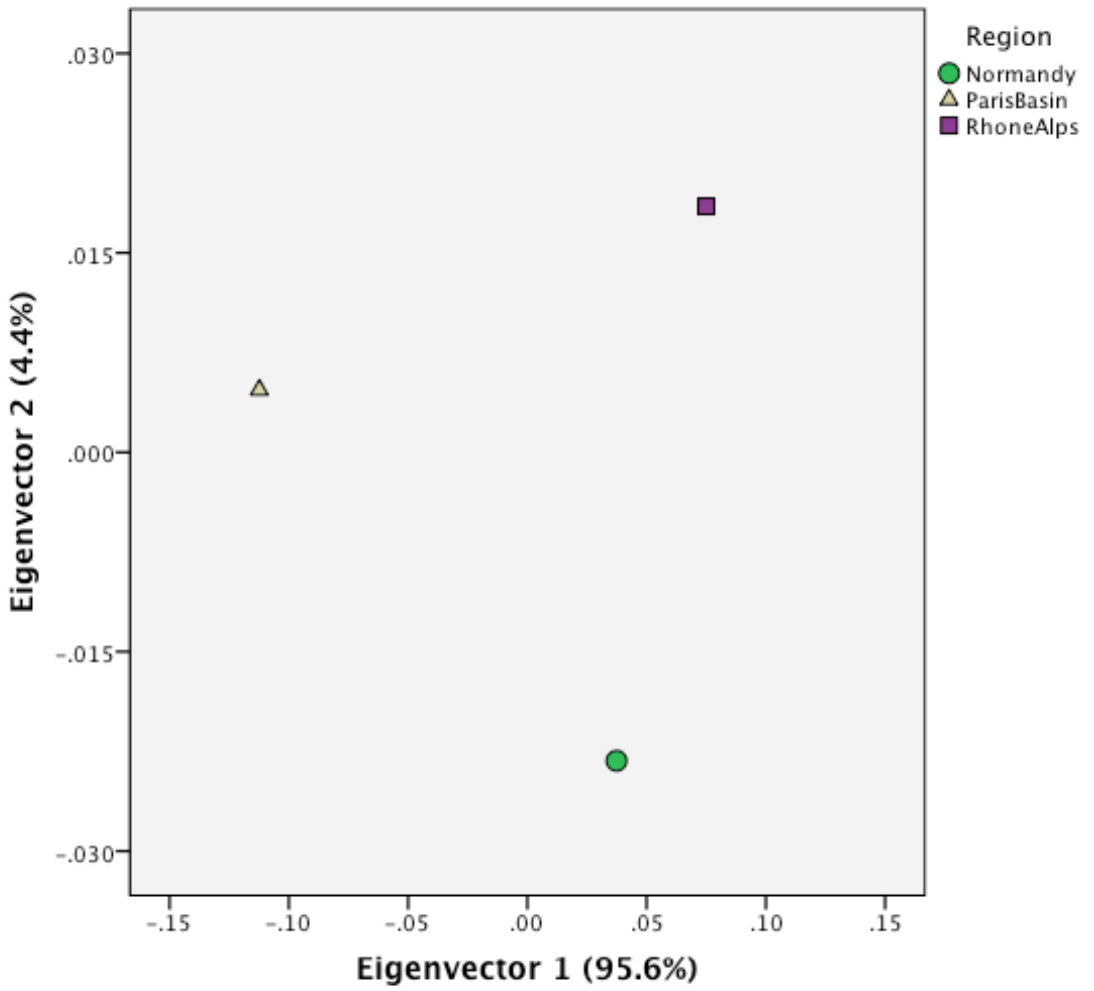

Figure 57. Scatterplot of PCO 1 vs. PCO 2 (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 3).

Table 50

Biological Distance (d^2) Matrix (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 3).

	Normandy	ParisBasin	Rhône-Alps
Normandy	-		
ParisBasin	0.023	-	
Rhône-Alps	0.003	0.035	-

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

Table 51

Relethford-Blangero Residuals (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 3).

Region	Residual
Normandy	0.041
ParisBasin	-0.077**
Rhône-Alps	0.073**

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

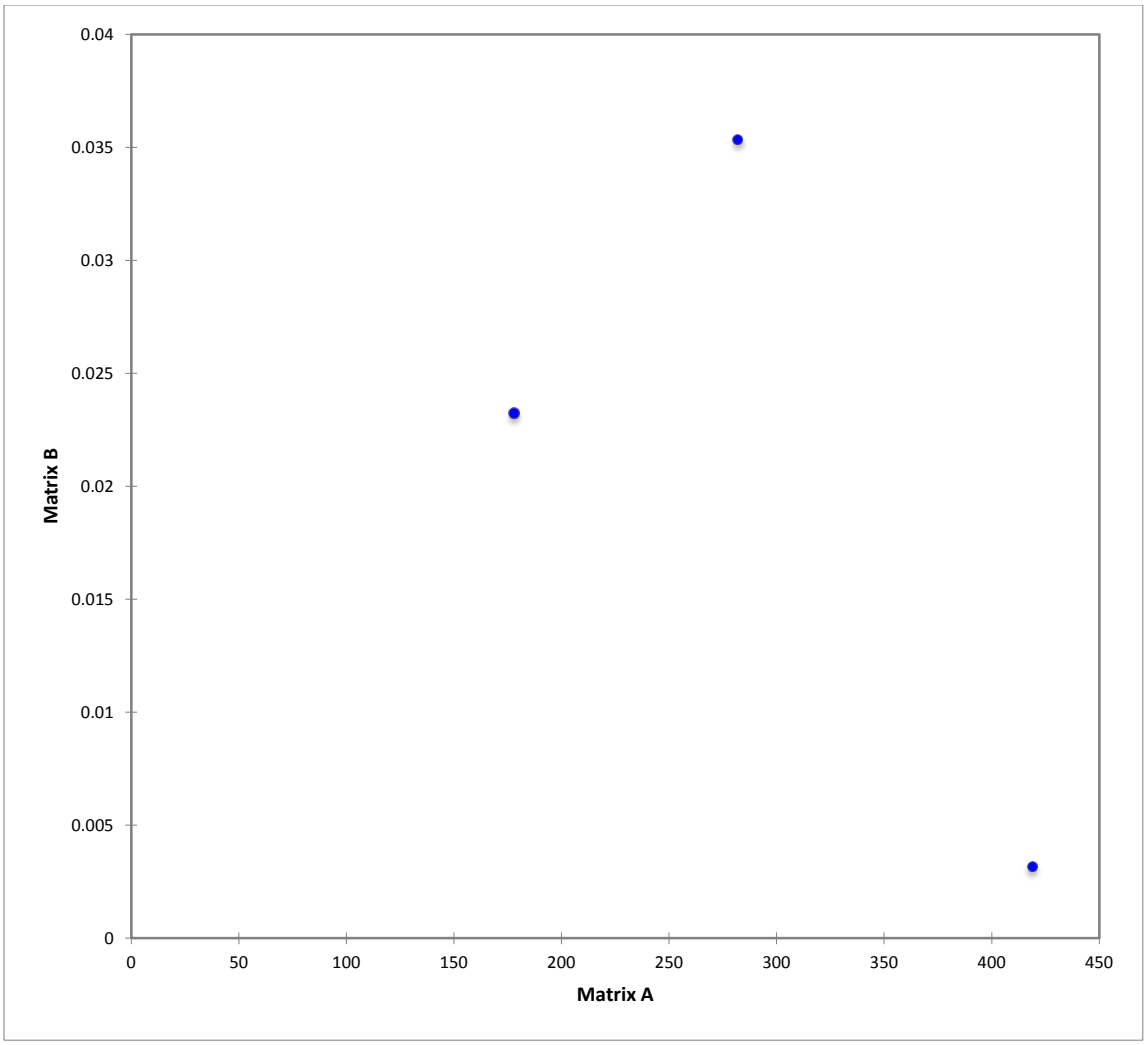

Figure 58. Scatterplot of the Mantel Test (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 3).

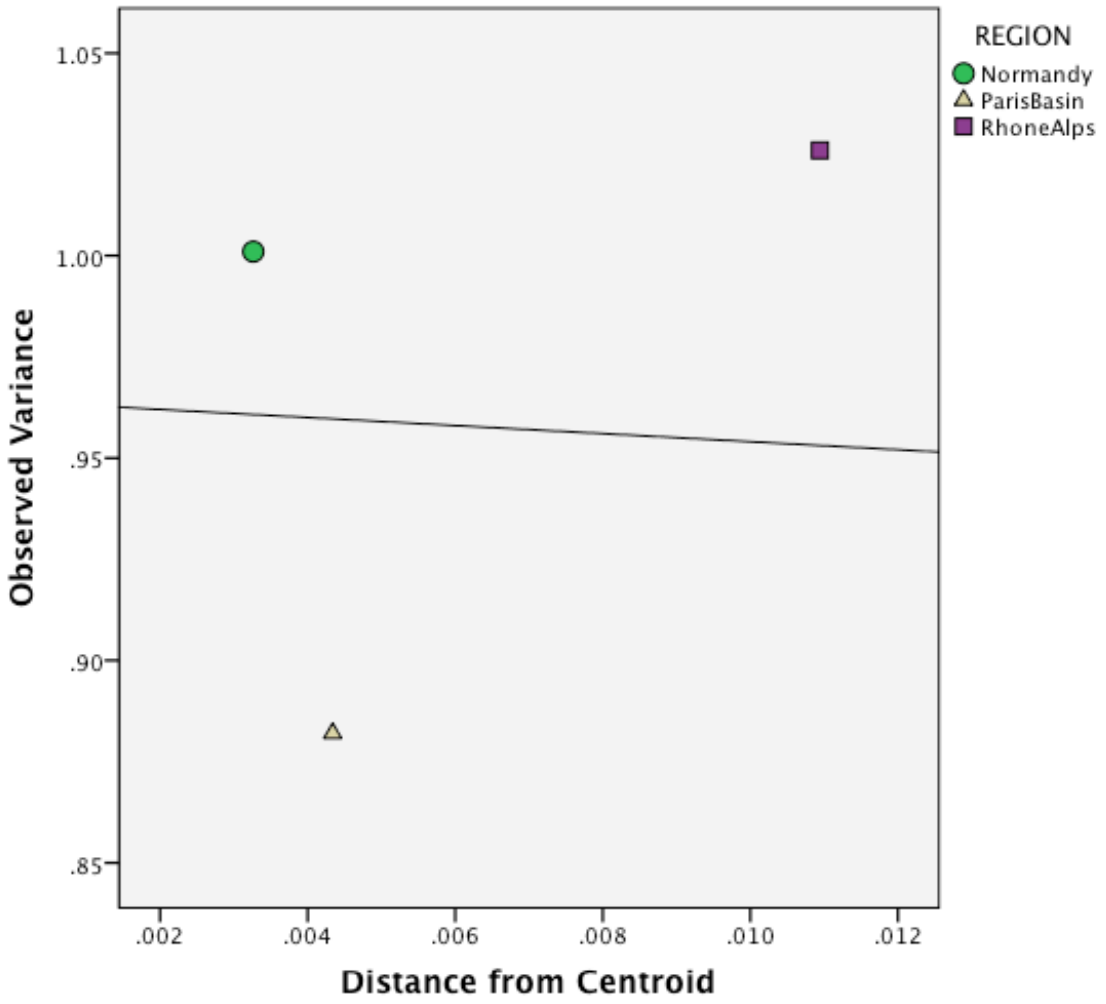

Figure 59. Scatterplot of Relethford-Blangero Residuals (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 3).

11.1.4 Demographic Scenario 4

The first two eigenvectors explain all of the variation from the R-matrix and should reflect spatially any of the underlying biological relationships among the regions. However, the final demographic scenario mirrors the previous ones. In other words, the three regions appear to be roughly equidistant from each other, showing little structure, save along individual axes (Figure 60).

Indeed, even the Mahalanobis d^2 matrix shows a consistent lack of significant biological distances (Table 52). These results would seem to confirm that any structure noted in Figure 60 is inconsequential from the perspective of biological differences. Likewise, the Mantel Test result does not support an interpretation of correlation between geographic and biological distances ($R^2 = -0.500$, $p = 0.667$; Figure 61).

These results seem to be mirrored by the very low and insignificant estimate of regional heterogeneity ($F_{ST} = 0.014$), which would suggest a large amount of gene flow amongst these regions. However, the Relethford-Blangero residuals (Table 53 and Figure 62) reveal that the Paris Basin Region exhibits significantly less than expected extra-local gene flow, so not all of these regions shared a similar population structure. Regardless, these results overall suggest a significant amount of regional homogeneity and an implied high degree of inter-regional gene flow.

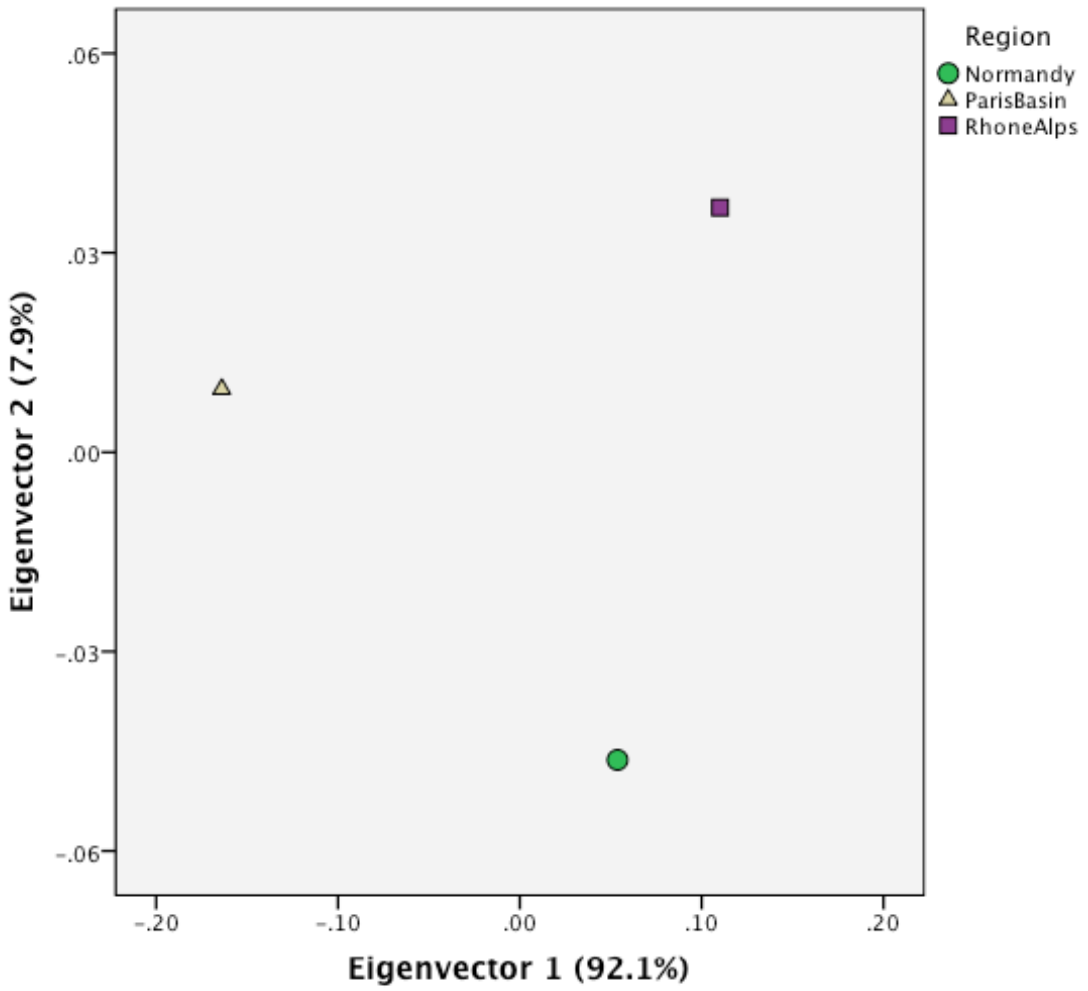

Figure 60. Scatterplot of PCO 1 vs. PCO 2 (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 4).

Table 52

Biological Distance (d^2) Matrix (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 4).

	Normandy	ParisBasin	Rhône-Alps
Normandy	-		
ParisBasin	0.050	-	
Rhône-Alps	0.010	0.076	-

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

Table 53

Relethford-Blangero Residuals (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 4).

Region	Residual
Normandy	0.035
ParisBasin	-0.075**
Rhône-Alps	0.080*

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

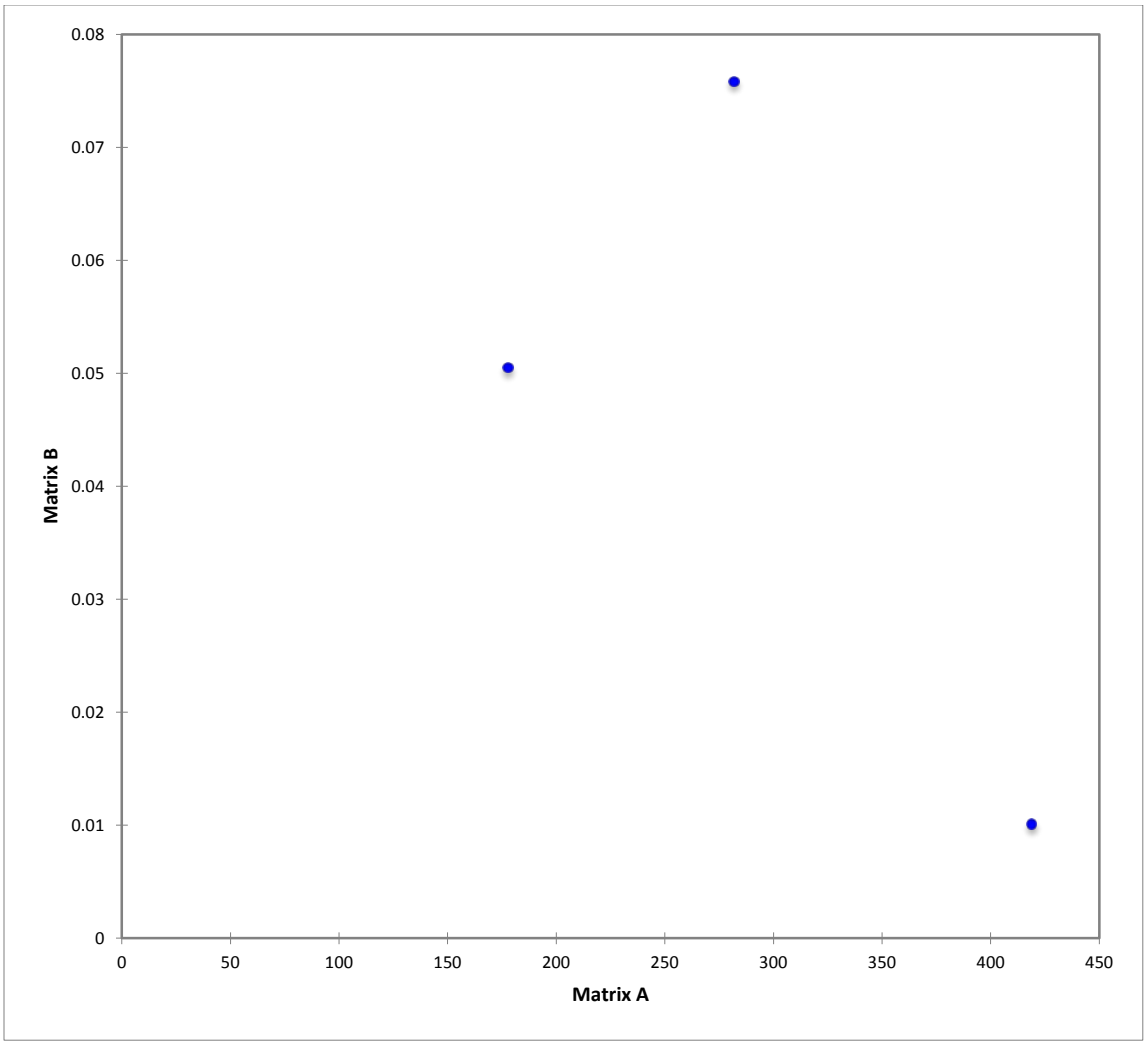

Figure 61. Scatterplot of the Mantel Test (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 4).

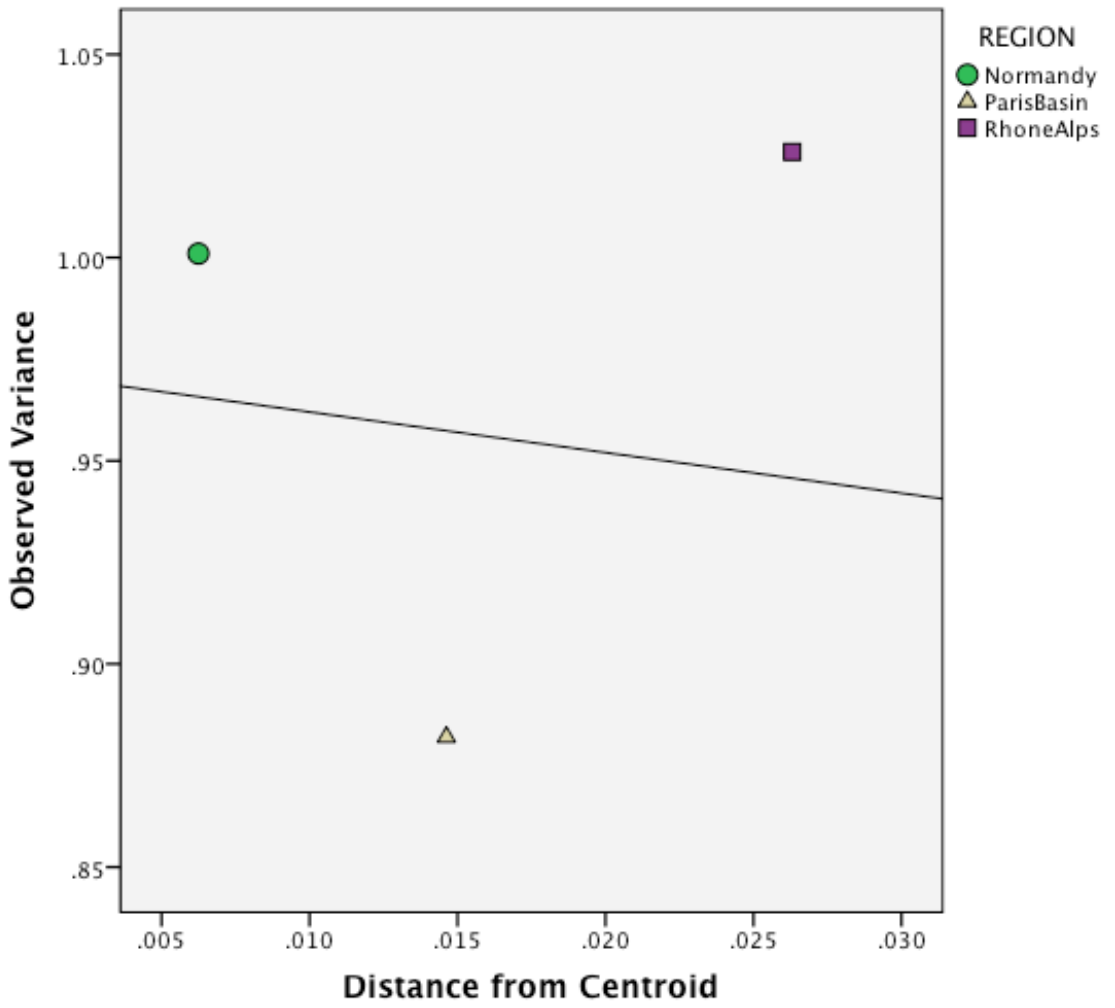

Figure 62. Scatterplot of Relethford-Blangero Residuals (Craniometric Analysis: Synchronic, Regional-Level, Demographic Scenario 4).

11.2.0 SUMMARY

There are few clear patterns for this portion of the analysis. Although a large percentage of the variation present in the relationship matrix is explained by the first two eigenvectors, there is little structure evident in the scatterplots. Perhaps the only observation consistently visible for these results is the slight distinction of the Paris Basin Region relative to the other regions. This possible trend is also consistent with results from the regional-level biodistance analysis of the odontometric data.

However, an assessment of the strength of the biological distances between the Paris Basin Region and the other regions yields a lack of significant differences. In fact, all biological distances represented by Mahalanobis d^2 matrices were not significant. These results contradict those of the odontometric biodistance analysis, which showed that the Paris Basin Region was both consistently and significantly different from all other regions. Likewise, these results give no indication that the Normandy Region is significantly different from other regions with changing demographic scenarios. This latter trend was itself noted for the regional-level analysis of the odontometric data.

Although there are fewer spatial patterns on the scatterplots for the principal coordinates, it is possible that a latitudinal gradient might be observed along the second eigenvector. This observation would be consistent with the regional-level analyses of the odontometric data. However, the gradient is not as obvious, and the Mantel Test results were all insignificant. Thus, geographic and biological distances are not correlated, both for regional-level craniometric data and the regional-level odontometric data.

Perhaps the most striking disparity between the regional-level analyses for the craniometric and odontometric data is the difference in estimates of inter-regional

heterogeneity (F_{ST}). For the former, all results were not significantly different from zero. For the latter, all results were significantly different from zero. The lack of significance for the craniometric data could be a simple product of statistical sampling, or it could reflect an underlying difference in the nature of craniometric and odontometric data.

Despite the lack of significant inter-regional heterogeneity, there is evidence in the craniometric data for extra-local gene flow into certain regions based on Relethford-Blangero residuals. More specifically, the Rhône-Alps Region often has significantly positive residuals, which paralleled results from the regional-level odontometric analysis. In contrast, the Paris Basin Region exhibits significantly negative extra-local gene flow, a result not consistently found in the regional-level odontometric analysis. Similarly, the Normandy Region, which typically exhibited significantly negative residuals in the odontometric analysis, did not possess any significant residuals in the craniometric analysis.

How can these differences between the odontometric and craniometric data be explained? As previously stated, issues of statistical sampling are a possible explanation. For example, no contemporaneous craniometric data were available for the Midi-Pyrénées, and thus they could not be included in the regional-level biodistance analysis. This absence could easily account for a lack of significance in inter-regional heterogeneity since the wider the area that is sampled, the greater the biological variation. Another possibility is that there are some inherent differences between craniometric and odontometric data. For example, researchers have pointed to the greater effects of environmental variance on craniometric variables than on odontometric variables (for

more discussion on this topic, see Chapter 13). Odontometric variables may be more sensitive to intra-population differences than craniometric data.

CHAPTER 12

RESULTS: CRANIOMETRIC DIACHRONIC ANALYSIS

12.0.0 INTRODUCTION

This chapter introduces the results for diachronic biodistance analyses performed on the craniometric dataset. These results stem from 16 craniometric variables collected from 20 sites (see Table 54). Sites were grouped into one of three geographic regions and subdivided according to associated time period. The goal of this portion of the analysis was to assess 1) how each region changes over time; 2) how contemporaneous regions relate to each other; and 3) to elucidate any additional trends by comparing these results with those obtained by the diachronic regional-level odontometric analysis.

Unfortunately, contemporaneous craniometric data for the Midi-Pyrénées Region were not available. Consequently, these results reflect only three of the four geographic regions (Normandy, Paris Basin, and Rhône-Alps). However, all time periods (Gallo-Roman, Merovingian, and Carolingian) are represented. Furthermore, an additional time period (Frankish) is incorporated. The Frankish Period encompasses both the Merovingian and Carolingian Periods, and several sites could not or were not dated more specifically than this. Thus, the first of the diachronic analyses takes into account those regional samples with a generic "Frankish" dating, resulting in four time periods being assessed: 1) Gallo-Roman, 2) Merovingian, 3) Carolingian, and 4) "Frankish". The second of the diachronic analyses combines all Merovingian, Carolingian, and Frankish regional samples together under a generic heading of Frankish for the ultimate goal to

assess any global changes from Gallo-Roman through Early Medieval times, especially since the distinction between late Merovingian and early Carolingian may not be always clear. Consequently, there are two time periods being assessed: 1) Gallo-Roman, and 2) Frankish.

Results are presented using four demographic scenarios based on different permutations of population sizes (equal or relative) and of narrow-sense heritability estimates ($h^2 = 1.0$ or $h^2 = 0.55$). Each report includes details on the following: 1) the percentage of variation accounted for by the relationship matrix; 2) the spatial relationship among the regions depicted by a scatterplot of principal coordinates; 3) the results of the Mahalanobis d^2 matrix; 4) the results of the Mantel Test; 5) the estimate of between-unit variance (i.e., the estimate of genetic diversity; F_{ST}); 6) the average within-region phenotypic variance; and 7) the Relethford-Blangero residuals (i.e., estimate of gene flow).

Table 54

Craniometric Sample Sizes: Regions and Time Periods

Region and Time Period	Relative Population Size	Sample Size (n)
Gallo-Roman:		
Normandy	0.5	94
Rhône-Alps	0.5	26
Merovingian:		
Normandy	0.75	809
Paris Basin	0.75	59
Rhône-Alps	0.60	31
Carolingian:		
Normandy	1	169
“Frankish”:		
Normandy	1	34
Rhône-Alps	0.85	3
Total		1225

12.1.0 REGIONAL-LEVEL 1 (GALLO-ROMAN, MEROVINGIAN, CAROLINGIAN, FRANKISH)

12.1.1 Demographic Scenario 1

Under this scenario, over 96% of the variance is explained by the first two eigenvectors, with the majority (87.7%) explained by eigenvector one. Interestingly, the Normandy Region is the sole region with representation in each time period, and the scatterplot of the principal coordinates shows a clear shift over time for this region (Figure 63). Yet, a consideration of the broadly dated "Frankish" regional sample from Normandy reveals a significant deviation from this trend, since it plots heavily positive along the first axis.

The Rhône-Alps Region also exhibits a similar pattern to that of the Normandy Region. In other words, there seems to be a temporal trend from the Gallo-Roman to at least the Merovingian Period. In fact, the Merovingian Rhône-Alps Region is tightly clustered with the Carolingian Normandy Region. Even the more broadly dated "Frankish" regional sample from the Rhône-Alps remains roughly consistent with this temporal trend. Unfortunately, the Paris Basin Region is represented only during the Merovingian Period, and nothing of its relationship can be ascertained other than to note that it appears to be more closely grouped to the Gallo-Roman Region than to any other regional time period.

Although a temporal shift may be occurring, this demographic scenario does not reveal a clear trend even via Mahalanobis d^2 distances (Table 55). For example, no region/time period, save the already anomalous "Frankish" Normandy Region, exhibits a significant biological distance (lower d^2 matrix). It is only by changing the alpha value

that any other region/time period shows distinction. Specifically, the Gallo-Roman Normandy Region becomes significantly different from the Carolingian Normandy Region when $\alpha = 0.10$. This result is intriguing and hints at a possible shift during the Carolingian Period.

However, considering only those time periods with multiple regional representations, there are no significant biological distances (upper d^2 matrix). In other words, the Gallo-Roman Rhône-Alps Region is not significantly different from the Gallo-Roman Normandy Region, while the Merovingian Paris Basin Region is not significantly different from the Merovingian Normandy or Rhône-Alps Regions.

Despite the lack of significant biological distances, a Mantel Test for isolation-by-distance is significant ($R^2 = -1.000$, $p < 0.0001$; Figure 64). In other words, there is a strong correlation between biological and geographic distances. However, this association could easily be due to the small sample size (n=3) of Merovingian Period regions that could actually be tested for isolation-by-distance. To illustrate, the Mantel Test applied to the odontometric data was not significant and was tested against a sample of four regions from the Merovingian Period, rather than three.

Tables 56 and 57 show values of inter-regional heterogeneity for each of the time periods having more than one regional representation, as well as for changes in heterogeneity over time. These estimates were not generated for the broadly defined "Frankish" Period regional samples because their chronological dispersion could not be fully determined. Estimates of inter-regional heterogeneity remain somewhat static and insignificant for both the Gallo-Roman and Merovingian Periods (Table 56), the sole periods for which estimates could be generated. Similarly, changes in F_{ST} over time

yielding no significant results based on *Z*-tests (Table 57). These estimates of diachronic inter-regional heterogeneity are remarkably low, despite increasing slightly from the Gallo-Roman to Merovingian Periods. This result perhaps indicates that gene flow between regions remained elevated during both the Gallo-Roman and Merovingian Periods. Average within-region phenotypic variation, by contrast, increases from the Gallo-Roman and Merovingian Periods. These combined results would not only suggest that regions were quite integrated over time, but that the biological variation of communities within each region increased over time. The latter result could be due to the introduction of new alleles from outside sources.

Despite the low estimates for inter-regional heterogeneity, it is still suggestive that a definable change occurs from the Gallo-Roman to the Carolingian Periods, at least for the Normandy Region. In fact, Relethford-Blangero residuals show that the Gallo-Roman and Merovingian Periods of the Normandy Region have significantly less than expected extra-local gene flow, while the Carolingian Normandy region exhibits significantly greater than expected extra-local gene flow (Table 58 and Figure 65). Although the results from the odontometric analysis (Chapter 10) revealed an overall trend whereby the Normandy Region had significantly less than expected extra-local gene flow during the Gallo-Roman and Merovingian Periods, this initial analysis of the craniometric data would also suggest that this pattern reverses for the Normandy region during the Carolingian Period. Unfortunately, no odontometric data are available for the Carolingian Period of the Normandy Region.

A reversal in residuals also occurs for the Paris Basin region. In the odontometric analysis (Chapter 10), the Paris Basin Region often exhibited significantly greater than

expected extra-local gene flow, even over time (for example, see Table 36). However, in this analysis, the Merovingian Period of the Paris Basin Region clearly has significantly less than expected extra-local gene flow. Likewise, the Merovingian Period of the Rhône-Alps Region exhibits a reversal in the direction of significant extra-local gene flow. More specifically, the Merovingian Rhône-Alps Region exhibited significantly greater than expected extra-local gene flow in the odontometric analysis (for example, see Table 44), while the craniometric data clearly reveal it to possess significantly less than expected extra-local gene flow.

A final observation concerning the Relethford-Blangero residuals is for the two regions (Normandy, Rhône-Alps) representing the more broadly defined "Frankish" Period. Both are greatly divergent from their respective Merovingian Period regional samples. While the Merovingian Normandy and Rhône-Alps Regions are significantly negative, both the "Frankish" Normandy and Rhône-Alps Regions are significantly positive. Although it is possible that the chronological dating of these particular regions was not entirely secure, a number of other factors could be involved, namely that their regional designation was inappropriate, and/or that they were both individually unique in being the recipients of significant amounts of extra-local gene flow from an unknown source or sources.

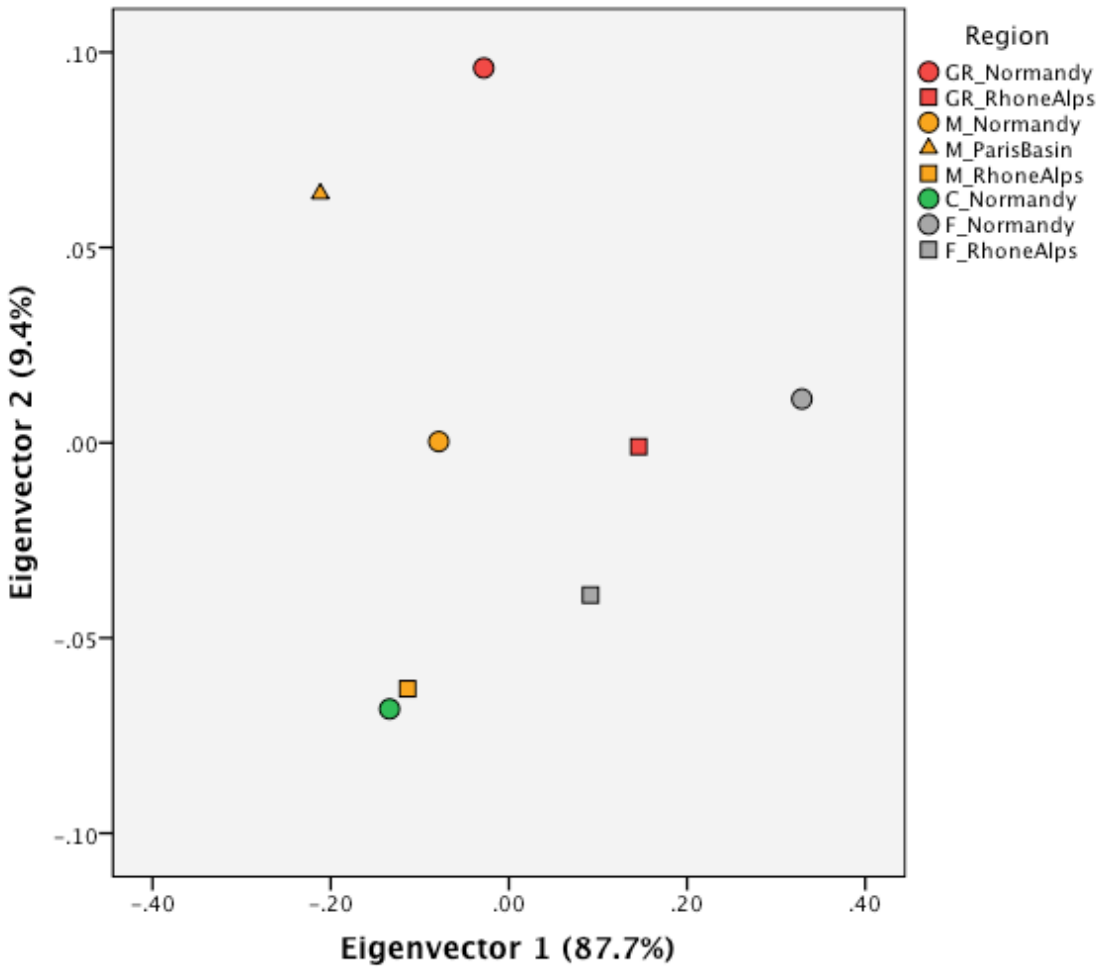

Figure 63. Scatterplot of PCO 1 vs. PCO 2 (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 1).

Table 55

Biological Distance (d^2) Matrix (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 1).

	(GR)_Rhône	(GR)_Norm	(M)_Norm	(M)_ParisB	(M)_Rhône	(C)_Norm	(F)_Norm	(F)_Rhône
(GR)_Rhône-Alps	-	0.025	-	-	-	-	-	-
(GR)_Normandy	0.022	-	-	-	-	-	-	-
(M)_Normandy	0.034	0.011	-	0.023	0.007	-	-	-
(M)_ParisBasin	0.119*	0.027	0.024	-	0.020	-	-	-
(M)_Rhône-Alps	0.049	0.030	0.000	0.014	-	-	-	-
(C)_Normandy	0.068	0.034*	0.006	0.019	0.000	-	-	-
(F)_Normandy	0.007	0.133**	0.164**	0.291**	0.195**	0.216**	-	-
(F)_Rhône-Alps	0.000	0.025	0.043	0.103	0.033	0.048	0.061	-

Notes: Lower matrix represents biological distances regardless of time period; upper matrix represents biological distances only for contemporaneous regions. $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 56

Estimates of Inter-Regional Heterogeneity and Average Within-Region Phenotypic Variance (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 1).

Period	F_{ST}	Average Within-Region Phenotypic Variance
Gallo-Roman	0.002	0.986
Merovingian	0.004	1.032
Carolingian	-	-
“Frankish”	-	-

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 57

Z-Test Results (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 1).

Change in F_{ST}	Z
Gallo-Roman to Merovingian (GR-M)	-0.148
Merovingian to Carolingian (M-C)	-
Gallo-Roman to Carolingian (GR-C)	-
Gallo-Roman to “Frankish” (GR-F)	-
Merovingian to “Frankish” (M-F)	-
Carolingian to “Frankish” (C-F)	-

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 58

Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 1).

Region and Time Period	Residual
Gallo-Roman:	
Rhône-Alps	-0.262**
Normandy	-0.267**
Merovingian:	
Normandy	-0.278**
ParisBasin	-0.256**
Rhône-Alps	-0.178**
Carolingian:	
Normandy	0.065**
“Frankish”:	
Normandy	0.748**
Rhône-Alps	0.427**

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

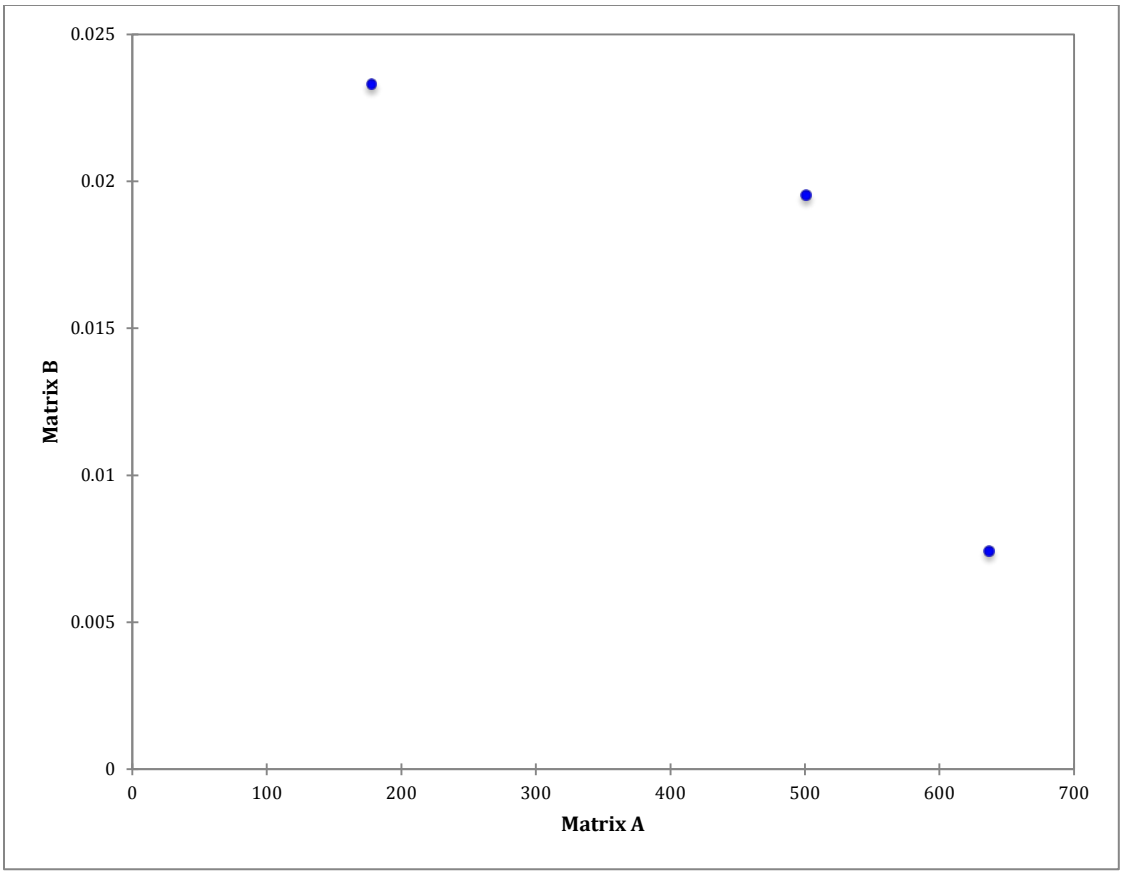

Figure 64. Scatterplot of the Mantel Test (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 1).

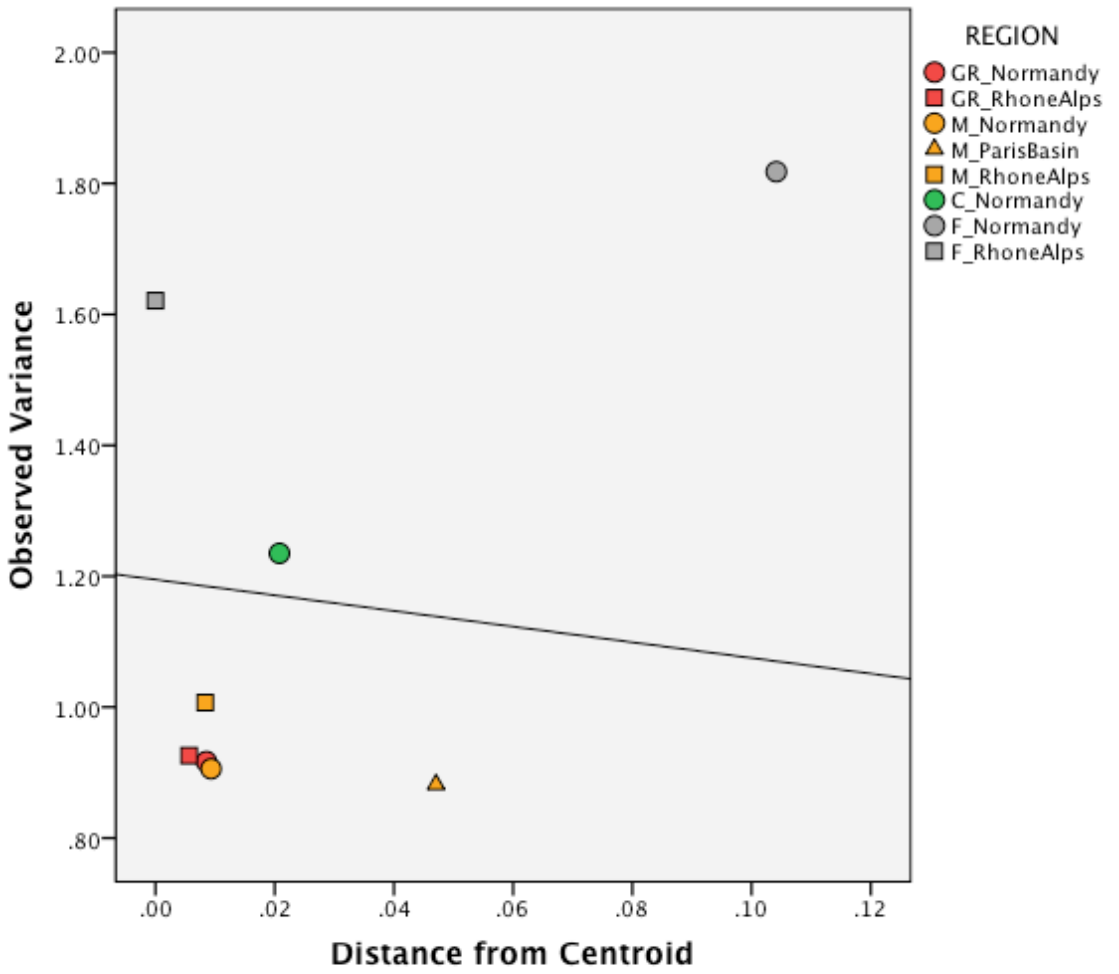

Figure 65. Scatterplot of Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 1).

12.1.2 Demographic Scenario 2

When narrow-sense heritability is altered to 0.55, the previous patterns are replicated (Figure 66). Nearly all of the variance is explained by the first two eigenvectors, the bulk of which falls along eigenvector one. Again, there is a perceptible shift in the Normandy and Rhône-Alps Regions over time. As time passes from the Gallo-Roman to the Merovingian and Carolingian Periods, these regions become closer to each other. In fact, the Merovingian Rhône-Alps Region clusters tightly with the Carolingian Normandy Region. Unfortunately, the Rhône-Alps Region has no craniometric representation during the Carolingian Period.

Other observations include the closer proximity of the Merovingian Paris Basin Region to the Gallo-Roman Normandy Region than to other regional time periods. Likewise, the broadly defined "Frankish" Normandy and Rhône-Alps Regions are equally divergent from their antecedent and contemporaneous regional samples, although that of the "Frankish" Rhône-Alps appears to flow in the same general direction exhibited by the change from Gallo-Roman to Carolingian Periods.

As indicated in the previous demographic scenario (see Table 55), significant biological distances are present, primarily for the broadly defined "Frankish" Normandy region (lower d^2 matrix). However, other regional periods also show significant distances (Table 59). Specifically, the Gallo-Roman Normandy Region is also significantly different from the Carolingian Normandy Region. This last observation seems to confirm the obvious diachronic trend noted earlier, at least for the region of Normandy. The distance between the Gallo-Roman and Merovingian Periods of the Rhône-Alps Region, however, is not significant.

In contrast, a consideration of regions by time period (upper d^2 matrix) yields no significant results, possibly indicating a greater homogeneity within time periods, despite the obvious dispersion noted in the scatterplot of the principal coordinates (Figure 66). Yet, tests for isolation-by-distance for regions of the Merovingian Period are significant ($R^2 = -1.000$, $p < 0.0001$; Figure 67), which suggests that geographic distance may structure the biological distances from the upper d^2 matrix. However, the issue of small sample size (n=3) provides an obvious constraint on this interpretation.

Ignoring time period, regional heterogeneity ($F_{ST} = 0.051$) is significantly different from zero (Table 60). However, this estimation may not reflect the level of inter-regional heterogeneity in each time period or over time. Indeed, each time period has very low, insignificant F_{ST} values, and (unsurprisingly) no significance to their values over time (Table 61). The F_{ST} values do increase slightly from the Gallo-Roman to Merovingian Periods, but not in a significant way. These results would suggest that the bulk of the variation noted by the overall significant F_{ST} of 0.051 originates from the Carolingian and Frankish Periods. Combined with a slight increase in average within-region phenotypic variation, it is possible to suggest that inter-regional gene flow was common within the Gallo-Roman and Merovingian Periods and that biological variation of communities within regions increased over time.

Nearly all regions, regardless of time period, have significantly negative Relethford-Blangero residuals. Only the "Frankish" Normandy and Rhône-Alps Regions have significant residuals, indicating greater than expected extra-local gene flow during this time period and regions (Table 62 and Figure 68). Interestingly, the Carolingian Normandy Region also exhibits greater than expected extra-local gene flow, although it is

not significant at the $\alpha = 0.05$ level. These results are in striking contrast to the same regions during the antecedent time periods during which the Normandy and the Rhône-Alps Regions exhibit significantly less than expected extra-local gene flow. Likewise, the Paris Basin Region during the Merovingian Period has significantly less than expected extra-local gene flow. It is unclear why the Merovingian and Gallo-Roman Periods would exhibit such a dearth of extra-local gene flow, especially considering the diversity of results presented by the odontometric analysis. However, these results continue to suggest that a significant change occurred at some point during the Carolingian Period.

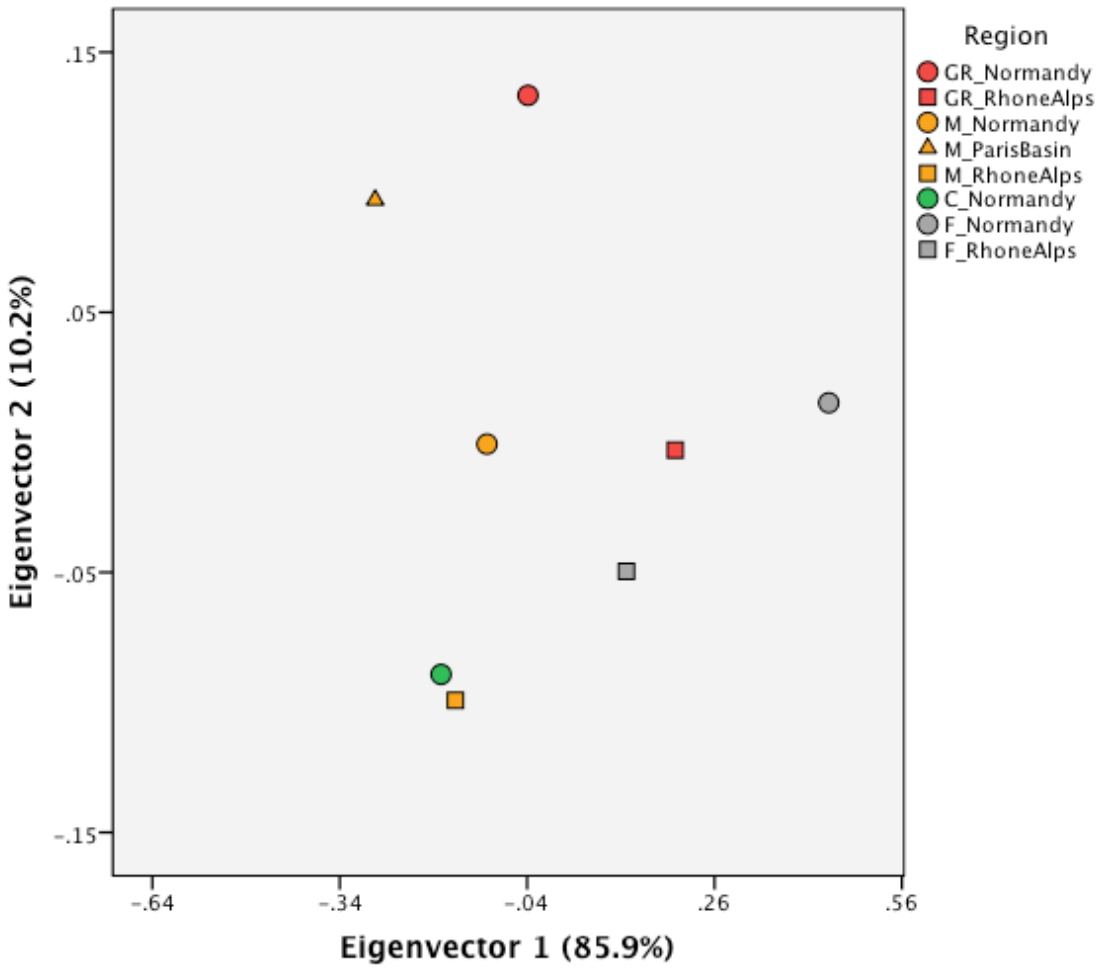

Figure 66. Scatterplot of PCO 1 vs. PCO 2 (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 2).

Table 59

Biological Distance (d^2) Matrix (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 2).

	(GR)_Rhône	(GR)_Norm	(M)_Norm	(M)_ParisB	(M)_Rhône	(C)_Norm	(F)_Norm	(F)_Rhône
(GR)_Rhône-Alps	-	0.050	-	-	-	-	-	-
(GR)_Normandy	0.058	-	-	-	-	-	-	-
(M)_Normandy	0.075*	0.025*	-	0.049	0.014	-	-	-
(M)_ParisBasin	0.231**	0.058*	0.049**	-	0.042	-	-	-
(M)_Rhône-Alps	0.113	0.068	0.007	0.044	-	-	-	-
(C)_Normandy	0.136**	0.066**	0.013*	0.041*	0.000	-	-	-
(F)_Normandy	0.039	0.250**	0.301**	0.529**	0.366**	0.393**	-	-
(F)_Rhône-Alps	0.000	0.049	0.077	0.189	0.070	0.087	0.118	-

Notes: Lower matrix represents biological distances regardless of time period; upper matrix represents biological distances only for contemporaneous regions. $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 60

Estimates of Inter-Regional Heterogeneity and Average Within-Region Phenotypic Variance (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 2).

Period	F_{ST}	Average Within-Region Phenotypic Variance
Gallo-Roman	0.007	0.986
Merovingian	0.009	1.032
Carolingian	-	-
“Frankish”	-	-

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 61

Z-Test Results (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 2).

Change in F_{ST}	Z
Gallo-Roman to Merovingian (GR-M)	-0.229
Merovingian to Carolingian (M-C)	-
Gallo-Roman to Carolingian (GR-C)	-
Gallo-Roman to "Frankish" (GR-F)	-
Merovingian to "Frankish" (M-F)	-
Carolingian to "Frankish" (C-F)	-

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 62

Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 2).

Region and Time Period	Residual
Gallo-Roman:	
Rhône-Alps	-0.271**
Normandy	-0.287**
Merovingian:	
Normandy	-0.300**
ParisBasin	-0.235**
Rhône-Alps	-0.187**
Carolingian:	
Normandy	0.055*
"Frankish":	
Normandy	0.830**
Rhône-Alps	0.394**

Notes: $^{**}\ p \leq 0.05$, $^{*}\ p \leq 0.10$.

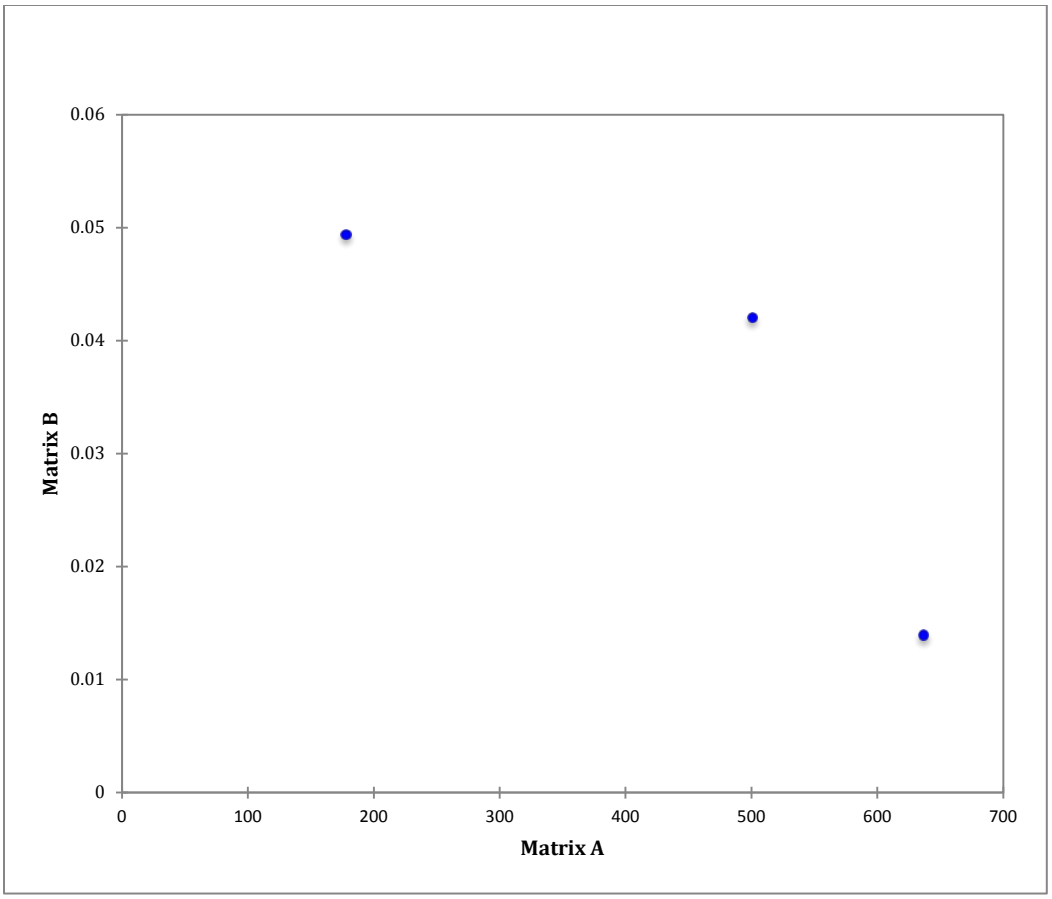

Figure 67. Scatterplot of the Mantel Test (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 2).

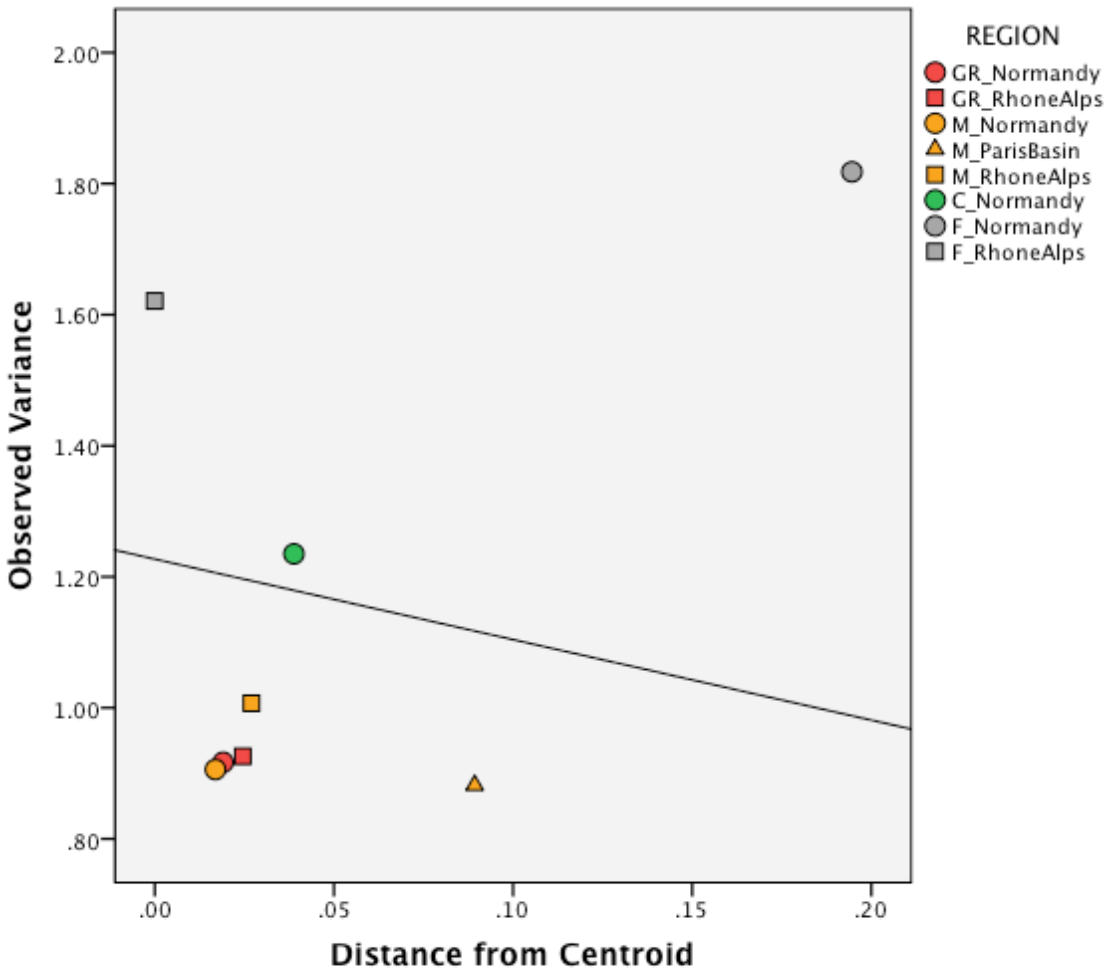

Figure 68. Scatterplot of Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 2).

12.1.3 Demographic Scenario 3

Factoring in population sizes (Figure 69) appears to shift the placement of the "Frankish" Rhône-Alps Region and little else. Again, most of the variance is explained by the first two eigenvectors, of which eigenvector one holds nearly 90%. Consequently, the dispersion of points along these eigenvectors suggests a degree of differentiation, as well as a shift occurring for the Normandy and Rhône-Alps Regions over time. However, the Merovingian Paris Basin Region is still closer to the Gallo-Roman Normandy Region than to any other regional time period. Likewise, the Merovingian Rhône-Alps and Carolingian Normandy Regions still cluster together.

The Mahalanobis d^2 matrix (Table 63) is very similar to that obtained in demographic scenario 1 (see Table 55), wherein the broadly defined "Frankish" Normandy region is significantly different from all other regional periods save one—the Gallo-Roman Rhône-Alps Region (lower d^2 matrix). Thus, the issue of relative population size does not appear initially to play a role in the dispersion of points in Figure 69. More interesting, however, are the significant biological distances between the Gallo-Roman and Carolingian Periods of the Normandy Region and the Gallo-Roman and Merovingian Periods of the Rhône-Alps Region. These results would imply that some regions did not remain biologically homogeneous over time. Likewise, considering time periods, no region is biologically distinct from another (upper d^2 matrix). However, despite the lack of significant biological distances between contemporaneous regions (upper d^2 matrix), a Mantel Test for isolation-by-distance of regions from the Merovingian Period still yield significant results ($R^2 = -1.000, p < 0.0001$; Figure 70). This result would suggest that geographic distance is a structuring agent to the biological

distances noted above. Nevertheless, sample size (n=3) likely plays an important part in this significant Mantel Test result.

Estimations of inter-regional heterogeneity for each time period remain roughly equivalent and insignificant, although they do increase slightly from the Gallo-Roman to Merovingian Periods (Table 64). Similarly, the change in F_{ST} over time is not significant as based on *Z*-tests (Table 65). In contrast, the average within-region phenotypic variability rises slightly from the Gallo-Roman to Merovingian Periods. These combined results would suggest that, although regions likely engaged in gene flow between each other, communities within each region also increased in their diversity, possibly via gene flow from outside sources.

Unfortunately, gene flow from extra-local sources is not supported by Relethford-Blangero residuals. Five of the eight regions have significantly less than expected extra-local gene flow (Table 66). Only the "Frankish" Period of the Rhône-Alps Region has significantly greater than expected extra-local gene flow. The "Frankish" Period of the Normandy Region is also far above the line of expected extra-local gene flow (Figure 71). However, its residual is only significant at the $\alpha = 0.10$ level. Interestingly, *all* of the Gallo-Roman and Merovingian regions have significantly less than expected extra-local gene flow, a result that appears to be consistently important.

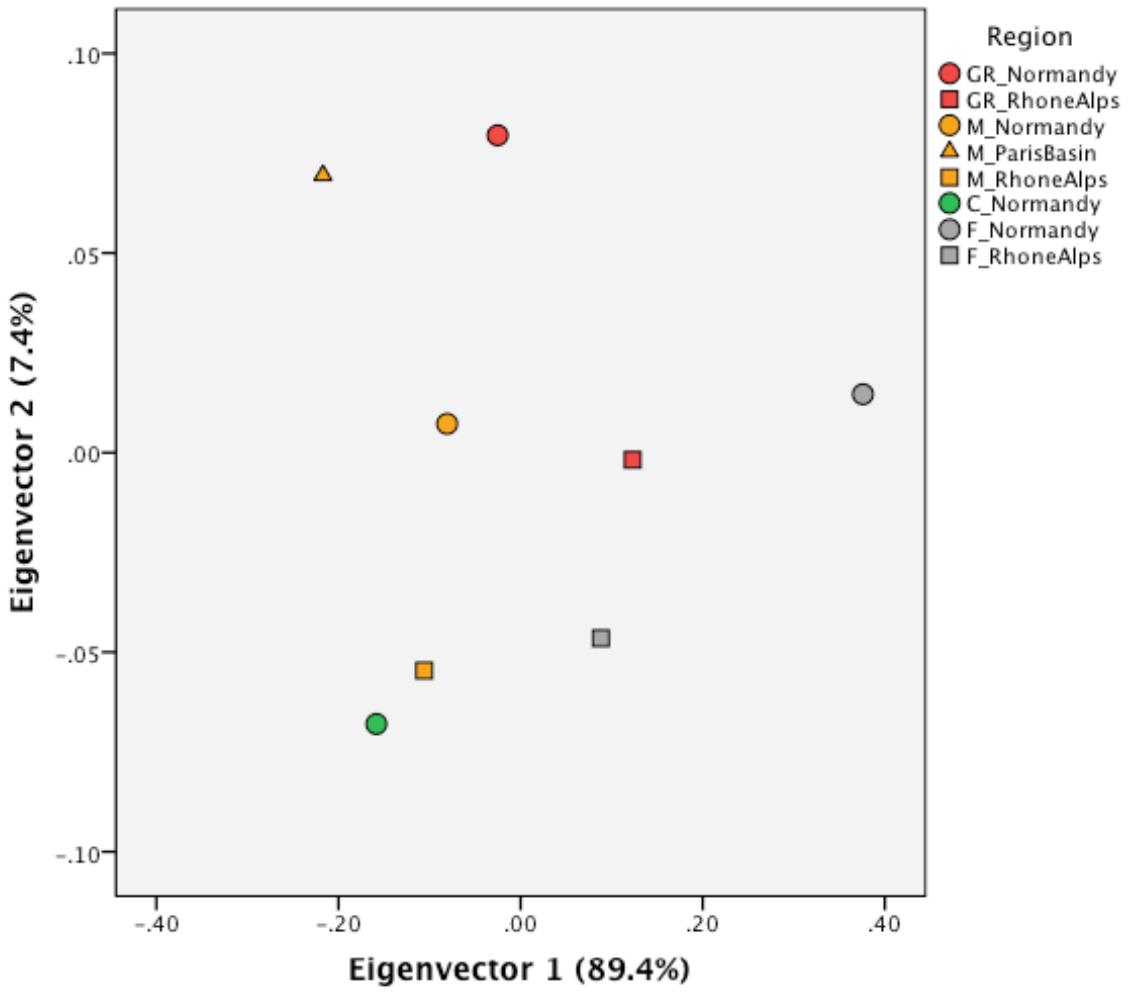

Figure 69. Scatterplot of PCO 1 vs. PCO 2 (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 3).

Table 63

Biological Distance (d^2) Matrix (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 3).

	(GR)_Rhône	(GR)_Norm	(M)_Norm	(M)_ParisB	(M)_Rhône	(C)_Norm	(F)_Norm	(F)_Rhône
(GR)_Rhône-Alps	-	0.012	-	-	-	-	-	-
(GR)_Normandy	0.015	-	-	-	-	-	-	-
(M)_Normandy	0.029	0.010	-	0.025	0.006	-	-	-
(M)_ParisBasin	0.109*	0.030	0.025*	-	0.012	-	-	-
(M)_Rhône-Alps	0.036	0.021	0.000	0.018	-	-	-	-
(C)_Normandy	0.071*	0.037**	0.009	0.018	0.000	-	-	-
(F)_Normandy	0.045	0.165**	0.207**	0.353**	0.231**	0.289**	-	-
(F)_Rhône-Alps	0.000	0.022	0.046	0.108	0.030	0.062	0.091	-

Notes: Lower matrix represents biological distances regardless of time period; upper matrix represents biological distances only for contemporaneous regions. $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 64

Estimates of Inter-Regional Heterogeneity and Average Within-Region Phenotypic Variance (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 3).

Period	F_{ST}	Average Within-Region Phenotypic Variance
Gallo-Roman	0.001	0.991
Merovingian	0.003	1.013
Carolingian	-	-
“Frankish”	-	-

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 65

Z-Test Results (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 3).

Change in F_{ST}	Z
Gallo-Roman to Merovingian (GR-M)	-0.299
Merovingian to Carolingian (M-C)	-
Gallo-Roman to Carolingian (GR-C)	-
Gallo-Roman to “Frankish” (GR-F)	-
Merovingian to “Frankish” (M-F)	-
Carolingian to “Frankish” (C-F)	-

Notes: $^{**}p \leq 0.05$, $^{*}\ p \leq 0.10$.

Table 66

Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 3).

Region and Time Period	Residual
Gallo-Roman:	
Rhône-Alps	-0.333**
Normandy	-0.333**
Merovingian:	
Normandy	-0.345**
ParisBasin	-0.316**
Rhône-Alps	-0.245**
Carolingian:	
Normandy	-0.002
“Frankish”:	
Normandy	0.680*
Rhône-Alps	0.358**

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

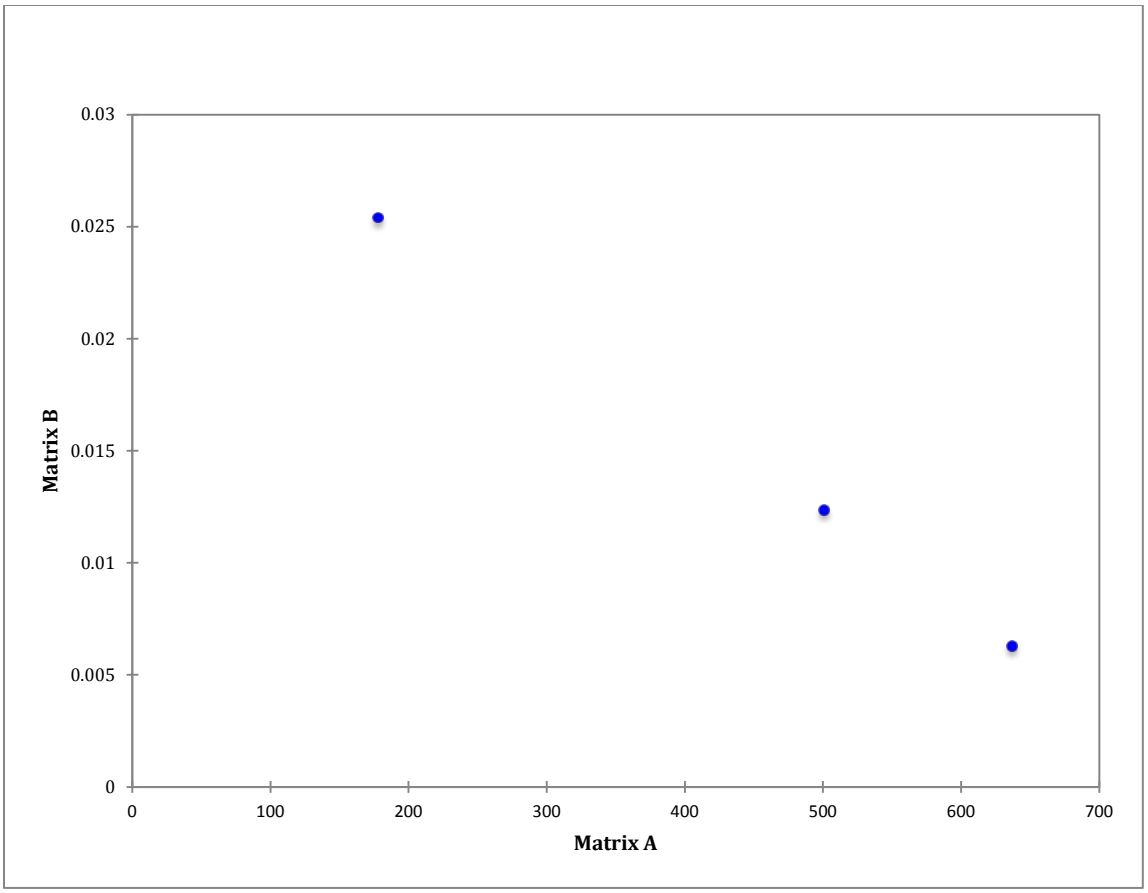

Figure 70. Scatterplot of the Mantel Test (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 3).

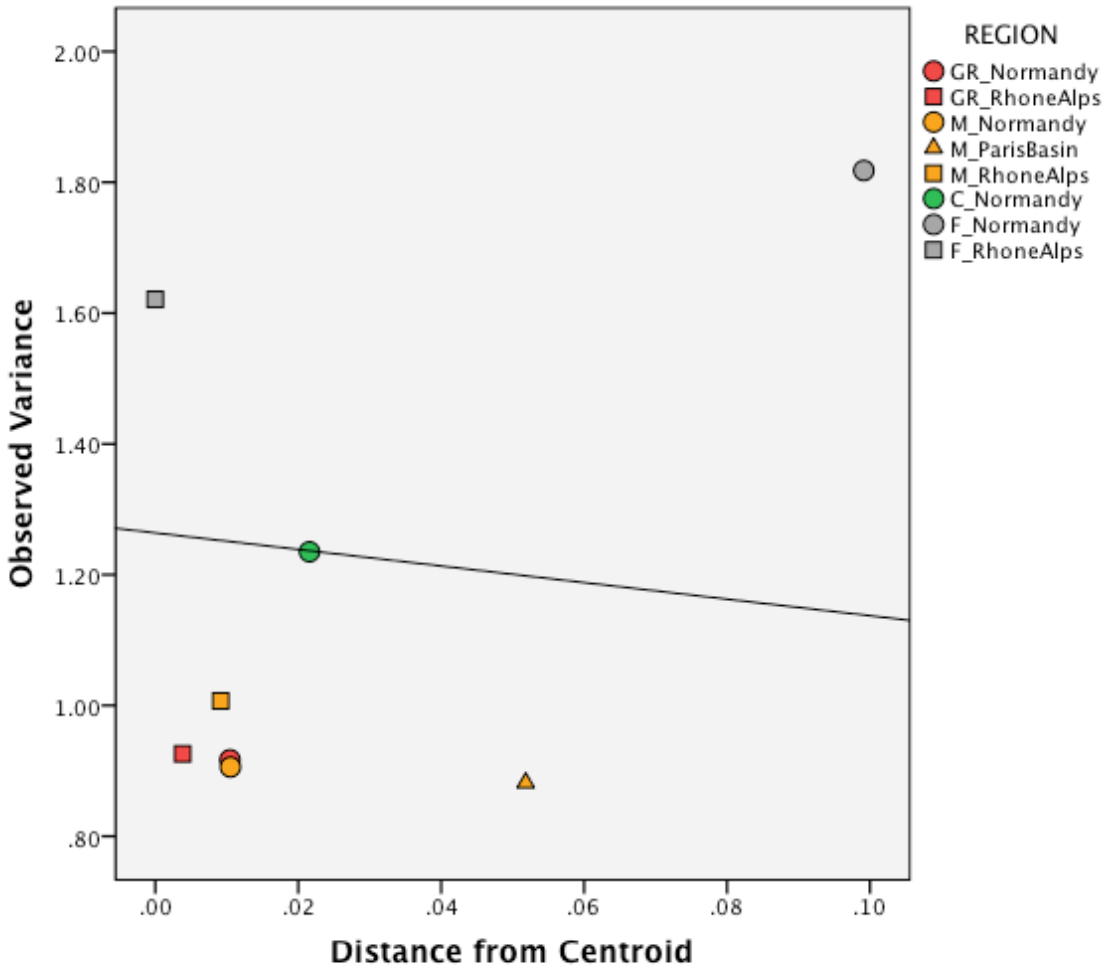

Figure 71. Scatterplot of Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 3).

12.1.4 Demographic Scenario 4

The final scenario seems to vary little from the previous one (Figure 72). A large part of the variation inherent in the R-matrix can be explained by the first two eigenvectors of the principal coordinates. Spatially, the Normandy and Rhône-Alps Regions seem to shift closer together over time, while the broadly defined "Frankish" Normandy Region is somewhat divergent. The Merovingian Paris Basin Region remains closer to the Gallo-Roman Normandy Region than to any other regional period. Likewise, the Merovingian Rhône-Alps Region remains clustered with the Carolingian Normandy Region. Overall, there is a diachronic shift from Gallo-Roman to Carolingian Periods that is apparent.

However, unlike in the previous scenario, many of the biological distances found in Table 67 are significant. Specifically, and perhaps most revealing, is that the Carolingian and "Frankish" Normandy Regions are significantly different from both the Gallo-Roman and Merovingian Normandy Regions (lower d^2 matrix) These results would suggest that there is *not* biological continuity over time for this specific region. The same cannot be said for the Rhône-Alps, as no biological distance between regional periods is significantly different. Likewise, there are no significant biological distances when restricting the analysis to those regions from the same time period (upper d^2 matrix), perhaps indicating greater homogeneity within time periods. Yet, the Mantel Test for isolation-by-distance performed on the Merovingian Period regions of the upper d^2 matrix do reveal significant correlations between the geographic and biological distances ($R^2 = -1.000, p < 0.0001$; Figure 73). The limited sample size (n=3) for

contemporaneous regions in the Merovingian Period likely limits the interpretive value of such a significant Mantel Test result.

Despite the biological distinction carried by the Carolingian and "Frankish" Normandy Regions in particular, inter-regional heterogeneity during the Gallo-Roman and Merovingian Periods is low and insignificant, even if it does increase slightly over time (Table 68). Likewise, the change in F_{ST} over time is insignificant (Table 69). Unfortunately, only a single region represents the Carolingian Period, and thus no estimate of inter-regional heterogeneity can be generated for this time period. Regardless, these results suggest that either gene flow was high during the Gallo-Roman and Merovingian Periods, that population sizes were quite large, or some combination thereof. An increase in average within-region phenotypic variance from the Gallo-Roman to Merovingian Periods might also suggest that communities within regions were becoming more diverse. However, this is a tentative interpretation.

The Relethford-Blangero residuals again confirm the patterns noted under other demographic scenarios (Table 70 and Figure 74). The broadly defined "Frankish" regions exhibit significantly greater than expected extra-local gene flow, while those of the Gallo-Roman and Merovingian Periods have significantly less than expected extra-local gene flow. It is entirely possible that the inclusion of these generic "Frankish" regions in this analysis skew much of the results.

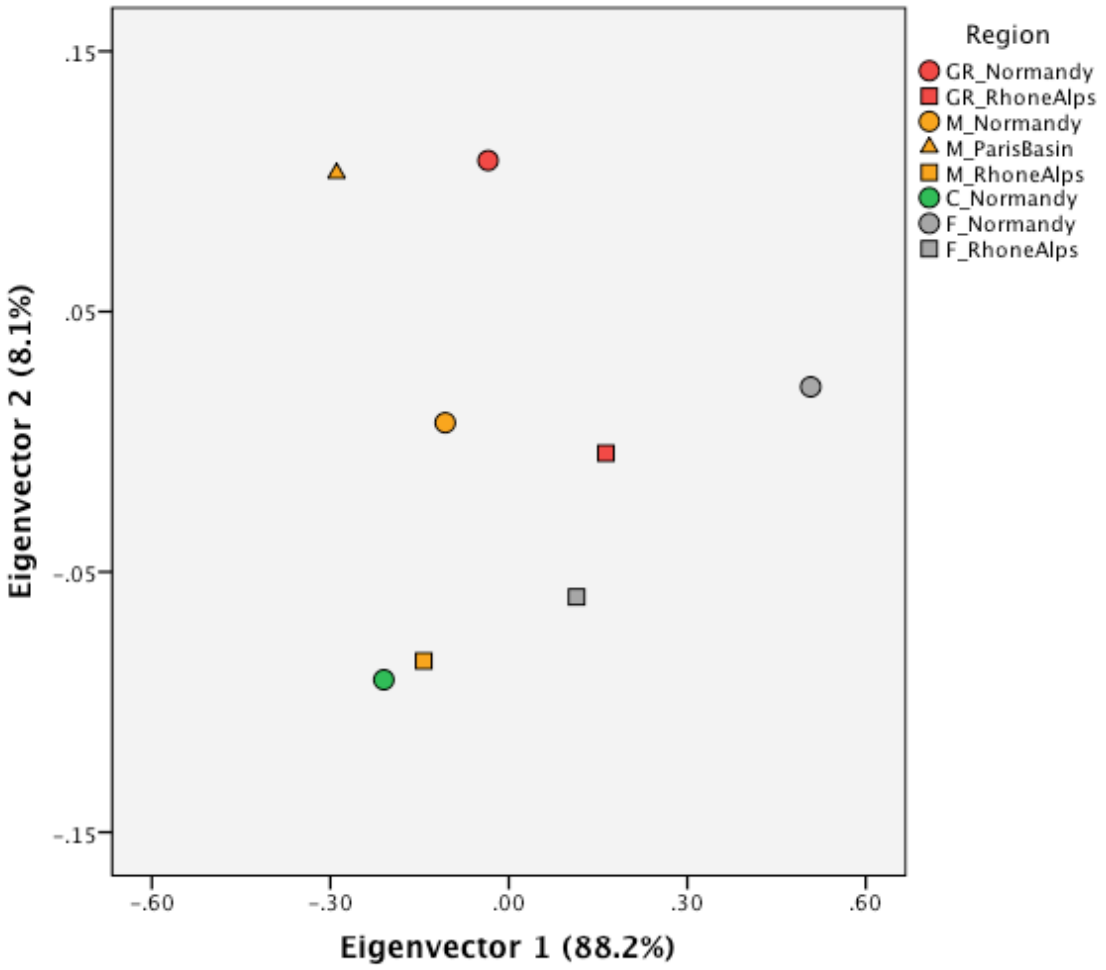

Figure 72. Scatterplot of PCO 1 vs. PCO 2 (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 4).

Table 67

Biological Distance (d^2) Matrix (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 4).

	(GR)_Rhône	(GR)_Norm	(M)_Norm	(M)_ParisB	(M)_Rhône	(C)_Norm	(F)_Norm	(F)_Rhône
(GR)_Rhône-Alps	-	0.029	-	-	-	-	-	-
(GR)_Normandy	0.040	-	-	-	-	-	-	-
(M)_Normandy	0.061*	0.020*	-	0.055	0.015	-	-	-
(M)_ParisBasin	0.207**	0.062**	0.051**	-	0.033	-	-	-
(M)_Rhône-Alps	0.083	0.049	0.005	0.048	-	-	-	-
(C)_Normandy	0.137**	0.071**	0.019**	0.041*	0.000	-	-	-
(F)_Normandy	0.104*	0.306**	0.378**	0.640**	0.430**	0.524**	-	-
(F)_Rhône-Alps	0.000	0.042	0.081	0.197	0.062	0.111	0.175	-

Notes: Lower matrix represents biological distances regardless of time period; upper matrix represents biological distances only for contemporaneous regions. $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 68

Estimates of Inter-Regional Heterogeneity and Average Within-Region Phenotypic Variance (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 4).

Period	F_{ST}	Average Within-Region Phenotypic Variance
Gallo-Roman	0.005	0.991
Merovingian	0.009	1.013
Carolingian	-	-
“Frankish”	-	-

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 69

Z-Test Results (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 4).

Change in F_{ST}	Z
Gallo-Roman to Merovingian (GR-M)	-0.492
Merovingian to Carolingian (M-C)	-
Gallo-Roman to Carolingian (GR-C)	-
Gallo-Roman to "Frankish" (GR-F)	-
Merovingian to "Frankish" (M-F)	-
Carolingian to "Frankish" (C-F)	-

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 70

Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 4).

Region and Time Period	Residual
Gallo-Roman:	
Rhône-Alps	-0.348**
Normandy	-0.356**
Merovingian:	
Normandy	-0.372**
ParisBasin	-0.293**
Rhône-Alps	-0.259**
Carolingian:	
Normandy	-0.015*
"Frankish":	
Normandy	0.757**
Rhône-Alps	0.319**

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

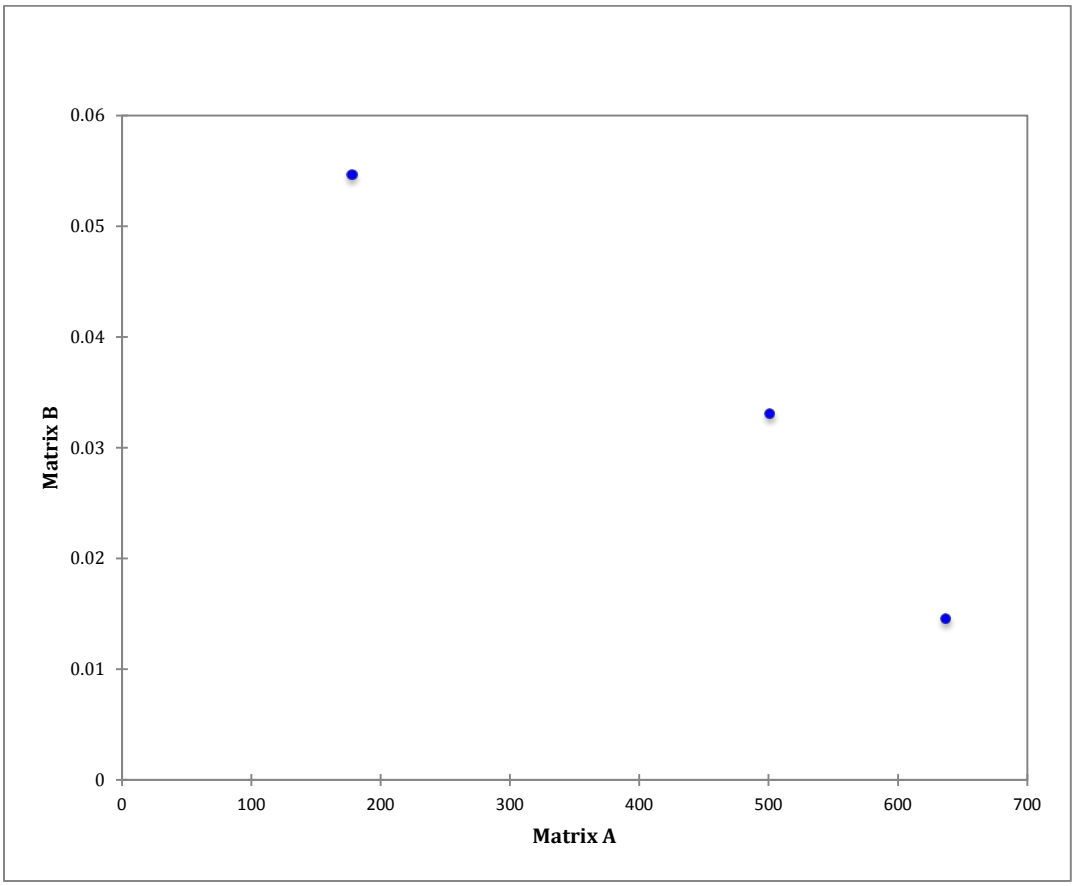

Figure 73. Scatterplot of the Mantel Test (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 4).

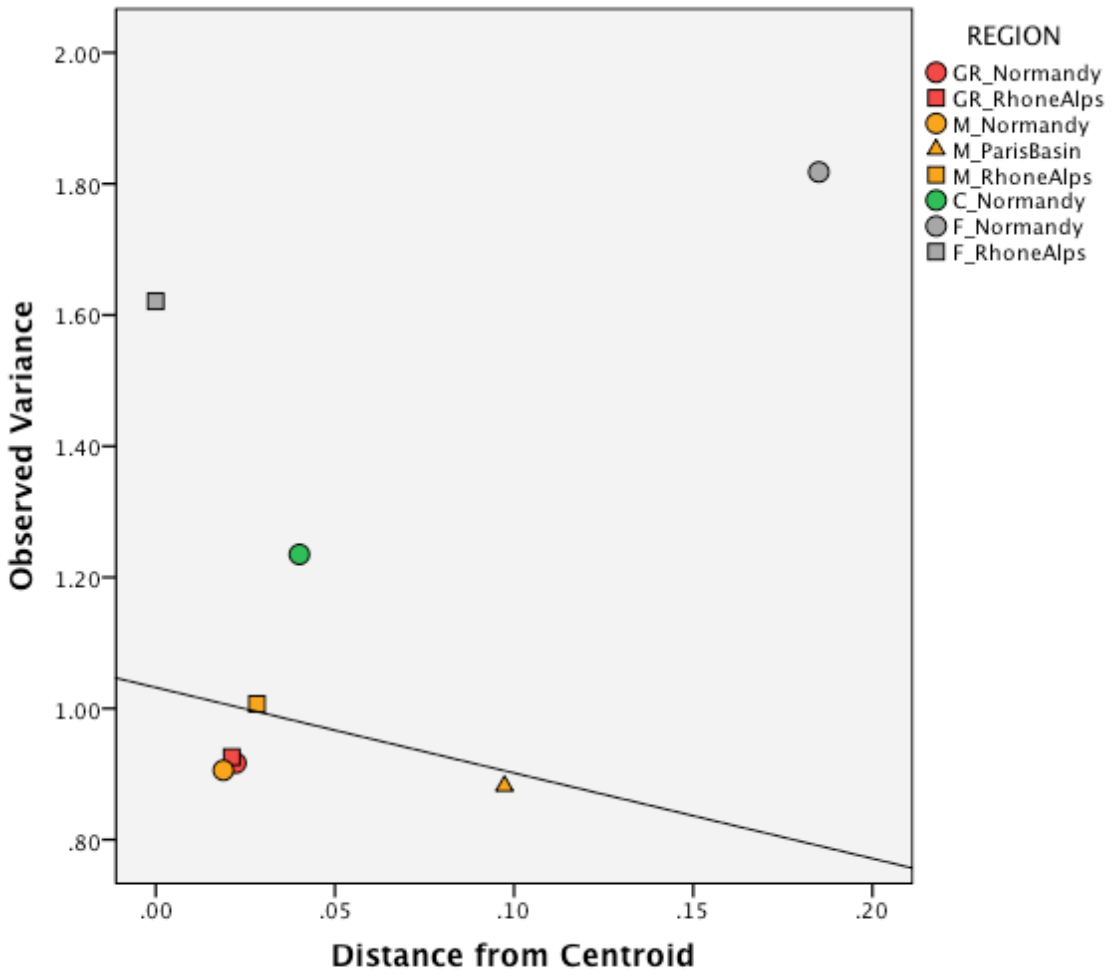

Figure 74. Scatterplot of Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 1, Regional-Level, Demographic Scenario 4).

12.1.5 Review

Nearly all of the variance of the R-matrix can be explained by the first two eigenvectors, which provides a level of certainty in the spatial patterning evident on the scatterplots of the principal coordinates. Regardless, the most striking pattern visible on the scatterplots is the clear temporal shift for regions. Not only do points representing the Normandy Region appear to shift more negatively along each axis from Gallo-Roman to Carolingian Periods, but points for the Rhône-Alps Region also shift negatively along each axis from Gallo-Roman to Merovingian Periods. This apparent temporal shift is similar to the results obtained in the diachronic odontometric analyses (see Chapter 10). In those analyses and scatterplots, the points representing regions became more distinct from each from the Gallo-Roman to Merovingian Periods, and then reversed from the Merovingian to Carolingian Periods when points clustered more closely together.

The Mahalanobis d^2 matrices also reveal some clear trends. Because subpopulations from different time periods could not interbreed, each matrix was visually and analytically divided into halves. The lower halves represented tests on the significance of biological distances between all regions regardless of time period and are best used to assess how a region compares to itself over time. The upper halves reflected tests on the significance of biological distances between regions from contemporary time periods. When considering the lower halves of the matrices, it is apparent that the Rhône-Alps Region exhibits a certain degree of homogeneity over time. Likewise, the Gallo-Roman Period of the Normandy Region is not significantly different from the Merovingian Period of the Normandy Region. In other words, for some regions represented diachronically, there is evidence for biological continuity. This trend is also

true of the results obtained in the diachronic odontometric analysis. However, it is interesting to note that the biological distance between the Gallo-Roman and Carolingian Periods of the Normandy Region is significant for the craniometric data. Unfortunately, no comparable odontometric data are available for the Carolingian Period of the Normandy Region. But the possibility of a change occurring during the Carolingian Period has been suggested in previous analyses and may be equally valid in this instance as well.

The upper halves of the d^2 matrices reveal that there are no significant biological distances for regions from the Gallo-Roman or Merovingian Periods. In other words, subpopulations from these two time periods are indistinct from each other. These results contrast to those obtained in the diachronic odontometric analysis, wherein the Paris Basin Region during the Merovingian Period is significantly different from all other regions from the same time period. In fact, it is striking that the Merovingian Period of the Paris Basin Region, which is so distinct in results for the odontometric analysis, is indistinguishable from contemporaneous regions in this analysis.

It is possible that the smaller sample of available regions for the craniometric analysis in comparison to the odontometric analysis (n=3 vs. n=4) could account for some of the apparent inter-regional homogeneity of the Merovingian Period, though not all. Likewise, the consistently significant Mantel Test results would also suggest that sample size plays a role. The potential issue of statistical sampling aside, there is still a significant correlation between geographical and biological distances, which would imply that any differences found for biological distances between contemporaneous regions would be due to isolation-by-distance. Unfortunately, no significant biological distances

were obtained, and thus these significant Mantel Test results have limited interpretive value.

Estimates for inter-regional heterogeneity (F_{ST}) and average intra-regional phenotypic variation were also generated for each time period having the minimum number of regions. Thus, estimates were made for only the Gallo-Roman and Merovingian Periods. Although showing a slight increase over time, both of these estimates were extremely low and not significant. Moreover, the actual change in F_{ST} from the Gallo-Roman to Merovingian Periods was not significant. These results suggest that inter-regional gene flow was similarly elevated during both time periods. In contrast, the average within-region phenotypic variance increases from the Gallo-Roman to Merovingian Periods. This suggests that, although regions were highly integrated from the Gallo-Roman to Merovingian Periods, they were also becoming more phenotypically diverse within each other over time, perhaps due to increasing effective population sizes and/or to extra-local gene flow.

When compared to estimates of inter-regional heterogeneity obtained in the odontometric analysis, these results are in striking contrast. In the odontometric analysis, F_{ST} increases from the Gallo-Roman to Carolingian Periods, in some cases up to a three- or four-fold increase. Furthermore, the odontometric analysis showed that while inter-regional heterogeneity was increasing over time, average intra-regional phenotypic variation was decreasing over time. In both instances, the odontometric and craniometric analyses contradict each other.

Relethford-Blangero residuals provide an estimation of the amount of gene flow into specific regions from sources not included in the analysis. For this particular

evaluation, nearly all regions had either significantly negative or positive residuals. In fact, all regions from the Gallo-Roman and Merovingian Periods exhibited significantly less than expected extra-local gene flow. Only those regions from the "Frankish" Period had consistently and significantly greater than expected extra-local gene flow. It is unclear what makes the "Frankish" Period unique in this possibility of gene flow from extra-local sources. It is possible that the attribution of the skeletal material to the "Frankish" Period was incorrect. It is also possible that the samples comprising the "Frankish" Period are reflecting a change occurring in the Carolingian (i.e., late "Frankish") Period to which other results also allude. It should be noted, though, that the diachronic analysis of the odontometric data contradicts some of the results for Relethford-Blangero residuals. Specifically, in the odontometric analysis, the Normandy Region almost always exhibits significantly negative residuals, regardless of time period.

12.2.2 REGIONAL-LEVEL 2 (GALLO-ROMAN, FRANKISH)

12.2.1 Demographic Scenario 1

This scatterplot of principal coordinates shows a number of interesting trends (Figure 75). First, the Gallo-Roman and Frankish Regions are quite distinct from each other. Likewise, regions are different from each other within each time period. The exceptions to this last observation are the Frankish Normandy and Rhône-Alps Regions that cluster together. There is a clear differentiation between the Merovingian Paris Basin Region and the other regions from this time period. This result is more consistent with those obtained in the diachronic odontometric analysis (Chapter 10), and less consistent with what was observed in the previous section (12.1.0) on diachronic regional trends

using more refined temporal periods. Most interesting, though, is that both the Gallo-Roman Normandy and Rhône-Alps Regions appear to shift over time, becoming more similar to each other.

Although some temporal shifts appear to be present, no biological distance between regions, regardless of time period, proves to be significant (lower d^2 matrix, Table 71). Likewise, no region is significantly different from others within the same time period (upper d^2 matrix). These results are in contrast to those obtained using the more refined chronological designations (for example, see Table 67), wherein the generically dated "Frankish" Normandy Region was significantly different from nearly all other regional periods. Although there were no significant biological differences between regions from the Frankish Period, the Mantel Test for isolation-by-distance was significant ($R^2 = -1.000$, $p < 0.0001$; Figure 76). Thus, geographic distance and biological distance are significantly correlated. However, with a sample size of three regions, this result warrants as much scrutiny as the significant Mantel Test results obtained using more refined chronological categorizations.

The overall estimate of inter-regional heterogeneity ($F_{ST} = 0.011$) regardless of time period is not statistically significant, nor is the estimate of heterogeneity for each time period (Table 72). Likewise, based on *Z*-tests, the change in F_{ST} over time is not significant, despite the fact that the estimate of F_{ST} increases slightly over time (Table 73). In summary, regional heterogeneity for each time period is quite low, suggesting that inter-regional gene flow was high and/or that effective population sizes for each time period were large. Interestingly, the average within-region phenotypic variance remains roughly consistent from the Gallo-Roman to Frankish Periods. This result contrasts with

that obtained using the more refined chronological designations, which showed an increase over time. Combined, the average intra-regional variances and F_{ST} imply that there was a large degree of homogeneity between and within regions over time.

Consideration of the Relethford-Blangero residuals also appears to confirm the overall impression of homogeneity amongst regions and time periods (Table 74 and Figure 77). The sole region to exhibit a significantly different than expected amount of extra-local gene flow is the Frankish Rhône-Alps Region. In fact, this region has much greater than expected levels of extra-local gene flow, which is similar to findings in the diachronic odontometric analysis (Chapter 10). It is interesting to note, however, that extra-local gene flow does seem to increase over time, with the exception of the Frankish Paris Basin Region that exhibits an unexpectedly low (albeit non-significant) negative residual.

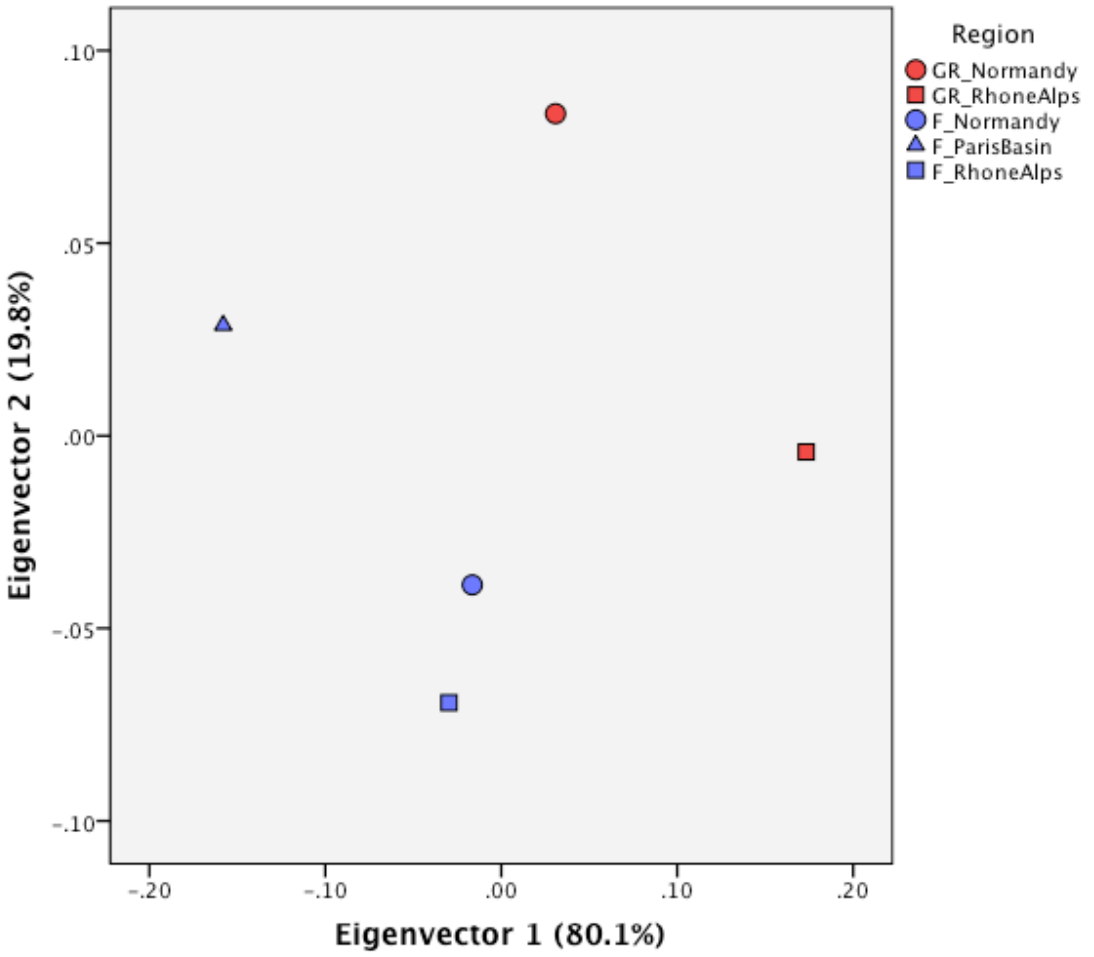

Figure 75. Scatterplot of PCO 1 vs. PCO 2 (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 1).

Table 71

Biological Distance (d^2) Matrix (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 1).

	(GR)_Rhône	(GR)_Norm	(F)_Norm	(F)_ParisB	(F)_Rhône
(GR)_Rhône-Alps	-	0.025	-	-	-
(GR)_Normandy	0.019	-	-	-	-
(F)_Normandy	0.035	0.014	-	0.024	0.004
(F)_ParisBasin	0.111	0.029	0.023	-	0.024
(F)_Rhône-Alps	0.037	0.027	0.000	0.017	-

Notes: Lower matrix represents biological distances regardless of time period; upper matrix represents biological distances only for contemporaneous regions. $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 72

Estimates of Inter-Regional Heterogeneity and Average Within-Region Phenotypic Variance (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 1).

Period	F_{ST}	Average Within-Region Phenotypic Variance
Gallo-Roman	0.002	0.986
Frankish	0.004	0.981

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 73

Z-Test Results (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 1).

Change in F_{ST}	Z
Gallo-Roman to Frankish (GR-F)	-0.177

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 74

Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 1).

Region and Time Period	Residual
Gallo-Roman:	
Rhône-Alps	-0.022
Normandy	-0.047*
Frankish:	
Normandy	0.041
ParisBasin	-0.066*
Rhône-Alps	0.094**

Notes: $^{**}\ p \leq 0.05$, $^{*}\ p \leq 0.10$.

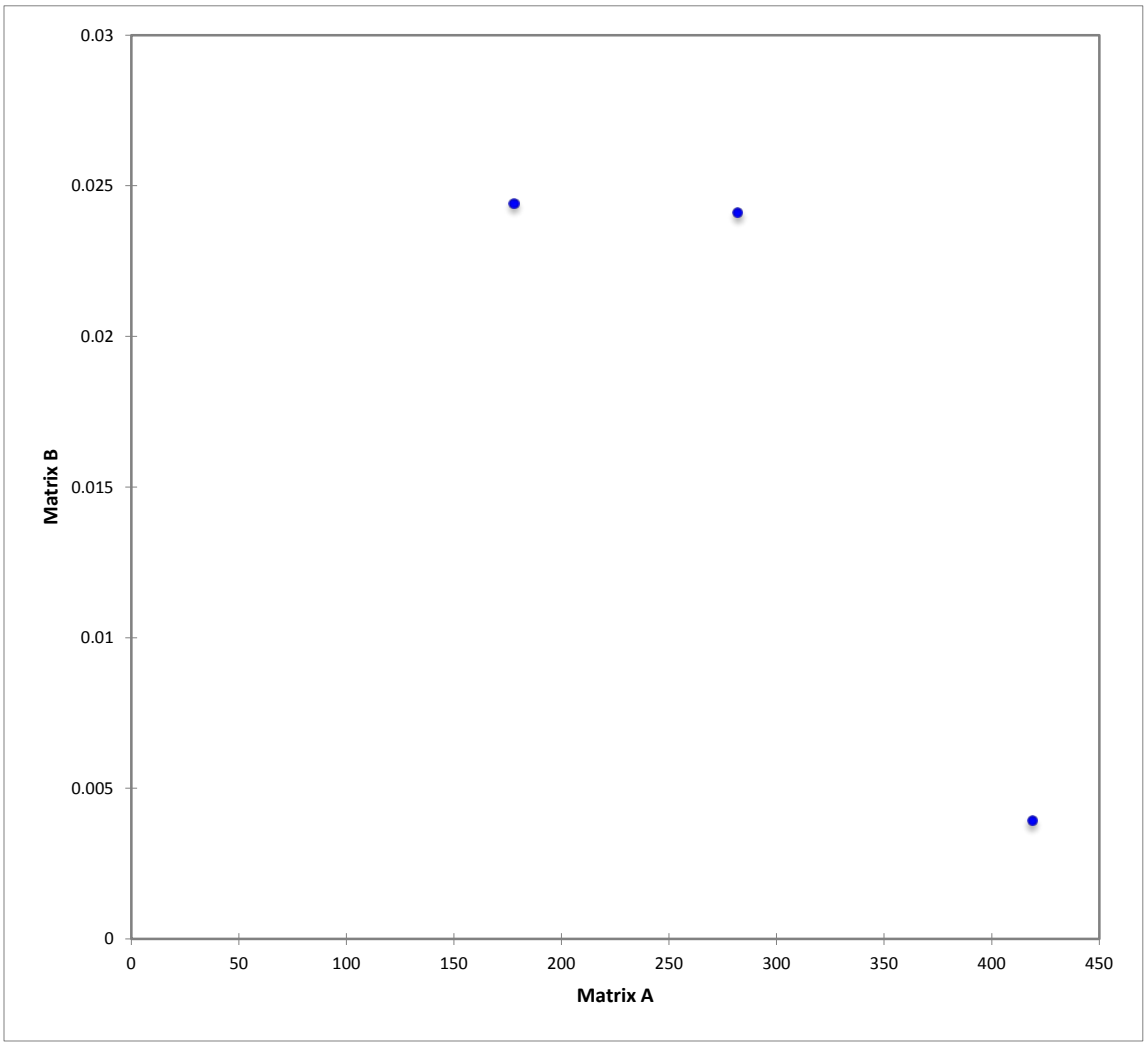

Figure 76. Scatterplot of the Mantel Test (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 1).

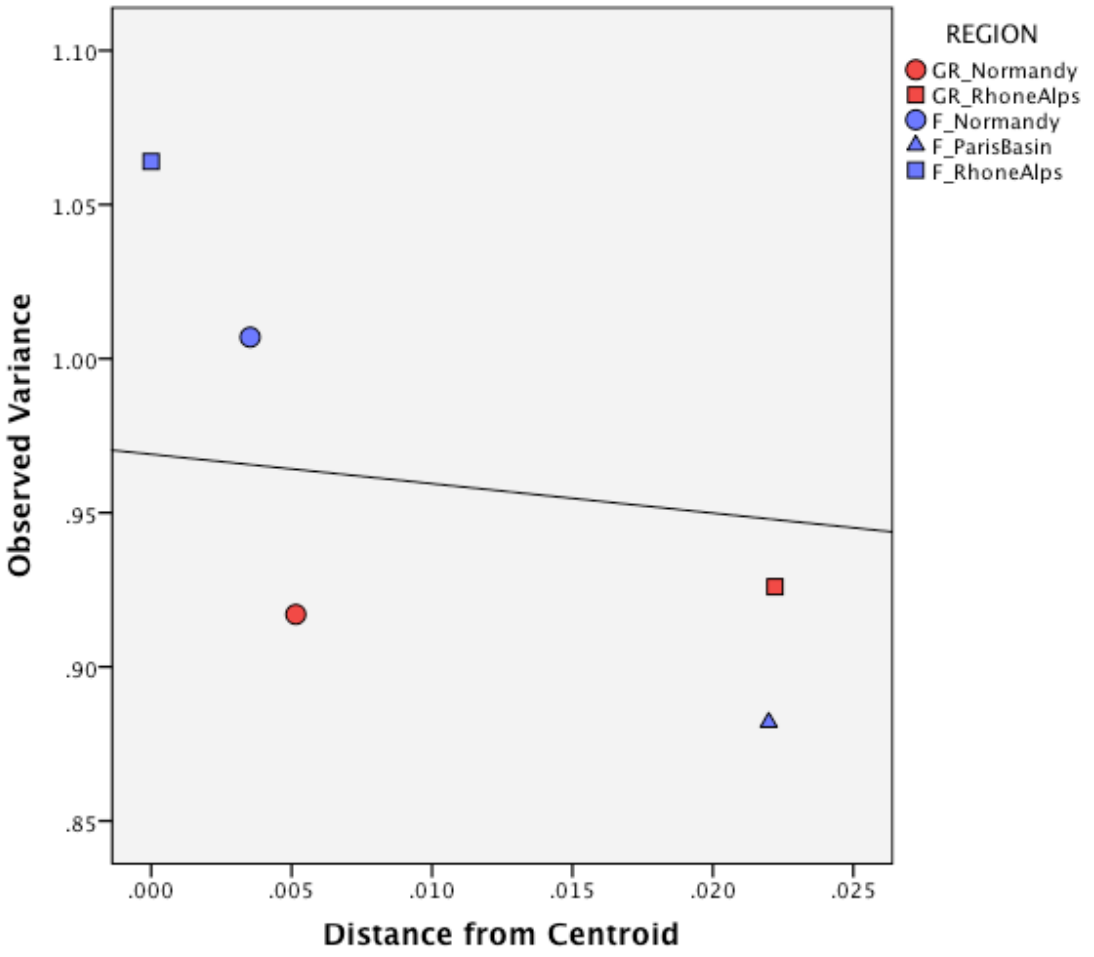

Figure 77. Scatterplot of Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 1).

12.2.2 Demographic Scenario 2

Changing the parameters to reflect a lower narrow-sense heritability does not seem to change the general pattern noted in the Demographic Scenario 1. Although the Frankish Normandy Region shifts away from the Frankish Rhône-Alps Region, they still cluster closer to each other than to the other regional time periods (Figure 78). A temporal shift is also indicated by the change in the Gallo-Roman Normandy and Rhône-Alps Regions to their placement during the subsequent time period. Moreover, the Merovingian Paris-Basin Region continues to remain distinct from other contemporaneous regions.

Most biological distance estimates between regions regardless of time period are non-significant (lower d^2 matrix, Table 75). Only the Frankish Paris Basin Region proves to be significantly distinct from the Gallo-Roman Rhône-Alps Region, and given the overall distinction held by the Paris Basin Region, this result is not surprising. Indeed, when $\alpha = 0.10$, the Frankish Paris Basin Region becomes significantly different from all other regional periods save the Frankish Rhône-Alps Region (Table 75). Even more interesting, however, is the biological difference between the Gallo-Roman and Frankish Periods of the Normandy Region (when $\alpha = 0.10$) In other words, this region becomes increasingly biologically distinct from itself over time. These results hint at changes occurring for these regions during the Frankish Period, changes which are realized when examining Table 67 from the previous section that considers more refined chronological designations. Regardless, there are no significant differences between regions from the same time period (upper d^2 matrix), even given the apparent dispersion seen in Figure 78. However, much like the previous demographic scenario, a Mantel Test for isolation-

by-distance yields significant results ($R^2 = -1.000$, $p < 0.0001$; Figure 79), suggesting that geographic distance can account for the biological distances reported in Table 75. However, with a sample size of three regions, this result warrants as much scrutiny as the significant Mantel Test results obtained using more refined chronological categorizations.

Although the overall estimate of inter-regional heterogeneity is significant ($F_{ST} = 0.026$), each time period has a remarkably similar estimate of F_{ST} (albeit increasingly slightly over time), both of which are quite low and non-significant (Table 76). Even the change in F_{ST} over time is non-significant (Table 77). Finally, the average within-region phenotypic variance shows little change over time. Together, these results signal for both time periods that 1) within-region phenotypic variance was constant; 2) inter-regional gene flow may have been high; and 3) effective population sizes may have been high.

Relethford-Blangero residuals do not clarify these issues (Table 78 and Figure 80). In fact, only the Frankish Rhône-Alps Region has significantly greater than expected extra-local gene flow. The remaining regions and periods are not significant and/or fall close to the expected line of phenotypic variance. It should be noted, however, that even though only one region had a significant residual, there does appear to be an increase in extra-local gene flow during the Frankish Period.

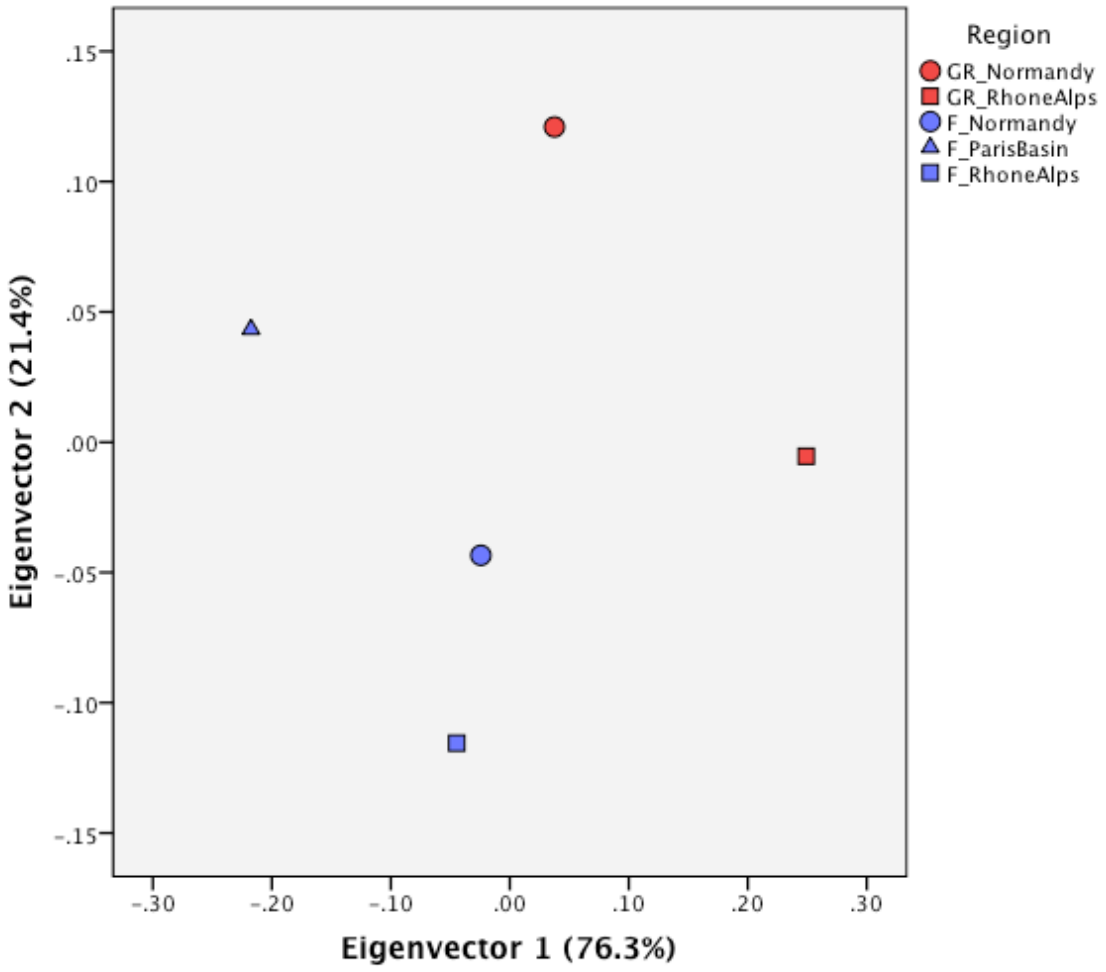

Figure 78. Scatterplot of PCO 1 vs. PCO 2 (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 2).

Table 75

Biological Distance (d^2) Matrix (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 2).

	(GR)_Rhône	(GR)_Norm	(F)_Norm	(F)_ParisB	(F)_Rhône
(GR)_Rhône-Alps	-	0.050	-	-	-
(GR)_Normandy	0.053	-	-	-	-
(F)_Normandy	0.079	0.030*	-	0.051	0.008
(F)_ParisBasin	0.220**	0.063*	0.048*	-	0.051
(F)_Rhône-Alps	0.092	0.063	0.009	0.048	-

Notes: Lower matrix represents biological distances regardless of time period; upper matrix represents biological distances only for contemporaneous regions. $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 76

Estimates of Inter-Regional Heterogeneity and Average Within-Region Phenotypic Variance (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 2).

Period	F_{ST}	Average Within-Region Phenotypic Variance
Gallo-Roman	0.007	0.986
Frankish	0.010	0.981

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 77

Z-Test Results (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 2).

Change in F_{ST}	Z
Gallo-Roman to Frankish (GR-F)	-0.275

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 78

Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 2).

Region and Time Period	Residual
Gallo-Roman:	
Rhône-Alps	-0.005
Normandy	-0.055*
Frankish:	
Normandy	0.028
ParisBasin	-0.057
Rhône-Alps	0.089**

Notes: $^{**}\ p \leq 0.05$, $^{*}\ p \leq 0.10$.

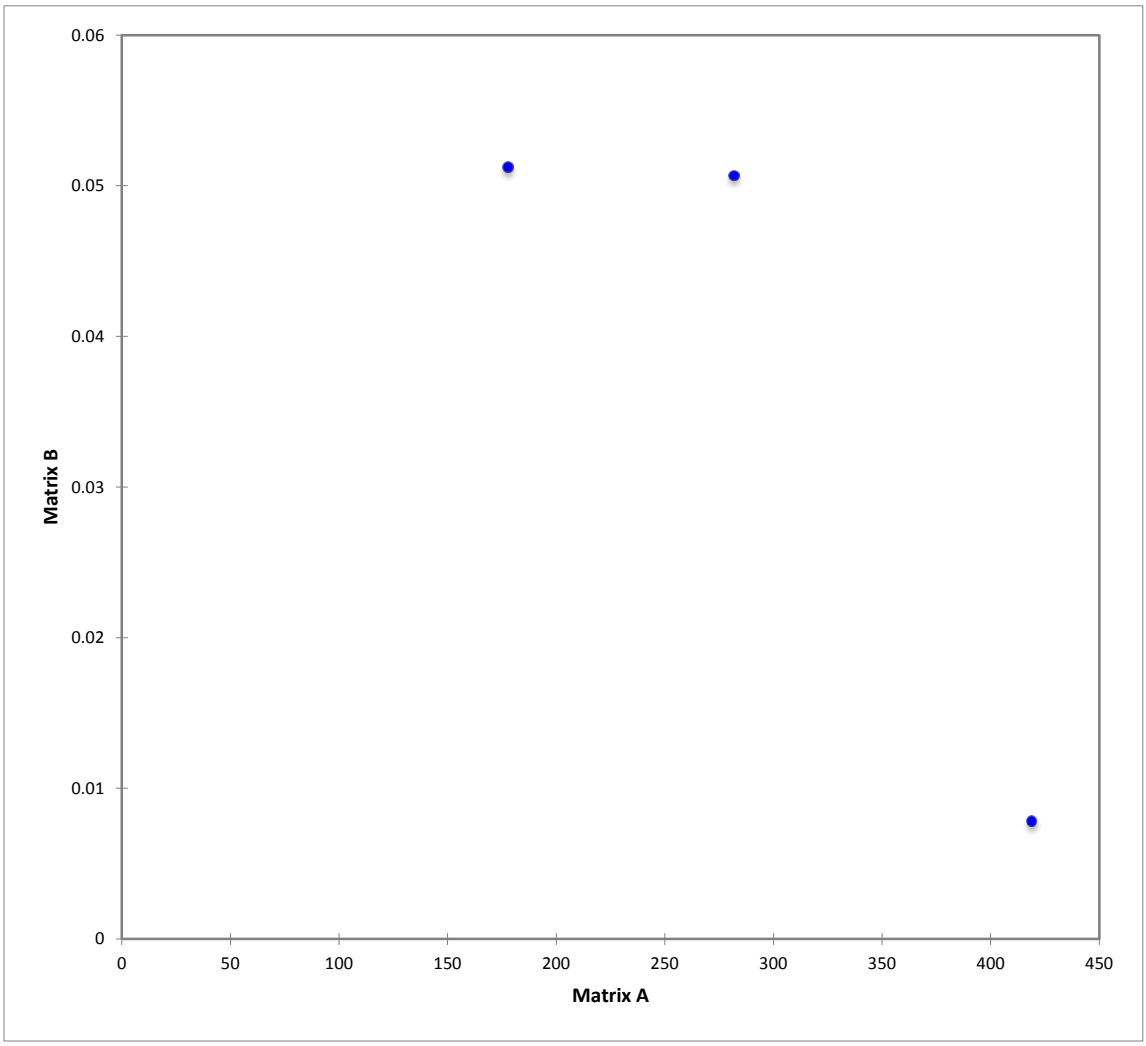

Figure 79. Scatterplot of the Mantel Test (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 2).

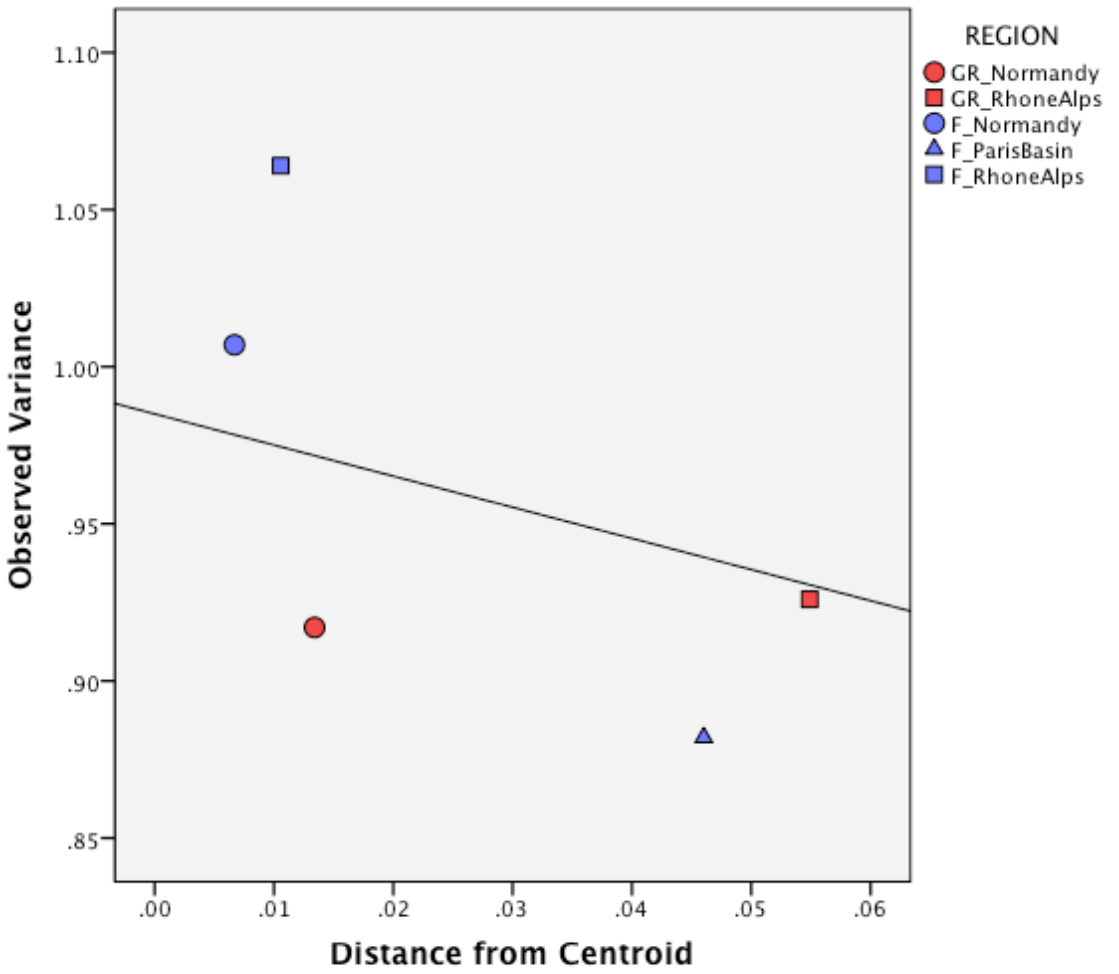

Figure 80. Scatterplot of Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 2).

12.2.3 Demographic Scenario 3

Altering the parameters to include relative population sizes does not change the overall pattern noted in the previous demographic scenarios. Again, the Frankish Normandy and Rhône-Alps Regions cluster together, while the Frankish Paris Basin Region remains distinct from its contemporaries (Figure 81). Also, the Gallo-Roman Normandy and Rhône-Alps Regions appear to shift closer to each other over time.

Although the distinctions between regions and time periods appear clear, all biological distances between regions, or between a region and itself, regardless of time period are not significant (lower d^2 matrix, Table 79). Furthermore, considering only those regions that are contemporaries, no region is significantly different from another (upper d^2 matrix). Yet, a Mantel Test on those contemporaneous Frankish Regions produced a significant correlation between the geographic and biological distance matrices ($R^2 = -1.000$, $p < 0.0001$; Figure 82). Given that the number of Frankish Regions available for assessment of isolation-by-distance (n=3), sample size issues likely play a role in this positive Mantel Test result.

The overall estimate of inter-regional heritability ($F_{ST} = 0.009$) is not significant; neither are the estimates of regional heterogeneity for each time period individually (Table 80). Likewise, the change in F_{ST} over time is not significant (Table 81), despite the fact that there is a slight increase in F_{ST} from the Gallo-Roman to Frankish Periods. These results further suggest that inter-regional gene flow was elevated, population sizes were large, or that a combination of these options occurred. The similarity in average within-group phenotypic variance also implies that communities within regions shared comparable amounts of biological variation over time. Together, these results indicate

that regions in both the Gallo-Roman and Frankish Periods were similarly diverse and yet highly integrated.

Relethford-Blangero residuals do not clarify much of the underlying population structure, especially since extra-local gene flow seems not be indicated for the majority of regions and time periods. While the Frankish Rhône-Alps Region has significantly positive residuals, the Frankish Paris Basin region has significantly less than expected extra-local gene flow (Table 82 and Figure 83). This latter observation is a reversal from patterns noted in the diachronic odontometric analysis (for example, see Table 25) but consistent with craniometric results that use more refined chronological categories.

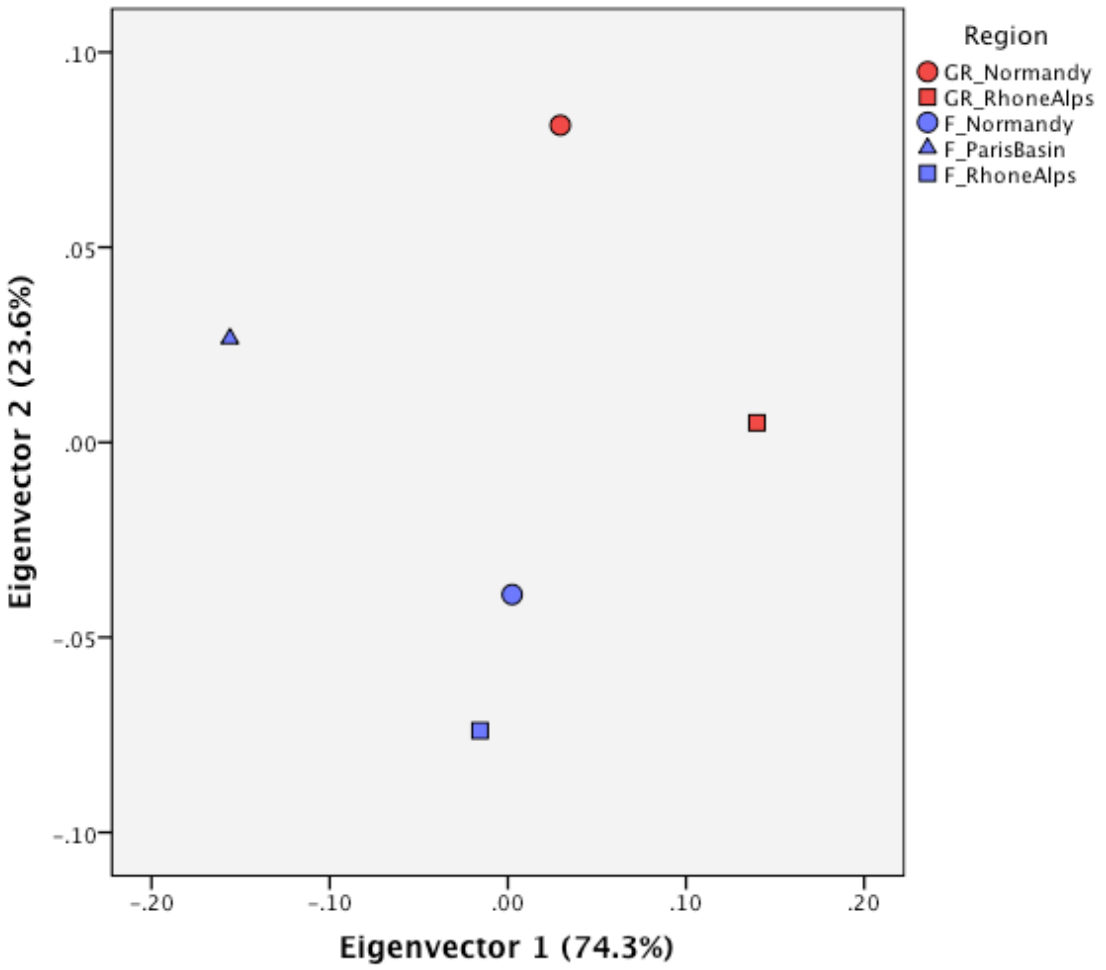

Figure 81. Scatterplot of PCO 1 vs. PCO 2 (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 3).

Table 79

Biological Distance (d^2) Matrix (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 3).

	(GR)_Rhône	(GR)_Norm	(F)_Norm	(F)_ParisB	(F)_Rhône
(GR)_Rhône-Alps	-	0.012	-	-	-
(GR)_Normandy	0.010	-	-	-	-
(F)_Normandy	0.020	0.013	-	0.026	0.003
(F)_ParisBasin	0.088	0.031	0.030	-	0.016
(F)_Rhône-Alps	0.024	0.026	0.002	0.025	-

Notes: Lower matrix represents biological distances regardless of time period; upper matrix represents biological distances only for contemporaneous regions. $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 80

Estimates of Inter-Regional Heterogeneity and Average Within-Region Phenotypic Variance (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 3).

Period	F_{ST}	Average Within-Region Phenotypic Variance
Gallo-Roman	0.001	0.991
Frankish	0.003	0.965

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 81

Z-Test Results (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 3).

Change in F_{ST}	Z
Gallo-Roman to Frankish (GR-F)	-0.325

Notes: **$p \leq 0.05$, * $p \leq 0.10$.

Table 82

Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 3).

Region and Time Period	Residual
Gallo-Roman:	
Rhône-Alps	-0.012
Normandy	-0.049*
Frankish:	
Normandy	0.035
ParisBasin	-0.080**
Rhône-Alps	0.089**

Notes: ** $p \leq 0.05$, * $p \leq 0.10$.

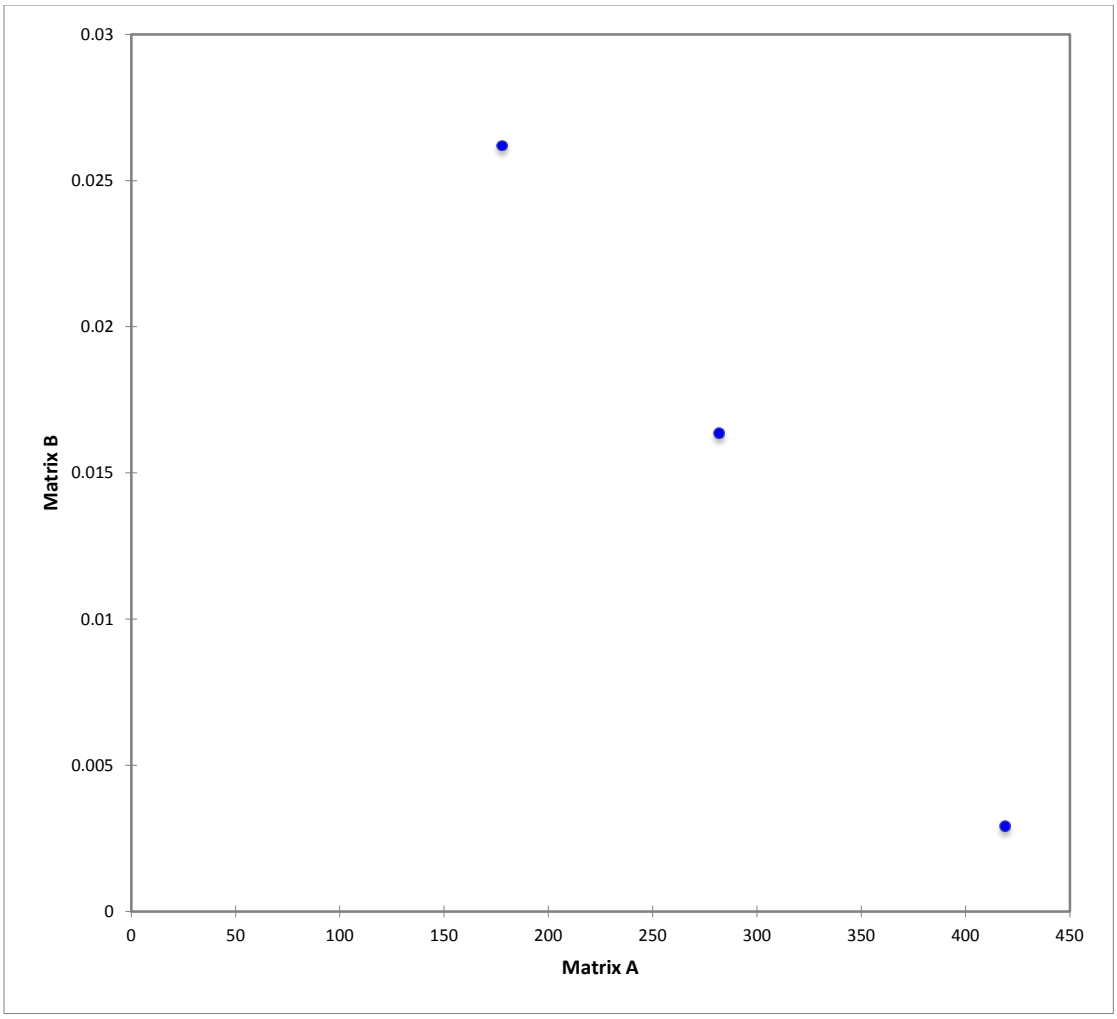

Figure 82. Scatterplot of the Mantel Test (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 3).

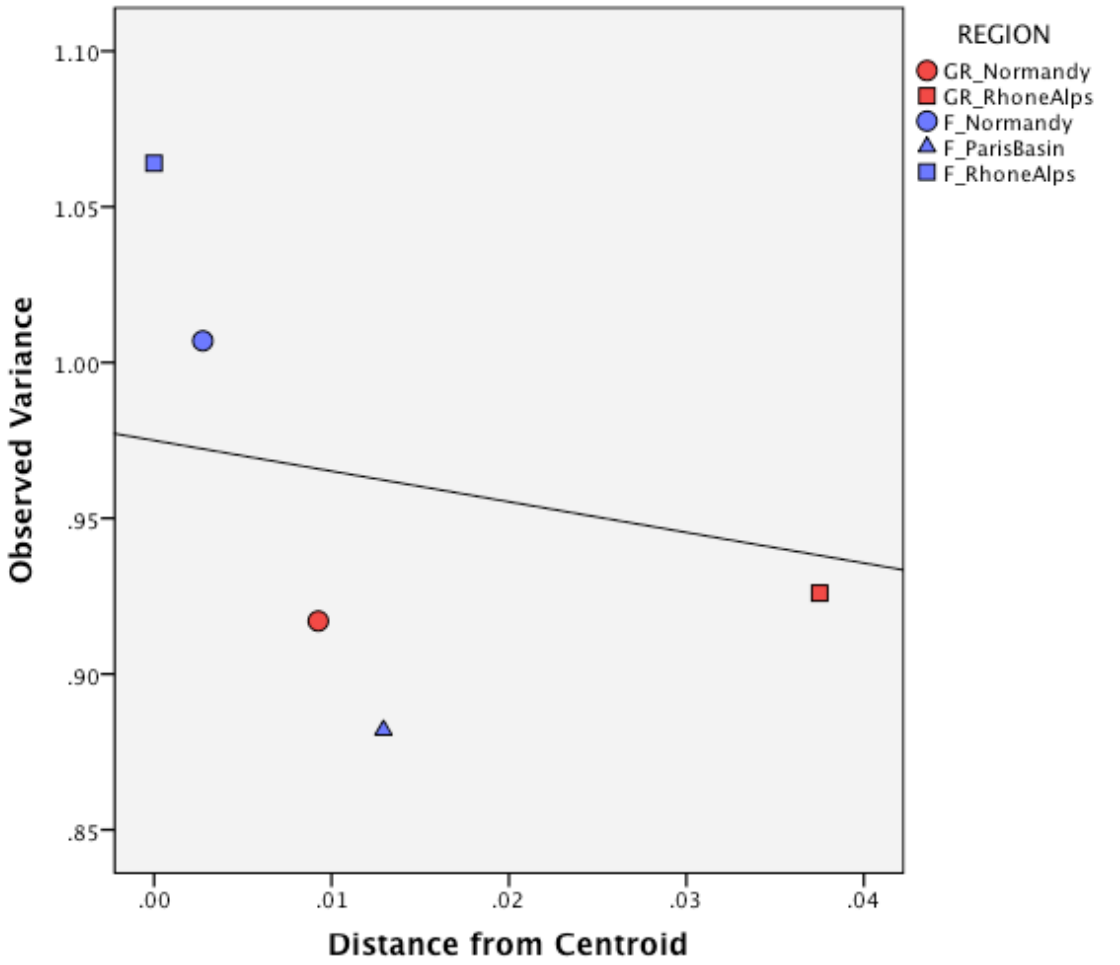

Figure 83. Scatterplot of Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 3).

12.2.4 Demographic Scenario 4

Considering a less conservative estimate of narrow-sense heritability, as well as relative population sizes, maintains the patterns previously noted (Figure 84). The Merovingian Normandy and Rhône-Alps Regions cluster together and exhibit a dramatic temporal shift from their counterparts in the Gallo-Roman Period. Likewise, the Merovingian Paris Basin Region remains distinct from its contemporaries.

Under this scenario, however, several of the biological distances between regional periods are significantly different (lower d^2 matrix, Table 83). Specifically, the Frankish Paris Basin region is significantly different from the Gallo-Roman Rhône-Alps and Frankish Normandy regions. More importantly, though, no region is significantly different from itself over time when $\alpha = 0.05$. It is only when $\alpha = 0.10$ that the Gallo-Roman Period of the Normandy Region becomes significantly different from the Frankish Period of the Normandy Region. This result perhaps confirms the dramatic shift of these regions over time that was noted in Figure 84. Unfortunately, an assessment of biological distances for Frankish Period regions (upper d^2 matrix) yielded no significant results. This would suggest that regions were quite homogeneous between themselves during the Frankish Period. Despite the lack of significant biological distances, a Mantel Test for isolation-by-distance yielded a significant correlation between the geographic and biological matrices of the contemporary Frankish Period regions ($R^2 = -1.000$, $p < 0.0001$; Figure 85). Normally, such a result would suggest that isolation-by-distance could account for the patterns observed in the upper portion of the Mahalanobis d^2 matrix. Yet, no indication of genetic isolation is evident.

In contrast to the other demographic scenarios, overall inter-regional heterogeneity ($F_{ST} = 0.022$) is significantly different from zero. However, individual estimates of inter-regional heterogeneity for each time period, despite increasing slightly over time, are quite a bit lower, insignificant, and are still very similar to each other in both the Gallo-Roman and Frankish Periods (Table 84). Thus, it is not surprising that the change in F_{ST} over time is also not significant (Table 85). These results may suggest inter-regional gene flow within each time period was high, as described previously. The average within-region phenotypic variation is also similar between the Gallo-Roman and Frankish Periods. This result would also indicate that communities within each region and time period shared a similar amount of biological variation.

Evidence for extra-local gene flow is rather mixed (Table 86 and Figure 86). Although the Frankish Paris Basin Region has significantly less than expected extra-local gene flow, the Frankish Rhône-Alps Region has significantly greater than expected extra-local gene flow. These combined results may suggest that some regions were subject to more or less gene flow from outside sources not included in this analysis.

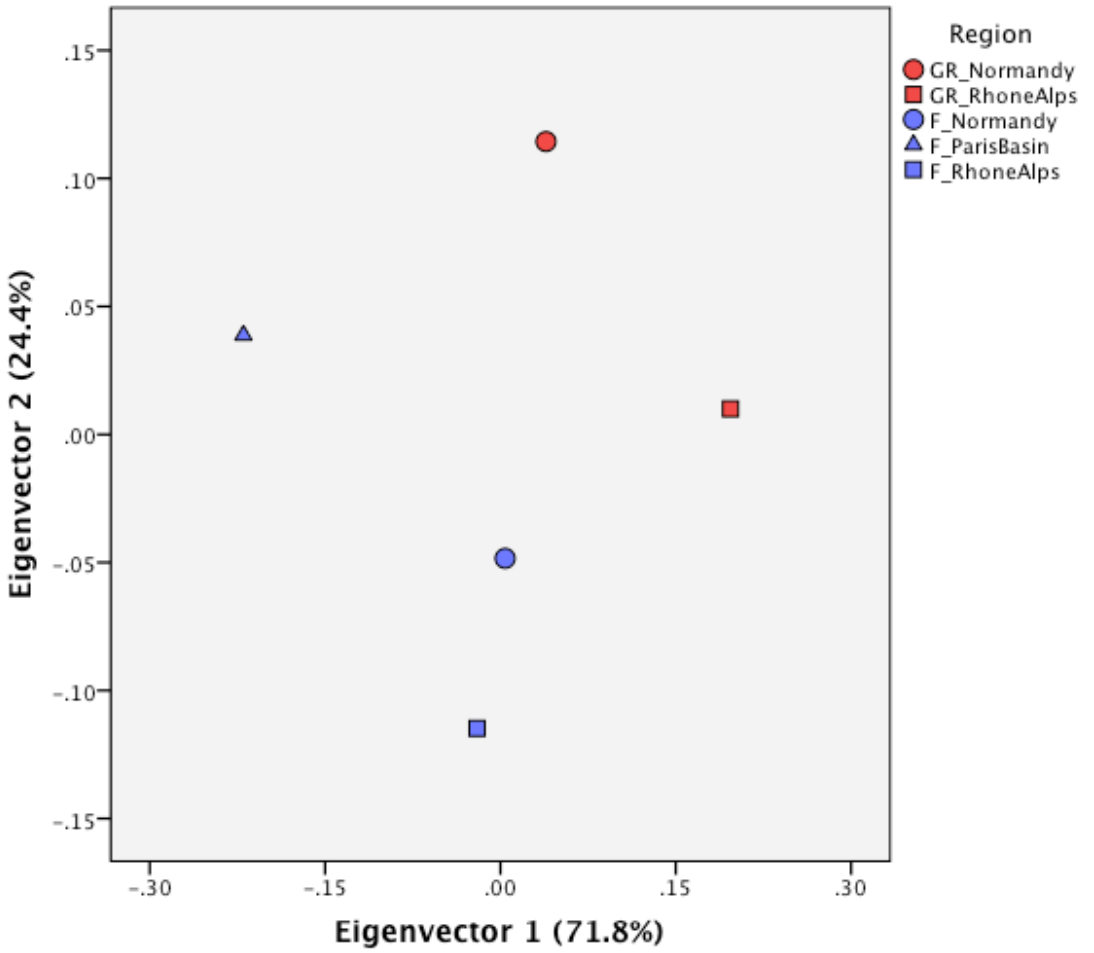

Figure 84. Scatterplot of PCO 1 vs. PCO 2 (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 4).

Table 83

Biological Distance (d^2) Matrix (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 4).

	(GR)_Rhône	(GR)_Norm	(F)_Norm	(F)_ParisB	(F)_Rhône
(GR)_Rhône-Alps	-	0.029	-	-	-
(GR)_Normandy	0.028	-	-	-	-
(F)_Normandy	0.045	0.028*	-	0.056	0.010
(F)_ParisBasin	0.174**	0.067*	0.062**	-	0.042
(F)_Rhône-Alps	0.057	0.057	0.011	0.059	-

Notes: Lower matrix represents biological distances regardless of time period; upper matrix represents biological distances only for contemporaneous regions. $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 84

Estimates of Inter-Regional Heterogeneity and Average Within-Region Phenotypic Variance (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 4).

Period	F_{ST}	Average Within-Region Phenotypic Variance
Gallo-Roman	0.005	0.991
Frankish	0.010	0.965

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 85

Z-Test Results (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 4).

Change in F_{ST}	Z
Gallo-Roman to Frankish (GR-F)	-0.577

Notes: $^{**}p \leq 0.05$, $^{*}p \leq 0.10$.

Table 86

Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 4).

Region and Time Period	Residual
Gallo-Roman:	
Rhône-Alps	0.020
Normandy	-0.050*
Frankish:	
Normandy	0.024
ParisBasin	-0.075**
Rhône-Alps	0.082**

Notes: $^{**}\ p \leq 0.05$, $^{*}\ p \leq 0.10$.

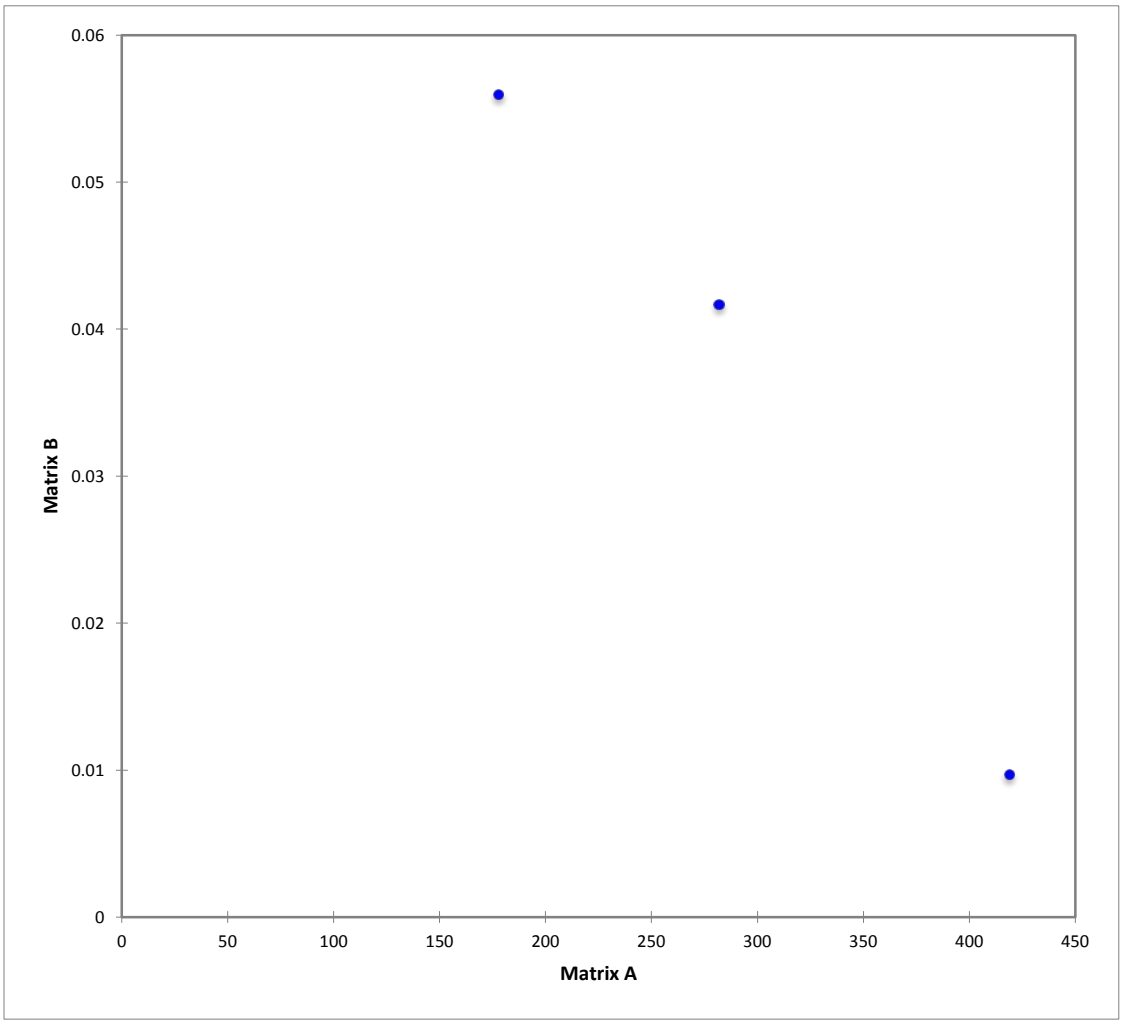

Figure 85. Scatterplot of the Mantel Test (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 4).

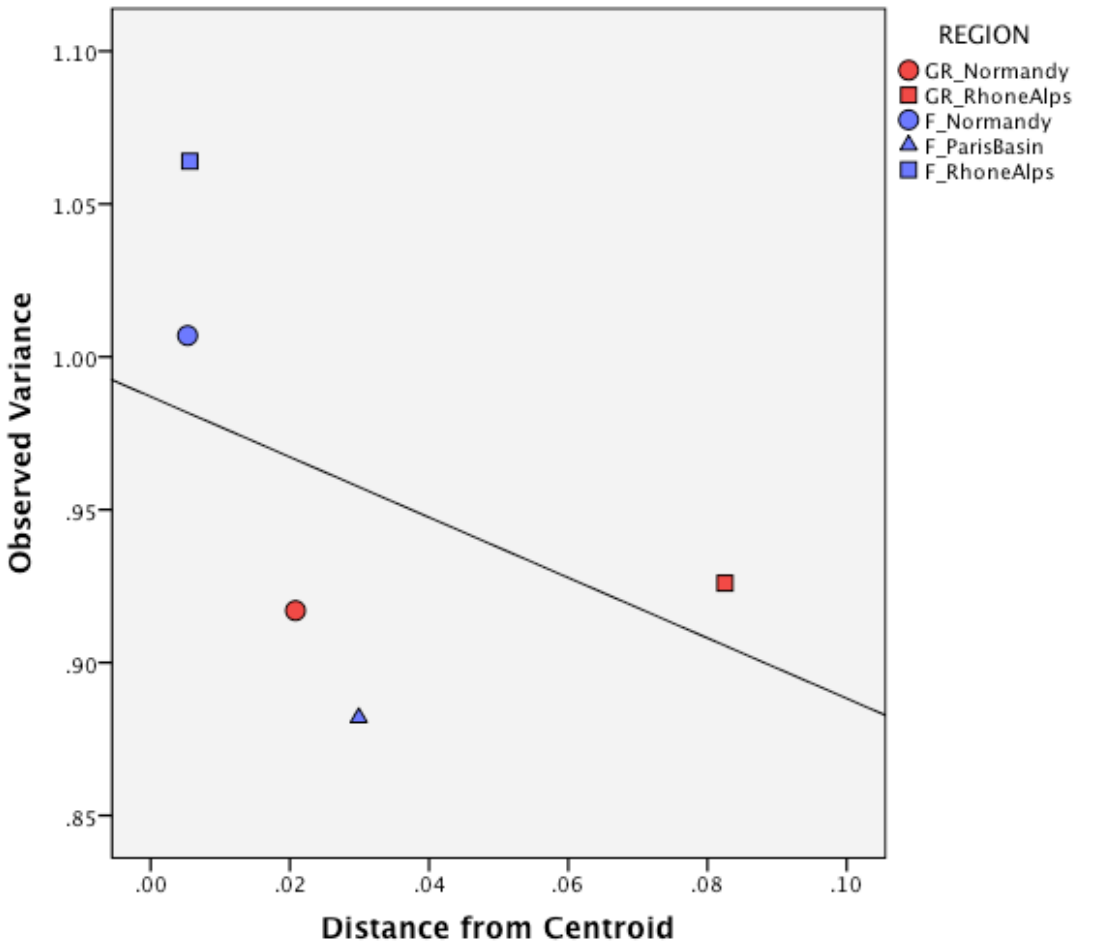

Figure 86. Scatterplot of Relethford-Blangero Residuals (Craniometric Analysis: Diachronic 2, Regional-Level, Demographic Scenario 4).

12.2.5 Review

Even using gross divisions of time periods, the scatterplots of the principal coordinates reveal a clear shift in points over time. Not only do points representing the Normandy Region appear to shift more negatively along each axis from the Gallo-Roman to Frankish Periods, but points from the Rhône-Alps Region also shifts negatively along both axes. Since most of the variation in the R-matrix can be explained by the first two eigenvectors, this temporal shift is likely an accurate reflection of an underlying pattern among the regions. This diachronic change is similar to results using more refined chronological, and it is also similar to results obtained in the diachronic odontometric analysis.

Despite the large visual disparity evident between regions in the Gallo-Roman Period and their counterparts in the Frankish Period, the biological distances are overwhelmingly insignificant. In other words, a region like Normandy is largely not significantly different from itself over time, as indicated by the results depicted in the lower halves of the Mahalanobis d^2 matrices. It is only when $\alpha = 0.10$ and the parameters are set to relative population sizes and $h^2 = 0.55$ (i.e., demographic scenario 4) that the biological distance between the Gallo-Roman and Frankish Periods of the Normandy Region is significant. A consideration of only those regions that are contemporaneous also yields no significant biological distances (upper d^2 matrices). These results would suggest that regions are remarkably similar to each other within particular time periods and over the course of time.

Interestingly, despite the lack of significant biological distances, all of the Mantel Test results were statistically significant. These findings would appear to confirm a

correlation between biological and geographic distances, at least for the Frankish Period. However, it is unclear to what effect small sample size (n=3) has on this correlation. Similarly, it is uncertain how these results fit with the evidence for gene flow between contemporaneous regions or for gene flow between regions over time.

Estimates of inter-regional heterogeneity for individual time periods were not statistically significant. Nor were the changes in F_{ST} over time. In fact, all estimates were very low, showing a weak increase from the Gallo-Roman to Frankish Periods. Regardless, the consistently low F_{ST} suggest that inter-regional gene flow was high. Even average within-region phenotypic variation was relatively constant over time, which indicates that the biological diversity of communities with regions stayed consistent from the Gallo-Roman to Frankish Periods.

Finally, the Relethford-Blangero residuals yield no significant results for any region from the Gallo-Roman Period. Only the Frankish Period of the Rhône-Alps Region has statistically significant residuals for all demographic scenarios under consideration. In fact, it always exhibits significant positive residuals, indicating that it was the recipient of greater than expected extra-local gene flow. Interestingly, when considering relative population sizes as a parameter of the R-matrix analysis (i.e., demographic scenarios 3 and 4), the Frankish Period of the Paris Basin has a significantly less than expected extra-local gene flow. This result is likely synonymous with the negative residuals for the Paris Basin Region that were obtained when using more refined chronological divisions (for example, see Table 70). It may also reflect the same aspect of the Paris Basin Region that was noted in the diachronic analysis of the odontometric dataset (for example, see Table 44).

12.3.0 SUMMARY

This chapter introduced the results for the diachronic analysis of the craniometric dataset. Regional samples were categorized according to their associated time periods, which extended from the Gallo-Roman to the Carolingian Period. Unfortunately, craniometric data for some regions could not be dated more firmly than the Frankish Period. Consequently, two forms of the diachronic analysis were undertaken. The first considered changes over time using the following time periods: 1) Gallo-Roman; 2) Merovingian; 3) Carolingian; and 4) "Frankish". The latter chronological grouping encompasses both the Merovingian and Carolingian Periods and reflects a number of regions for which a more specific data could not be ascertained. However, given the possibility that holistic diachronic changes could be missed, a second form of diachronic analysis used the following two generalized time periods: 1) Gallo-Roman; and 2) Frankish.

Both forms of the diachronic analyses resulted in two eigenvectors that explained most of the variation inherent in the R-matrices. The scatterplots for both also showed similar patterns of diachronic changes. Specifically, there is a visible temporal shift for regions over time. Regions in the Gallo-Roman Period are quite distinct from each other. Yet, in the subsequent periods, whether Merovingian/Carolingian or Frankish, regions group more closely together. This pattern parallels results from the diachronic odontometric analysis, which also showed regions changing from more dispersed to more clustered, at least for the more conservative demographic scenarios. A slight difference, however, is that the synonymous odontometric analysis suggests that groups became

more diverse from the Gallo-Roman to Merovingian Periods before reversing from the Merovingian to Carolingian Periods.

The Mahalanobis d^2 matrices between each dating scheme of the diachronic craniometric analysis are also quite similar. Most regions having representation in multiple time periods are not significantly different from themselves when examined diachronically. This result is also true for the diachronic odontometric analysis. However, the Normandy Region does exhibit a significant change that occurs during the overall change from the Gallo-Roman to Carolingian/Frankish Period. Interestingly, the prospect of a biological change occurring during the Carolingian Period has been previously suggested for the Paris Basin Region too (see Chapter 10).

For regions that are contemporaneous, both forms of the analysis (specific and generalized chronological groupings) yield insignificant biological distances. These results would suggest that regions are remarkably similar to each other within particular time periods and over the course of time. These results contrast to those obtained in the diachronic odontometric analysis for which the Paris Basin Region during the Merovingian Period is significantly different from all other regions from the same time period. It is possible that the smaller sample of available regions for the craniometric analyses in comparison to the odontometric analysis (n=3 vs. n=4) could account for some of the apparent inter-regional homogeneity of the Merovingian/Frankish Period assessed in the diachronic craniometric analysis. Though differences in regional sample sizes is not likely to explain all divergences in the results between the craniometric and odontometric datasets.

The issue of sample sizes for the Merovingian/Frankish Period may also account for some of the positive Mantel Tests. Indeed, both diachronic analyses of the craniometric data yielded statistically significant results for isolation-by-distance. These results would suggest that any differences found for biological distances between regions in the Merovingian/Frankish Period could be due to geographic distance. However, no significant biological distances were found for these diachronic analyses. Furthermore, these significant Mantel Test results contrast with the non-significant results that were observed for the odontometric diachronic analysis.

Large differences in patterns of F_{ST} are also present between the odontometric and craniometric analyses. While both craniometric diachronic analyses resulted in extremely low, insignificant, and chronologically consistent estimates of inter-regional heterogeneity for different time periods, the opposite was found for the odontometric data. For the latter analysis, not only does F_{ST} increase steadily from the Gallo-Roman to Carolingian Periods in the odontometric analysis, the actual changes in F_{ST} from the Merovingian to Carolingian Periods and from the Gallo-Roman to Carolingian Periods are statistically significant. Interestingly, average within-region phenotypic variance also differs for each analysis. For the first craniometric diachronic analysis, average within-region phenotypic variance increases from the Gallo-Roman to Merovingian Periods. For the craniometric diachronic analysis that only uses two time periods (Gallo-Roman, Frankish), average within-region phenotypic variance remains relatively stable over time. For the odontometric diachronic analysis, average within-region phenotypic variance decreases from the Gallo-Roman to Carolingian Periods. It is possible that the lack of equivalent regional sample sizes for each analysis could account for some of these

differences, especially since the Carolingian Period has fewer regions representing it in the craniometric analyses than the Gallo-Roman and Merovingian Periods.

Relethford-Blangero residuals provide an estimation of the amount of gene flow into specific regions from sources not included in the analysis. For the two diachronic craniometric analyses, results somewhat contradict each other. In the first craniometric analysis, nearly all regions have either significantly negative or positive residuals. In fact, all regions from the Gallo-Roman and Merovingian Periods exhibit significantly less than expected extra-local gene flow. Only those regions from the "Frankish" Period (Normandy, Rhône-Alps) have consistently and significantly greater than expected extra-local gene flow. The second diachronic analysis yields a significantly positive residual only for the Frankish Period of the Rhône-Alps. It too exhibits significantly greater than expected extra-local gene flow, which likely reflects the presence of the same region (Rhône-Alps) in both analyses. However, it remains unclear why these analyses would exhibit differences in significant residuals for regions of the Gallo-Roman Period. The odontometric analysis, in contrast, shows mixed results. The Normandy Region almost always exhibits significantly less than expected extra-local gene flow, regardless of time period. And the Midi-Pyrénées Region almost always has significantly greater than expected extra-local gene flow, regardless of time period. Interestingly, both the odontometric analysis and the craniometric analysis using two generalized time periods (Gallo-Roman, Frankish) show significantly negative residuals for the Paris Basin Region in the Carolingian and Frankish Periods, respectively. This combined result suggests that some regions experienced a change in population structure during the Carolingian or (possibly later) Frankish Period.

CHAPTER 13

DISCUSSION

13.0.0 INTRODUCTION

In this study, I examined the historical, cultural, and genetic backgrounds related to possible Frankish ethnogenesis in an attempt to better understand the process and to evaluate how population structure changes at the turn of Late Antiquity. The case study of Frankish ethnogenesis is ideal, not only because of the potential afforded by ethnohistoric documents, but also for evaluating the utility of particular ethnogenetic models. Similarly, the rich biological record presents an unparalleled opportunity to complement existing historical and archaeological data and to explore the interstices of population movement, mate choice, and changing conceptions of group identity. By applying a bioarchaeological approach, I hoped to avoid a facile and descriptive study and to encourage one that would move beyond mere description.

In this final chapter I provide a summary of the results generated from both the odontometric and craniometric analyses. These results are subsequently compared to the generalized expectations presented in Chapter 6 and interpreted using the ethnogenetic model presented by Hickerson (1996). However, alternatives and other observed patterns are also discussed, since the applied ethnogenetic model is merely employed as a starting point for further research. The ultimate goal is to explore the possible intersectionality of these biological data with other data from this time period, to shed light on the transformations from the Roman to pre-European world, and to highlight the wider utility

of biological data to questions that interest historians and archaeologists of Late Antiquity and the Early Middle Ages.

13.1.0 RESULTS OVERVIEW

13.1.1 Odontometric Analysis: Synchronic

- The sites from within the Paris Basin Region are different from those in other regions. Similarly, the Paris Basin as a region is quite distinct from other regions.
- A latitudinal gradient may be structuring some of the differences between sites and regions.
- Many of the sites from the Normandy Region are significantly different from other sites. However, this result is not true on a regional-level.
- Tests for isolation-by-distance (Mantel Tests) were significant on the site-level, but not the regional-level. Sampling issues at the site-level likely account for the positive result, especially given the negative result at the regional-level.
- Estimates for heterogeneity (F_{ST}), both at the site- and regional-level, are significantly different from zero. These results suggest that communities were highly diverse, possibly due to stochastic effects (i.e., genetic drift) or due to a lack of gene flow between sites/regions.
- Lack of significant biological distances (d^2) between sites from within the same region suggest a certain degree of intra-regional homogeneity.

- Extra-local gene flow was not uniform across sites and regions. The Normandy Region almost always has significantly negative Relethford-Blangero residuals, while the Rhône-Alps Region has significantly positive.
- The Paris Basin Region mostly lacks significantly positive Relethford-Blangero residuals, implying that differential gene flow from extra-local sources cannot account for its distinction from other regions.

13.1.2 Odontometric Analysis: Diachronic

- The Paris Basin Region is distinct from all other regions over time.
- The latitudinal gradient among the regions is not as evident.
- There is an apparent diachronic shift from the Gallo-Roman to Carolingian Periods. Specifically, from the Gallo-Roman to Merovingian Periods, regions become more distinct from each other; this pattern reverses from the Merovingian to Carolingian Periods.
- Biological distances (d^2) show that regions were homogeneous when comparing the same region over time. This implies a degree of biological continuity within regions over time.
- Contemporary regions from the Gallo-Roman Period are not significantly different (d^2) from each other; neither are contemporary regions from the Carolingian Period. A lack of differentiation may be due to small regional sample sizes.
- The Paris Basin Region of the Merovingian Period is significantly different (d^2) from its contemporaries.

- Isolation-by-distance (Mantel Test) cannot account for the differences in biological distances.
- Estimates of inter-regional heterogeneity (F_{ST}) increase from the Gallo-Roman to Merovingian Period, and again from the Merovingian to Carolingian Period. These results suggest that gene flow between regions decreased over time. Other possibilities include decreases in effective population size or unequal distributions of extra-local gene flow.
- The greatest effect on inter-regional heterogeneity (F_{ST}) may stem from events in the Carolingian Period.
- Average intra-regional phenotypic variation decreased over time (i.e., from Gallo-Roman to Carolingian Periods), suggesting increasing homogeneity within individual regions over time.
- The Normandy Region had significantly less than expected extra-local gene flow (Relethford-Blangero residuals) in all time periods. The Paris Basin Region exhibited mixed results for significant residuals.

13.1.3 Craniometric Analysis: Synchronic

- The Paris Basin Region appears to be somewhat distinct from remaining regions, as based on principal coordinates of the relationship matrix. However, it is not significantly different based on tests of the Mahalanobis d^2 matrix.
- There are no consistent significant biological differences between regions.
- There is a possible latitudinal gradient.
- Results of the Mantels Test were all insignificant.

- Estimates of inter-regional heterogeneity (F_{ST}) are insignificant. This may suggest that gene flow between regions was elevated.
- The Rhône-Alps Region was subject to significant amounts of extra-local gene flow (Relethford-Blangero residuals).
- Neither the Normandy Region nor the Paris Basin Region had significant Relethford-Blangero residuals.

13.1.4 Craniometric Analysis: Diachronic

- There is a temporal shift from the Gallo-Roman to Frankish Period, wherein regions appear to group more closely to each other during the Frankish Period than during the Gallo-Roman Period (Principal Coordinates).
- Regions exhibit intra-homogeneity over time (d^2), which implies a degree of biological continuity. Interestingly, though, the Normandy Region does show a significant change from the Gallo-Roman to Frankish Period.
- Contemporary regions are not biologically distinct from each other (d^2), regardless of time period.
- Mantel Tests were all positive, suggesting that isolation-by-distance could account for the biological differences previously noted. However, no significant d^2 results were found, so it is unclear what this test is reflecting.
- Estimates of inter-regional heterogeneity (F_{ST}) are low and insignificant for each time period, suggesting large amounts of inter-regional gene flow and/or large effective population size (N_e).

- Average intra-regional phenotypic variation either decreases slightly or remains steady over time.
- Results for extra-local gene flow (Relethford-Blangero residuals) are mixed. If using more chronological distinctions, all regions have significantly negative residuals in the Gallo-Roman and Merovingian Periods. Only regions from the generically dated "Frankish" period have significantly positive residuals. If using less chronological distinctions, the only significant residuals are for the Rhône-Alps and Paris Basin Regions, which are positive and negative respectively.

13.2.0 EVALUTION OF EXPECTATIONS

In Chapter 6, I laid out a number of general expectations for population structure that were based on principals of population genetics and on Hickerson's (1996) ethnogenetic life-cycles (i.e., separation, liminal, reintegration). I review these expectations below and follow each with a comparison of my results.

`*13.2.1 Expectation 1*

I expect a difference in population structure for groups in the north and south of Gaul. In many of the analyses—synchronic, diachronic, odontometric, or craniometric—there is a clear difference between sites and/or regions in the northern part of Gaul and those that are further south. For example, when examining the principal coordinates of the relationship matrices for the synchronic site-level analysis of the odontometric data, those sites comprising the Normandy and Paris Basin Regions cluster

closely to other sites from their respective regions. Similarly, principal coordinates often differentiate these two regions as a whole from other regions. This is most obvious for the Paris Basin Region, which, for the odontometric analysis, is consistently spatially and biologically (Mahalanobis d^2) distinguished from other regions regardless of synchronic or diachronic delineation. This regional characteristic of the Paris Basin is still present but less obvious when using craniometric data because the spatial distinctions are more obscure and the inter-regional biological distances—though high—are insignificant. Overall, these patterns may be evident due to a number of factors: 1) northern parts of Gaul would likely have been subject to more prolonged Frankish interaction and influence than those further away (i.e., the "Francization" of the frontier); 2) southern parts of Gaul were not absorbed, conquered, or otherwise subject to hegemonic control by the Franks until roughly the mid-sixth century; 3) the Merovingians established their capitol in the north, specifically in Paris itself.

In many cases, though, the apparent clustering between sites and differences between regions are not always corroborated by tests of their biological distances. For example, those sites comprising the Paris Basin and Normandy Regions are quite diverse. This becomes more obvious with less constrained parameters for narrow-sense heritability (h^2) for the synchronic analysis of the site-level odontometric data. Here, sites from the Paris Basin and Normandy Region begin to show significant inter-site biological differences within their respective regions. Some of this biological difference could stem from temporal conflation (discussed below). Regardless, this intriguing result suggests a degree of intra-regional variability that is lost when combining some sites together into general regional categories.

If there were a structure based on latitude, it is entirely possible that simple geographic distance could account for any differences between sites and/or regions. Tests for isolation-by-distance (Mantel Tests) were used to assess this possibility. For the synchronic analysis of the site-level odontometric data, the Mantel Test results were surprisingly significant. These results would imply that isolation-by-distance does indeed account for any observed patterns in biological distances. However, it was ascertained that these results were likely a statistical by-product of the large number of individual sites in the Normandy Region. In fact, once these sites are assessed on a regional level, any evidence of isolation-by-distance disappears. Likewise, the Mantel Tests of the synchronic analysis of the craniometric data were not significant. Thus, geographic distance by itself does not account for any patterns observed for the synchronic analyses of the odontometric and craniometric data.

The diachronic analyses are different, however. Because assessments of isolation-by-distance are only valid between contemporaneous subpopulations, the Mantel Tests were performed just on those time periods having the requisite minimum number of regions. For the odontometric and craniometric data, this means that only the Merovingian and/or Frankish Period can be assessed for correlations between geographic and biological distances. In the former, results of the Mantel Tests between contemporaneous regions of the Merovingian Period were all non-significant. In the latter, they were all significant. The apparent discrepancy between these tests for isolation-by-distance is unlikely to be due to any inherent difference between odontometric and craniometric data. Rather, the significant results obtained by the craniometric data likely stem from the smaller number of regions comprising the sample

(n=3 rather than n=4), since it is far easier to obtain a significant correlation between three data points than between four. This possibility could easily form the basis of additional study in the future. Thus, isolation-by-distance is unlikely to account for the spatial patterns, biological relationships, and estimates for inter-regional phenotypic variance.

Overall, then, these results suggest that subpopulations were structured intra-regionally and inter-regionally, as well as differently over time. Notwithstanding the large amount of structure that is observed, there is also evidence for intra-regional homogeneity over time. Specifically, for those regions/subpopulations in the odontometric analysis having representation in more than one time period (i.e., Normandy, Paris Basin, Midi-Pyrénées), all are biologically indistinct from themselves over time. For example, the Normandy Region in the Gallo-Roman Period is not statistically different from the Normandy Region in the Merovingian Period. The same is true for the Midi-Pyrénées Region in the Gallo-Roman, Merovingian, and Carolingian Periods, and for the Paris Basin Region in the Merovingian and Carolingian Periods.

These results would strongly suggest that intra-regional homogeneity is an important structuring element over time. Indeed, these results parallel existing model free skeletal morphology studies by French physical anthropologists that repeatedly note consistent cranial morphological homogeneity within regions, such as Normandy (Alduc-Le Bagousse, 1980, Buchet and Torre, 1981; Alduc-Le Bagousse, 1983; Pilet et al., 1990) and the Paris Basin (Auboire, 1988). Clearly, evidence for population continuity is an important factor, especially as it relates to Frankish ethnogenesis. **As it relates to the initial expectation, then, there are indeed differences in population between regions**

in the north and those in the south of Gaul. More importantly, though, is 1) evidence for differences in population structure over time; and 2) evidence for population continuity over time. In other words, the basic genetic character of each region was stable over time, despite changing patterns of interaction during the first millennium AD.

13.2.2 Expectation 2

I expect that inter- and intra-group phenotypic variation to be high in the Gallo-Roman Period. Results are mixed, depending on which dataset is used. Estimates for regional heterogeneity (F_{ST}) using odontometric data ranged from 0.036 to 0.085 depending on the demographic scenario. These results are similar to other biodistance studies indicating population subdivisions (see Table 87). However, estimates for regional heterogeneity using craniometric data ranged from 0.001 to 0.007, which are more consistent with an inclusive regional mating network (i.e., gene flow between groups) (see Wright, 1951). Analysis of both datasets was based on two subpopulations, one of which (Normandy Region) was the same between each analysis. Thus, a difference in the number of units being analyzed (in this case, the number of regions) is unlikely to be a contributing factor. The second subpopulation used in each analysis, however, was different between the two datasets. For the odontometric analysis, the Midi-Pyrénées Region was used as the second subpopulation; for the craniometric analysis, the Rhône-Alps Region was used. It is possible that the extreme differences in estimates for regional heterogeneity between the odontometric and craniometric datasets reflect inherent differences between these two regions. However, synchronic analysis of

these two regions using odontometric data often shows them clustering together and lacking significant between-region biological distances. No craniometric data were available for the Midi-Pyrénées Region. Consequently, this apparent disparity in results is more likely caused by measurement error and the greater sensitivity of cranial shape and size to ecological and cultural factors (Boas, 1912; Sparks and Jantz, 2002; Gravelee et al., 2003; but see Relethford, 2004; von Cramon-Taubadel, 2014). In contrast, the developmental system integrating tooth formation, shape, and size in humans are subject to greater influence by canalization and developmental stability[39], as described in Chapter 8.

Much like the estimates of regional heterogeneity, results for average intra-regional phenotypic variation vary based on the dataset that is used. For the odontometric analysis, average within-region phenotypic variance ranges from 1.519 to 1.608. For the craniometric analysis, it ranges from 0.986 to 0.991. On the one hand, the former results would suggest a high amount of variation (greater than one) within the Gallo-Roman subpopulations comprising the odontometric analysis. On the other hand, the latter would suggest a lower degree of variation (less than one) within the Gallo-Roman subpopulations used in the craniometric analysis. The difference in these ranges likely stems from disparities in extra-local gene flow that the Midi-Pyrénées Region (odontometric analysis) and the Rhône-Alps Region (craniometric analysis) exhibit in their respective analyses. For the former, there is always significantly greater than expected extra-local gene flow; for the latter, the amount of extra-local gene flow either meets expectations or falls significantly below it. In contrast, the Gallo-Roman Period of

[39] For definitions and additional examples of developmental stability and canalization in humans, see Hallgrímsson et al. (2002).

the Normandy Region almost always has significantly less than expected amounts of extra-local gene flow, regardless of the dataset used. Thus, much of the average intra-regional phenotypic variation during this time period originates from the unique position held by the Midi-Pyrénées Region. It is possible, then, that people were immigrating to this region from outside the study areas used in these particular analyses. One intriguing, and historically viable, possibility is that the Midi-Pyrénées Region represents an area through which a variety of named barbarian groups and confederacies (i.e., Vandals, Visigoths) migrated or perhaps settled during the fifth century AD. Indeed, the Visigoths had settled in Roman territory as foederati in AD 418 and eventually established their capital at Toulouse, which is approximately 175 km from Granède (Midi-Pyrénées Region). **In sum, the expectation for high inter- and intra-regional phenotypic variation can be neither supported nor refuted.**

Table 87

Comparative Estimates of F_{ST}

F_{ST}	Reference
0.078	Ohio Valley (Tatarek and Sciulli, 2000)
0.055	Algonkian (Jantz and Meadows, 1995)
0.045	Iroquoian (Langdon, 1995)
0.027	Irish (Relethford and Blangero, 1990)
0.041	Ethnic Sicán (Klaus, 2008)
0.029	Pre- / Proto-historic Tewa (Schillaci and Stojanowski, 2005)
0.020	Azapa Valley and Coast (Varela and Cocilovo, 2002)
0.047	Late Chachapoya (Nystrom, 2006)

13.2.3 Expectation 3

I expect that inter-regional phenotypic variation will be lower in the Merovingian Period than in the preceding Gallo-Roman Period. Based on a model of ethnogenetic life-cycles, I expected that changing forms of group integration in the Merovingian Period would result in lower amounts inter-regional phenotypic variation than in earlier periods. However, the results are not consistent with this expectation. Both datasets show an increase in estimates of inter-regional heterogeneity (F_{ST}) from the Gallo-Roman to Merovingian Periods. Thus, for the odontometric analysis, these estimates change from a range of 0.036 to 0.085 in the Gallo-Roman Period to a range of 0.056 to 0.108 in the Merovingian Period. For the craniometric analysis, this change over time is less striking, showing a large degree of overlap. Estimates change from a range of 0.001 to 0.007 in the Gallo-Roman Period to a range of 0.003 to 0.009 in the Merovingian Period. Not surprisingly, then, the actual change over time in F_{ST} for these craniometric data is not significant. More interesting, however, is a lack of significance for the change over time in F_{ST} for the odontometric data, despite the apparently greater temporal difference.

Much like for the previous expectation, these results suggest contradictory factors impacting regional mating networks. For the larger estimates of F_{ST} generated by the odontometric analysis, the result implies a large degree of structure operating on populations at this time. In other words, inter-regional gene flow would appear to decrease over time, such that subpopulations are increasingly different from each other. Other factors, such as socially or religiously mediated beliefs on endogamy or changing demographic parameters, could also impact estimates of heterogeneity. More prosaically,

though, the absence of a Gallo-Roman sample from the Paris Basin Region could account for the perceived increase in F_{ST} in the Merovingian Period. As noted in the synchronic analysis of the odontometric data, the sites comprising the Paris Basin Region are often biologically distinct from the others. This pattern also carries over when considering the Paris Basin Region as a whole. Regardless, observation of the principal coordinates for the odontometric analysis shows a diachronic shift from the Gallo-Roman to the Merovingian Periods. In other words, regions/subpopulations become more differentiated over this time period. **Thus, the expectation for lower inter-regional phenotypic variance in the Merovingian Period relative to the Gallo-Roman Period does not appear to be supported.**

Interestingly, results for average intra-regional phenotypic variance also differ based on which dataset was analyzed. For the odontometric analysis, average within-region phenotypic variance during the Merovingian Period ranges from 1.074 to 1.141, which is a decrease relative to the Gallo-Roman Period (1.519 – 1.608). For the craniometric analysis, in contrast, average intra-regional phenotypic variance during the Merovingian Period ranges from 1.013 to 1.032, which is an increase relative to the Gallo-Roman Period (0.986 – 0.991). Some of the difference between these two analyses could stem from the absence of craniometric data for the Midi-Pyrénées Region. In other words, the fewer samples included in the analysis, especially potentially diverse ones like the Midi-Pyrénées Region, the less genetic variation that is potentially observed. Consequently, the craniometric analysis could simply show a smaller average inter-regional phenotypic variance due to a smaller sample size.

Another option to explain these divergent results could be inherent differences in the craniometric and odontometric data. As previously mentioned, the human cranium—more specifically, some regions of the cranium—is subject to greater effects of non-neutral microevolutionary mechanisms (i.e., natural selection) than the dentition (see von Cramon-Taubadel, 2014). Thus, individual regions of the cranium, such as the face, occipital, and mandible, have been shown to diverge from a neutral model of explanation. The use of data to understand population structure based on these cranial modules, then, could be misleading, referring instead to dietary or climatic adaptations.

The goals of this study were not to assess whether craniofacial data revealed an increase in diversity. However, given the limited number of facial dimensions used in the craniometrics analysis of this study (five out of 16 variables, see Table 6), it is unlikely that dietary adaptations account for the differences between the craniometric and odontometric results. This is especially true since "global patterns of modern human variation fit a largely neutral microevolutionary model of the overall shape of the human skull" (von Cramon-Taubadel, 2014: 64). A more likely explanation could stem from the visible aspect of the human cranium, making it subject to culturally specific vagaries of assortative mating. Either way, odontometrics have been shown to be more sensitive at smaller analytical scales than craniometrics (see Stojanowski and Schillaci, 2006).

13.2.4 Expectation 4

I expect that inter- and intra-regional phenotypic variation will be low in the Carolingian Period. As a validating ideology matures in Frankish Europe, and the extrinsic and intrinsic factors contributing to Late Roman and Early Frankish social

instability wane, inter-regional phenotypic variation was expected to be low. Interestingly, these results were not consistently observed. For the odontometric dataset, estimates of inter-regional heterogeneity (F_{ST}) actually increase relative to the preceding Merovingian Period, ranging from 0.121 to 0.232. These numbers are incredibly high and are more similar to heterogeneity estimates found between species. Given the comparatively small combined sample size for this time period (n=14) and high standard errors in the estimation of (F_{ST}), it is perhaps not surprising that these F_{ST} estimates were so high. Likewise, it explains the lack of statistical significance for these estimates of heterogeneity in the Carolingian Period overall.

Although these numbers are questionable, it is interesting to note that the actual change in F_{ST} over time *is* statistically significant when setting narrow-sense heritability (h^2) at 0.55. Thus, the changes in F_{ST} from the Merovingian to Carolingian Period, as well as the Gallo-Roman to Carolingian Period, are significant for two of the four demographic scenarios. These results likely stem from the effect of h^2 on F_{ST}, but it would be imprudent to dismiss them entirely. Those demographic scenarios that only use a narrow-sense heritability of 1.0 are extremely conservative. This approach, while preferred in some ways, can still obscure existing variation.

Unfortunately, the craniometric data available for the Carolingian Period only originated from one confirmed subpopulation. Consequently, an adequate analysis of the craniometric data was not possible when considering this time period alone. However, other data were available that possessed a more generalized date of “Frankish”. Although this chronological attribution could include both the Merovingian and/or Carolingian Period, it is still possible to assess patterns for the Frankish Period overall, as well as for

changes from the Gallo-Roman to Frankish Period. Thus, in contrast to the odontometric analysis, estimates of inter-regional phenotypic variance for craniometric data range from 0.003 to 0.010. These results strongly suggest a large degree of inter-regional gene flow that produces population homogeneity. Furthermore, the expectation of low inter-regional phenotypic variation generated using Hickerson's (1996) model appears to be confirmed. However, much like the odontometric analysis, the actual change in F_{ST} from the Gallo-Roman to Frankish Period is not significant, regardless of demographic scenario.

So, was inter-regional heterogeneity high or low during the Carolingian/Frankish Period? Did inter-regional gene flow occur or not during the later parts of the Frankish Period? One manner of shedding light on these contradictory results is observation of the principal coordinates for each demographic scenario of the diachronic odontometric and craniometric analyses. For example, scatterplots for the demographic scenarios 1 and 2 of the odontometric data show an apparent diachronic shift of regions/subpopulations over time. Thus, from the Gallo-Roman to the Merovingian Period, regions appear to become more differentiated from each other. From the Merovingian to the Carolingian Period, regions appear to become more similar to each other. Likewise examination of the principal coordinates for each demographic scenario of the diachronic craniometric analysis shows a clear temporal shift in which regions cluster more closely to each. **Overall, then, the Carolingian Period appears to have been characterized by a greater degree of gene flow between regions/subpopulations. In other words, inter-regional phenotypic variation did not increase during the Carolingian Period. Instead, it appears to have decreased over time.**

In addition to an expectation of low F_{ST}, intra-regional phenotypic variance was also expected to be low. This is indeed the case for both the odontometric and craniometric analyses. For the former, average within-region phenotypic variance ranged from 0.862 to 0.911, which is less than the range of averages obtained for the Merovingian Period (1.074 – 1.141) and less than the range of averages obtained for the Gallo-Roman Period (1.519 – 1.608). For the latter (using craniometric data attributed to the Frankish Period), average within-region phenotypic variance ranged from 0.965 to 0.981. These numbers, though less, are not drastically different from the range that was observed for the Gallo-Roman Period (0.986 – 0.991). They are, however, still low, which implies a certain degree of uniformity within regions/subpopulations at this time. **Thus, this overall pattern is consistent with the expectation for low intra-regional phenotypic variation during the Carolingian Period.**

13.2.5 Expectation 5

I expect that Late Roman populations experienced greater levels of extra-local gene flow than those in the Merovingian and Carolingian Periods. There is a general consensus that the Late Roman Period witnessed large amounts of population movement, best reflected in an overlapping term for this period, "The Migration Age". However, a growing number of scholars dispute the likelihood of migration and/or dispute the actual effect of particular migrating groups on indigenous Gallo-Roman populations. This question, however, can be assessed using Relethford-Blangero residuals.

For the odontometric analysis, the Midi-Pyrénées Region always has significantly greater than expected extra-local gene flow (0.583 – 0.742). In contrast, the Normandy Region always exhibits significantly less than expected extra-local gene flow during the Gallo-Roman Period (-0.460 – -0.344). For the craniometric analysis, the Normandy Region is the same, exhibiting low levels of extra-local gene flow (-0.356 – -0.267). The Rhône-Alps Region also has significantly less than expected extra-local gene flow during the Gallo-Roman Period (-0.348 – -0.262). If these regions were truly part of a larger population (i.e., breeding network) that had existed and interacted for generations, then there would be an expectation of panmixia, whereby every region/subpopulation would have the same rate of gene flow from outside sources. However, these results clearly show that this is not the case for the Gallo-Roman Period.

As previously mentioned, the Midi-Pyrénées Region is part of an area through which known groups, such as the Vandals and Visigoths, migrated or settled during the fifth century AD. Whether these migrating peoples were a/the source of the extra-local gene flow for the sample used in this analysis cannot be determined by this study. Future analysis could include skeletal samples from contemporaneous regions of putative Vandal or Visigothic settlement to test this hypothesis.

What of those regions/subpopulations during the Merovingian Period? Relethford-Blangero residuals are mixed, with most showing significant deviations from the expected amounts of extra-local gene flow. Specifically, the Normandy Region again exhibits significantly less than expected extra-local gene flow for both the odontometric and craniometric analyses (-0.398 – -0.296 and -0.372 – -0.278, respectively). The Midi-Pyrénées Region also exhibits significantly greater than expected extra-local gene flow

for the odontometric analysis (0.074 – 0.200). Likewise, the Rhône-Alps Region also has significantly positive residuals (0.168 – 0.305) for the odontometric analysis.

Interestingly, the Paris Basin Region, which appears to be so distinct on scatterplots of the principal coordinates for the relationship matrix of the odontometric analysis, only has significant residuals for demographic scenarios 2 and 4 (0.166 and 0.104, respectively). However, demographic scenarios 1 and 3 still yield positive (though non-significant) residuals (0.028 and 0.033, respectively). Thus, the overall pattern of elevated rates of extra-local gene flow based on odontometric data remains consistent for the Paris Basin Region. However, the opposite pattern was observed when using the craniometric data. In the craniometric analysis, the Paris Basin Region exhibited significantly less than expected extra-local gene flow during the Merovingian Period (-0.316 – -0.235).

The confounding patterns between the odontometric and craniometric analyses appear to be the general rule, rather than the exception, and they require an explanation that is beyond the scope of this study. Regardless, it is intriguing to note the differences between contemporaneous regions/subpopulations at this time, as they again suggest that there is degree of population structure during the Merovingian Period—one that differentiates the southern portions of Gaul from those further north. Why the Normandy Region would continue to exhibit such apparent deficits in extra-local gene flow may be due to intrinsic factors that discouraged such extra-local immigration. Other possibilities could include: 1) continuous gene flow between extra-local sources such that no differentiation is detectable; 2) recently shared common ancestor(s) between extra-local sources and those people inhabiting the Normandy Region during the Merovingian

Period; and 3) extremely high effective population size, such that any immigration from outside sources that may have occurred would have had little impact on existing allele frequencies. Even so, the concept of the "Francization" of the northeastern Roman frontiers could easily have consisted of more than hypothetical material culture.

In the Carolingian Period, the Midi-Pyrénées Region again exhibits significantly greater extra-local gene flow, as based on odontometric data (0.215 – 0.333). In contrast, the Paris Basin Region shows significantly negative residuals (-0.468– -0.350). Insufficient sampling prohibits a synonymous assessment using craniometric data. However, an assessment of the Frankish Period (i.e., combined Merovingian, Carolingian, and "Frankish" samples) using craniometric data is possible. In this analysis, the Rhône-Alps Region always has significantly positive residuals (0.082 – 0.094). The Paris Basin Region has consistently negative residuals, only two of which are statistically significant (-0.075 and -0.080). Interestingly, the Normandy Region, which overwhelmingly exhibits less than expected extra-local gene flow in all other analyses, has positive (albeit non-significant) residuals. This apparent reversal likely stems from the inclusion of a generically dated "Frankish" skeletal sample from the Normandy Region that repeatedly shows itself to be distinct biologically from other subpopulations/regions, and which exhibits *extremely* high residuals (0.680 – 0.830). In other words, the lumping of this "Frankish Period" sample with the more confidently dated Merovingian and Carolingian Period samples from the Normandy Region produces an averaging effect on residual variation, especially since those samples comprising the Merovingian and Carolingian Periods exhibit significantly less than expected extra-local gene flow.

Two conclusions can be drawn from this observation: 1) the grouping of samples into more inclusive temporal categories can obscure important aspects of population structure; and 2) the "Frankish Period" sample from the Normandy Region clearly demonstrates some unique characteristics. One intriguing possibility for this apparently irregular "Frankish Period" sample is Viking raids that occurred in the late 8th century and again in the late 9th century. Without additional study, it would be premature to assert that these results are 1) direct evidence of Scandinavian immigration; or 2) due to displacement of peoples subject to Viking raids. However, they suggest potential avenues of exploration for assessing Viking influence and migration on this particular region at the turn of the first millennium AD.

Together, these results do not support the expectation for greater amounts of extra-local gene flow during the Gallo-Roman Period than in subsequent periods. In fact, patterns of Relethford-Blangero residuals suggest that extra-local immigration better characterized the later Frankish Period/Carolingian Period than for earlier periods. These observations are not meant to imply, however, that extra-local gene flow was absent in the Gallo-Roman or early Frankish Period/Merovingian Period, or that the Carolingian Period was composed entirely of evidence for significantly greater than expected extra-local gene flow. As repeatedly shown, immigration from extra-local sources occurred on a differential basis, resulting in a mosaic of significantly negative and positive residuals in any given time period, including the Carolingian Period.

13.3.0 FRANKISH ETHNOGENESIS: A CONTESTED PROCESS

As the above discussion reveals, some of the expectations for population structure and how it changed over time from Late Antiquity through the Carolingian Period are met. Others are not. Rather than invalidating Hickerson's (1996) model of ethnogenetic life-cycles, though, I argue that these results enrich it. Ultimately, a pattern of decreasing inter- and intra-regional heterogeneity is observable during the Carolingian Period, as predicted by the extension of Hickerson's reintegration phase to population genetics, as employed in this study. What then can we infer about Frankish ethnogenesis? The following sections attempt to understand the observed results in relation to the process of ethnogenesis of the Franks. I propose that Frankish ethnogenesis, as it is understood in anthropological theory, did not truly "coalesce" until the Carolingian Period. Even then, it was still a contested process. Furthermore, I suggest that this interpretation reconciles some of the criticisms related to the subject of ethnogenesis in the Late Antique and Early Medieval world of Western Europe (see Chapter 1). Indeed, rather than being incompatible with recent criticisms, the interpretation presented here becomes one aspect of a larger discourse on identity and transformations in identity.

13.3.1 Contested Ethnogenesis during the Frankish Period

A growing number of scholars have noted important changes in discourse that occurred during the Carolingian Period (Nelson, 2008; Reimitz, 2008; Broome, 2014). The first of these are changes in the narrative of Frankish history. As Broome (2014: 9) shows, early Carolingian sources begin their narrative in the early 8th century with an emphasis on Charles Martel and his wars against peripheral, non-Frankish peoples. He

suggests that this served two purposes: 1) it paid a kind of political homage to Frankish provinces, especially Austrasia that shared a border at the eastern Rhineland frontier; and 2) it referenced common enemies of the Franks against whom they could unite (*ibid*: 8, 83). Broome also suggests that this allowed Carolingian authors to imagine a group identity that emerged from the actions of its rulers, like Charles Martel and his heirs (*ibid*: 37, 83-84). Most importantly, however, was a de-emphasis on internal politics within the Frankish heartland:

> [T]he Frankish sub-groups have all but disappeared in these accounts; there are very few references to Austrasians, Neustrians, and Burgundians… Instead, we primarily hear only of the Franks, unqualified by more specific terms… What we have here, then, is an emphasis on Frankish unity to a far greater extreme than the desire for consensus found in the Merovingian texts. Rather than highlighting the interplay between the three Frankish kingdoms [i.e., the teilreichen], the early Carolingian authors present the Franks as a single entity, and so the Neustrians, Austrasians and Burgundians fall completely out of site. (*ibid*: 83)

Hand in hand with this increasing focus on the Frankish peripheries came a greater emphasis on religious identity. Thus, "the late eight century saw the Carolingians constantly depicted as doing God's work and as undertaking wars and emerging victorious with his aid: such language had rarely, if ever been used in the Merovingian Period" (*ibid*: 10). Furthermore, Broome suggests that ethnic identity became more complex during the Carolingian Period because the relationship between the Franks and those areas along the frontiers were progressively being defined "in terms of loyalty to the Carolingian dynasty and in terms of Christianity" (*ibid*: 29, 86-87). Thus, as "wars undertaken by the Carolingian were expansionist and aimed at the conquest of peripheral peoples, it made sense to overlook Frankishness in favour of a less exclusive

characteristic like shared Christianity" (*ibid*: 87). He suggests that this was a kind of 'discourse of otherness', since enemies were often associated with paganism, rebellion, and disloyalty (*ibid*: 29, 87, 97-150). Indeed, the apparent importance of frontier zones during the Carolingian Period mirrors much of the theory of ethnic groups developed by Frederik Barth (1969). More specifically, Barth proposed that frontiers or boundaries functioned as structuring agents that contribute to the dichotomization of group members and non-members (e.g., "us" and "them").

A clearer picture of Frankish identity, then, is being painted during the Carolingian Period. This coalescence of identity seems to parallel the decrease in inter- and intra-regional heterogeneity that was observed in this study. Perhaps the discourse on Frankish identity during the Carolingian Period had an actual population-level effect on group behavior and mate choice?

To say that ethnogenesis occurred under the Carolingians as if it were a discrete event ignores the process through which it materialized and risks exaggerating state or elite sponsored rhetoric to the exclusion of other social dynamics. For example, during the Merovingian Period pre-existing divisions in the Frankish kingdom formed the main *Teilreichen*: Neustria, Austrasia, and Burgundy. These regionally-based dynamics are apparent by the clear differences in population structure among and between regions in both the Gallo-Roman and Merovingian Periods observed in this study. Even the evidence for biological continuity within some regions implies a degree of persistence in group identity between Gallo-Roman and Frankish peoples. Tensions in these divisions and how people identified themselves in relationship to them – regardless of how centripetal the politics of the royal court were during the Merovingian Period – meant

that “authors writing about the *regnum* had to negotiate what these identities meant in terms of the cohesion of the Frankish community” (*ibid*: 29, 43). They did this in several ways: 1) by emphasizing a common ancestry and shared origin story (*ibid*: 37-43); and 2) by attempting to balance regional identities within a framework of an overarching ideal of Frankish unity (*ibid*: 45-81).

Similar frictions between regional identities and an emerging Frankish identity also existed during the Carolingian Period, as noted by a regionally based population structure. In other words, regardless of the increase in inter- and intra-regional homogeneity during the Carolingian Period, there was still a large amount of inter-regional differentiation and intra-regional biological continuity over time. These results would suggest that not all people inhabiting the Frankish kingdom shared an equal sense of group identity as perhaps perpetuated by the Carolingian dynasty.

Regardless, there remain clear changes in population structure that parallel modifications in group identity discourse from Late Antiquity through the Early Middle Ages. These trends are highly suggestive, and when combined with established historical and archaeological methods, strongly suggest that Frankish identity coalesced during the Carolingian Period. Future research might expand from this foundation, not just by incorporating more biological data toward questions of relevance to this time period, but also by exploring 1) the interactions between emerging ethnic group identities and other social identities; 2) the role of other institutions in ethnogenetic processes (i.e., religious institutions); and 3) the dynamic between populations in liminal, contested, or frontier zones.

13.3.2 Ethnogenesis: Liberation from "Tyranny"

Much of the criticism aimed at research on ethnicity and ethnogenesis during Late Antiquity and Early Middle Ages claims that there is a lack of historiographical and literary awareness, especially as it relates to the impact of *Germanische Altertumskunde* on studies of the first millennium AD. However, this study reveals a number of important conclusions. First, it shows that historically laden concepts of "Germanic" culture and/or groups are not required to explore issues of group identity. Nor do we have to conceive of ethnohistoric texts as fossilized remains of ancient concepts. Similarly, it is possible to engage the theoretical literature on ethnogenesis without 1) reifying primordial notions of group identity that some scholars insist are lurking in current discussions, or 2) relying on concepts of migration or "tradition" to explain the formation of ethnic groups. Finally, and at no point, is ethnic self-identification presented as *the* explanatory model that governs Late Antiquity or the Early Middle Ages. Rather, emerging ethnogenesis during the Carolingian Period may be better seen as an outcome (though not pre-determined in an evolutionary or tautological sense) of a variety of changing social and biological processes during the Gallo-Roman and Merovingian Periods.

REFERENCES

Achilli A, Rengo C, Magri C, Battaglia V, Olivieri A, Scozzari R, Cruciani, Zeviani M, Briem E, Carelli V, Moral P, Dogoujon JM, Roostalu U, Loogvali EL, Kivisild T, Bandelt HJ, Richards M, Villems R, Santachiara-Benerecetti AS, Semino O, Torroni A. 2004. The molecular dissection of mtDNA haplogroup H confirms that the Franco-Cantabrian glacial refuge was a major source for the European gene pool. Am J Hum Genet 75:910-918.

Adams SM, Bosch E, Balaresque PL, Ballereau SJ, Lee AC, Arroyo E, López-Parra AM, Aler M, Grifo MSG, Brion M, Carracedo A, Lavinha J, Martínez-Jarreta B, Quintana-Murci L, Picornell A, Ramon M, Skorecki K, Behar DM, Calafell F, Jobling MA. 2008. The genetic legacy of religious diversity and intolerance: paternal lineages of Christians, Jews, and Muslims in the Iberian Peninsula. Am J Hum Gen 83:725-736.

Airlie S. 2005. Charlemagne and the aristocracy: captains and kings. In: Story J, editor. Charlemagne: Empire and society. Manchester: Manchester University Press. p 90-102.

Agarwal SC, Glencross BA. Social bioarchaeology. West Sussex: Wiley-Blackwell.

Albers PC. 1996. Changing patterns of ethnicity in the northeastern Plains. In: Hill JD, editor. History, power, and identity. Ethnogenesis in the Americas, 1492-1992. Iowa City: University of Iowa Press. p 90-118.

Alconini S. 2004. The southeastern Inka frontier against the Chiriguanos: structure and dynamics of the Inka imperial borderlands. Latin Am Antiq 15:389-418.

Alduc-Le Bagousse A. 1980. Contribution à l'étude des populations médiévales de Basse-Normandie: anthropologie du cimetière mérovingien de Verson (Calvados). PhD. Université de Caen.

Alduce-Le Bagousse A. 1983. État actuel des recherches anthropologiques en Normandie: l'époque gallo-romaine et médiévale. Bull Mém Soc Anthropol Paris 10:169-175.

Alduc-Le Bagousse A. 1985. Étude anthropologique des sépultures de la rue Eugénie. Annales de Normandie 35:183-196.

Alt KW, Pichler SL. 1998. Artificial modifications of human teeth. Vienna: Springer.

Alt KW, Vach W. 1992. Non-spatial analysis of "genetic kinship" in skeletal remains. In: Schader M, editor. Analysis and modeling data and knowledge. Berlin: Springer-Verlag. p 247-256.

Alt KW, Vach W. 1998. Kinship studies in skeletal remains—Concepts and examples. In: Alt KW, Rösing FW, Teschler-Nicola M, editors. Dental anthropology: Fundamentals, limits, and prospects. Wien: Spring. p 537-554.

Alvarez L, Jaffe K. 2004. Narcissism guides mate selection: humans mate assortatively, as revealed by facial resemblance, following an algorithm of self seeking life. Evol Psych 2:177-194.

Alvesalo L, Tigerstedt PMA. 1974. Heritabilities of human tooth dimensions. Hereditas 77:311-318.

Ambrosio B, Dugoujon JM, Hernández C, De La Fuente D, González-Martín A, Fortes-Lima CA, Novelletto A, Rodríguez JN, Calderón R. 2010. The Andalusian population from Huelva reveals a high diversification of Y-DNA paternal lineages from haplogroup E: identifying human male movements within the Mediterranean space. Annals Hum Biol 37:86-107.

Ammerman AJ, Cavalli-Sforza LL. 1984. Neolithic transition and the genetics of populations in Europe. Princeton: Princeton University Press.

Armelagos GJ, Van Gerven DP. 2003. A century of skeletal biology and paleopathology: Contrasts, contradictions, and conflicts. Am Anthropol 105:51–62.

Armstrong G, Wood I. 2000. Christianizing peoples and converting individuals. Turnhout: Brepols.

Auboire G. 1980. Les squelettes mérovingiens d'Épône (Yvelines, France). Bull Mém Soc Anthropol Paris 7:319-325.

Auboire G. 1981. L'évolution de la morphologie humaine dans le basin Parisien du paléolithique au Moyen-Âge. Ph.D., Université de Paris 7.

Auboire G. 1982. Les découvertes archéologiques de la région parisienne étudiées d'un point de vu anthropologique. Bull Mém Soc Anthropol Paris 9:57-74.

Auboire G. 1988. Étude comparative de populations gallo-romaines et mérovingiennes en Île-de-France et Normandie. Rév Archéol Ouest 5:109-120.

Aubry BS. 2009. Population structure and interregional interaction in pre-Hispanic Mesoamerica: a biodistance study. Ph.D. Dissertation, The Ohio State University.

Austin D. 1990. The 'proper study' of medieval archaeology. In: Austin D, Alcock L, editors. From the Baltic to the Black Sea: studies in medieval archaeology. London: Unwin Hyman.

Bachrach B. 2001 Early Carolingian warfare: Prelude to empire. Philadelphia: University of Pennsylvania Press.

Bachrach B. 2013. Charlemagne's early campaigns (768-777): a diplomatic and military analysis. London: Brill.

Ballantyne KN, Ralf A, Aboukhalid R, Achakzai NM, Anjia MJ, Ayub Q, Balažic J, Ballantyne J, Ballard DJ, Berger B, Bobillo C, Bouabdellah M, Burri H, Capal T, Caratti S, Cárdenas J, Cartault F, Carvalho EF, Carvalho M, Cheng B, Coble MD, Comas D, Corach D, D'Amato ME, Davison S, de Knijff P, De Ungria MCA, Decorte R, Dobosz T, Dupuy BM, Elmrghni S, Gliwiński M, Gomes SC, Grol L, Haas C, Hanson E, Henke J, Henke L, Herrera-Rodríguez F, Hill CR, Holmlund G, Honda K, Immel U-D, Inokuchi S, Jobling MA, Kaddura M, Kim JS, Kim SH, Kim W, King TE, Klausriegler E, Kling D, Kovačević L, Kovatsi L, Krajewski P, Kravchenko S, Larumuseau MHD, Lee EY, Lessig R, Livshits LA, Marjanović D, Minarik M, Mizuno N, Moreira H, Morling N, Mukherjee M, Munier P, Nagaraju J, Neuhuber F, Nie S, Nilasitsataporn P, Nisi T, Oh HH, Olofsson J, Onofri V, Palo JU, Pamjav H, Parson W, Petlach M, Phillips C, Ploski R, Prasad SPR, Primorac D, Purnomo GA, Purps J, Rangel-Villalobos H, Rębała K, Rerkamnuaychoke B, Gonzalez DR, Robino C, Roewer L, Rosa A, Sajantila L, Sala A, Salvador JM, Sans P, Schmitt C, Sharma AK, Silva DA, Shin K-J, Sijen T, Sirker M, Siváková D, Škaro V, Solano-Matamoros C, Souto L, Stenzl V, Sudoyo H, Syndercombe-Court D, Tagliabracci A, Taylor D, Tillmar A, Tsybovsky IS, Tyler-Smith C, van der Gaag KJ, Vanek D, Völgyi A, Ward D, Willemse P, Yap EPH, Yon RYY, Pajnič Iz, Kayser M. 2014. Toward male individualization with rapid mutating Y-chromosomall short tandem repeats. Hum Mutation 35:1021-1032.

Bandy MS. 2004. Fissioning, scalar stress, and social evolution in early village societies. Am Anthropol 106:322-333.

Barth F. 1969. Ethnic groups and boundaries: the social organization of culture difference. Boston: Little Brown.

Bateson W. Materials for the study of variation: treated with special regard to discontinuity in the origin of species. London: Macmillan.

Baudouin M. 1912. Description anatomique des neuf crânes de la station gallo-romain des Chaumes, en Saint-Hilaire-de-Riew (Vendée). Bull Mém Soc Anthropol 3:321-346.

Bawden G. 2005. Ethnogenesis at Galindo, Peru. In: Reycraft R, editor. Us and them: archaeology and ethnicity in the Andes. Los Angeles: Cotsen Institute of Archaeology, University of California. p 12-33.

Bawden G, Reycraft R. 2009. Exploration of punctuated equilibrium and culture change in the archaeology of Andean ethnogenesis. In: Marcus J, Williams PR, editors. Andean civilization: a tribute to Michael E. Moseley. Los Angeles: Cotsen Institute of Archaeology, University of California. p 195-210.

Beck H. 2004. The concept of Germanic antiquity. In: Murdoch B, Read M, editors. Early Germanic literature and culture. Rochester: Camden House. p 25-38.

Bell A. 2005. White ethnogenesis and gradual capitalism: perspectives from colonial archaeological sites in the Chesapeake. Am Anthropol 107:446-460.

Bentley GC. 1987. Ethnicity and practice. Comp Studies Soc Hist 29: 24-55.

Berger SL, Kouzarides T, Shiekhattar R, Shilatifard A. 2009. An operational definition of epigenetics. Genes Develop 23:781-783.

Betti L, Balloux F, Hanihara T, Manica A. 2010. The relative role of drift and selection in shaping the human skull. Am J Phys Anthropol 141:76-82.

Billy G. 1970. Contribution à l'étude du peuplement mérovingien en Poitou. Bull Mém Soc Anthropol Paris 6:243-263.

Binford LR. 1962. Archaeology as anthropology. Am Antiq 28:217-225.

Blangero J. 1988. The selective neutrality of dermatoglyphic variation. Int J Anthropol 3:289–299.

Blangero J. 1990. Population structure analysis using polygenic traits: estimation of migration matrices. Hum Biol 62:27-48.

Blakey ML, Rankin-Hill LM. 2004. The New York African burial ground. A synthesis of volumes 1-3. Washington, D.C.: Howard University for the United States General Services Administration.

Blom DE. 2005. Embodying borders: human body modification and diversity in Tiwanaku society. J Anthropol Archaeol 24:1-24.

Blondiaux J. 1986. Tentative de reconstruction paléodémographique d'une population mérovingienne du Nord de la Gaule: la nécropole de Les Rue des Vignes (Nord). Bull Mém Soc Anthropol Paris 3:163-175.

Blondiaux J. 1989. Essai d'anthropologie physique et de paleopathologie des populations du Nord de la Gaule au Haut Moyen-Âge. PhD. Université de Lille-III.

Blondiaux J, Buchet L. 1990. La place d'anthropologie morphologique dans l'étude des nécropoles. Bull Mém Soc Anthropol Paris 2:191-200.

Blumenbach JF. 1776. De generis humani varietate nativa. Goettingae: Vandenhoeck.

Boas F. 1905. The mythologies of the Indians. Intl Quart 12:157-173.

Boas F. 1912. Changes in the bodily form of descendants of immigrants. New York: Columbia University Press.

Bocquet-Appel J-P. 1985. Une méthode de réconstitution familiale dans les nécropolis. Table Ronde de la RCP 742. Méthodes d'Études des Sépultures. Saint-Germain-en-Laye, May 11-12, 1985.

Bocquet-Appel J-P. 1989. L'anthropologie physique en France et ses origines institutionnelles. Gradhiva 6:23-34.

Bocquet-Appel J-P. Masset C. 1982. Farewell to paleodemography. J Hum Evol 11:321-333.

Bodmer WF, Cavalli-Sforza LL. 1968. A migration matrix model for the study of random genetic drift. Genetics 59:565-592.

Bonzom Y. 1976. Quelque cas de paléopathologie infectieuse mediévale en Basse Normandie. Bull Mém Soc Anthropol Paris 3:137-145.

Børsting C, Pereira V, Andersen JP, Morling N. 2014. Single nucleotide polymorphism. In: Jamieson A, Moenssons A, editors. Wiley encyclopedia of forensic science. Chichester: Wiley and Sons. p 1-18.

Bosch E, Calafell F, Comas D, Oefner PJ, Underhill PA, Bertranpetit J. 2001. High-resolution analysis of human Y-chromosome variation shows a sharp discontinuity and limited gene flow between northwestern Africa and the Iberian Peninsula. Am J Hum Gen 68:1019-1029.

Bourdieu P. 1977. Outline of a theory of practice. Cambridge: Cambridge University Press.

Bowlus CR. 2002. Ethnogenesis: the tyranny of a concept. In: Gillett A, editor. On barbarian identity. Critical approaches to ethnicity in the Early Middle Ages. Vol. 4. Turnhout: Brepols. p 241-256.

Boyce AJ, Küchemann CF, Harrison GA. 1967. Neighbourhood knowledge and the distribution of marriage distances. Ann Hum Gen 30:335-338.

Boyd R. Silk J. 1997. How humans evolved. New York: W.W. Norton.

Brather S. 2005. Acculturation and ethnogenesis along the frontier: Rome and the ancient Germans in an archaeological perspective. In: Curta F, editor. Borders, barriers, and ethnogenesis: frontiers in Late Antiquity and the Middle Ages. Turnhout: Brepols. p 139-171.

Broca P. 1864. Sur l'état des crânes et des squelettes dans les anciennes sépultures. Bull Soc Anthropol Paris. 5:642-653.

Broca P. 1875. Instructions craniologiques et craniométriques. Bull Mém Soc Anthropol Paris 2:1-203.

Broca P. 1879. Instructions relatives à l'étude anthropologique du système dentaire. Bull Soc Anthropol Paris 2:128-163.

Bromley Y. 1974. Soviet ethnology and anthropology today. The Hague: Mouton.

Broome RC. 2014. Approaches to community and otherness in the late Merovingian and early Carolingian periods. PhD dissertation, School of History, University of Leeds.

Brook AH. 2009. Multilevel complex interactions between genetic, epigenetic and environmental factors in the aetiology of anomalies of dental development. 54:S3-S17.

Brown P. 1996. Authority and the sacred. Cambridge: Cambridge University Press.

Brumfield EM. 1994. Factional competition and political development in the New World: an introduction. In: Brumfield EM, Fox JW, editors. Factional competition and political development in the New World. Cambridge: Cambridge University Press. p -13.

Buchet L. 1977. Étude anthropologique d'une population de Basse Normandie, Frénouville (fin III siècle – fin VII siècle). Ph.D., Université de Caen.

Buchet L. 1978. La nécropole gallo-romaine et mérovingienne de Frénouville. Étude anthropologique. Archaeol Med 8:5-53.

Buchet L. 1988. La déformation cranienne en Gaule et dans les régions limitrophes pendant le Haut Moyen Âge: son origine, sa valeur historique. Archéol Médiévale 18:55-71.

Buchet L, Séguy I. 2003. Mort probable, mort certaine. Réflexions en paléodémographie à partir de squelettes modernes et contemporains. Revue Archéol Picardie 21:101-111.

Buchet L, Torre S. 1981. Étude anthropologique des squelettes adultes découverts dans la nécropole mérovingienne de Réville (Manche). Soma 2:1-21.

Buchignani N. 1982. Anthropological approaches to the study of ethnicity: occasional papers in ethnic and immigration studies. Toronto: The Multicultural Society of Ontario.

Buikstra JE. 1977. Biocultural dimensions of archaeological study: a regional perspective. In: Blakely RL, editor. Biocultural adaptation in prehistoric America. Athens: University of Georgia Press. p 67-84.

Buikstra JE. 1980. Epigenetic distance: a study of biological variability in the Lower Illinois River region. In: Browman DL, editor. Early native Americans: prehistoric demography, economy, and technology. New York: Mouton. p 271-299.

Buikstra JE, Beck LA. 2006. Bioarchaeology: the contextual analysis of human remains. New York: Academic Press.

Buikstra JE, Scott RE. 2009. Key concepts in identity studies. In: Knudson KJ, Stojanowski CM, editors. Bioarchaeology and identity in the Americas. Gainesville: University Press of Florida. p 24-55.

Buikstra JE, Ubelaker DH. 1994. Standards for data collection from human skeletal remains. Arkansas Archaeological Survey Research Series No. 44. Arkansas Archaeological Survey, Fayetteville.

Buikstra JE, Frankenberg SR, Konigsberg LW. 1990. Skeletal biological distance studies in American physical anthropology: recent trends. Am J Phys Anthropol 82:1-7.

Burns TS, Eadie JW. 2001. Urban centers and rural contexts in Late Antiquity. East Lansing: Michigan State University Press.

Butler PM. 1939. Studies of the mammalian dentition. Differentiation of the post-canine dentition. Proc Zool Soc London B 109:1-36.

Butler J. 1990. Gender troubles: feminism and the subversion of identity. London: Routledge.

Buzon MR. 2011. Nubian identity in the Bronze Age. Bioarchaeol Near East 5:19-40.

Byrd JE, Jantz RL. 1994. Osteological evidence for distinct social groups at the Leavenworth site. In: Owsley DH, Jantz RL, editors. Skeletal biology in the Great Plains. Washington, DC: Smithsonian Institution Press. p 203-208.

Byrd RM. 2014. Phenotypic variation in transitional forager-farmers in the Sonoroan Desert. Am J Phys Anthropol 155: 579-590.

Cai J, Cho S-W, Kim J-Y, Lee M-J, Cha Y-G, Jung H-S. 2007. Patterning the size and number of tooth and its cusps. Develop Biol 304:499-507.

Cadien JD, Harris EF, Jones WP, Mandarino LJ. 1974. Biological lineages, skeletal populations, and microevolution. Yrbk Phys Anthropol 18:194–201.

Capelli C, Redhead N, Abernethy JK, Gratix F, Wilson JF, Moen T, Hervig T, Richards M, Stumpf MPH, Underhill PA, Bradshaw P, Shaha A, Thomas MG, Bradman N, Goldstein DB. 2003. A Y chromosome census of the British Isles. Curr Biol 13:979-984.

Carlier C. 1764. Histoire du Duché de Valois, contenant ce qui est arrivée dans ce pays depuis le temps des Gaulois, et depuis l'origine de la monarchie françoise, jusqu'en l'année 1703. Paris: Chez Guillyn.

Carson EA. 2006. Maximum likelihood estimation of human craniometric heritabilities. Am J Phys Anthropol 131:169-180.

Castex D, Depierre G, Maureille B. 1995. Population indigène, population allogène à Beaune (Côte-d'Or) aux V-Ve siècles. In: Gaillard de Semainville H., editor. Les Burgondes. Apports de l'archéologie. Actes du colloque international de Dijon (5-6 novembre 1992). Dijon: Conseil Regional de Bourgogne et du Ministère de la Culture. p 167-184.

Catón J, Tucker AS. 2009. Current knowledge of tooth development: patterning and mineralization of the murine dentition. J Anat 214:502-515.

Cauchemé V. 1900-1902. Description des fouilles archéologiques exécutées dans la forêt de Compiègne sous la direction de Mr A. de Roucy. Paris: H. Lefevre.

Chabeuf M. 1976. Recherches sur les origins anthropologiques de la population dijonnaise. Rev Archéol Est Centre-Est 27:285-305.

Chabeuf M. 1977. Sur le peuplement ancien de la Bourgogne. Bull Mém Soc Anthropol Paris 4:127-134.

Chabeuf M. 1978. Note sur la population gallo-romaine en Bourgogne. Bull Mém Soc Anthropol Paris 5:107-115.

Chadwick HM. 1907. The origin of the English nation. Cambridge: Cambridge University Press.

Chakraborty R. 1990. Quantitative traits in relation to population structure: why and how are they used and what do they imply? Hum Biol 62:147-162.

Chamberlain A. 2009. Archaeological demography. Hum Biol 81: 275-286.

Chappell D. 1993. Ethnogenesis and frontiers. J World Hist 4:267-275.

Cheverud JM. 1988. A comparison of genetic and phenotypic correlations. Evol 42:958-968.

Cheverud JM, Buikstra JE, Twitchell E. 1979. Relationships between non-metric skeletal traits and cranial size and shape. Am J Phys Anthropol 50:191-209.

Chikhi L, Nichols RA, Barubjani G, Beaumont MA. 2002. Y genetic data support the Neolithic demic diffusion model. Proc Natl Acad Sci 99: 11008-11013.

Childe VG. 1929. The Danube in prehistory. Oxford: Clarendon.

Childe VG. 1933. Races, peoples and cultures in prehistoric Europe. Hist 18:193-203.

Christlein R, Natter K. 1978. Die Alamannen: Archäologie eines lebendigen Volkes. K. Theiss.

Clifford J. 1988. The predicament of culture. Cambridge: Harvard University Press.

Codrington T. 1905. Early Britain: Roman roads in Britain. New York: ES Gorham.

Colson E. 1968. Contemporary tribes and the development of nationalism. In: Helm J, editor. Essays on the problem of tribe. Seattle: University of Washington Press. p 201-206.

Cohen A. 1969. Custom and politics in urban Africa. London: Routledge.

Cohen A. 1974. Urban ethnicity. London: Tavistock.

Cohen R. 1978. Ethnicity: problem and focus in anthropology. Ann Rev Anthropol 7:379-403.

Comaroff J, Comaroff JL. 1991. Of revelation and revolution: Christianity, colonialism and consciousness in South Africa. Chicago: University of Chicago Press.

Connor W. 1978. A nation is a nation, is a state, is an ethnic group, is a…. Ethnic Racial Studies 1:377-400.

Côrtes-Real HBSM, Macauley V, Richards MB, Hariti G, Issad MS, Cambon-Thomsen A, Papiha S, Bertranpetit J, Sykes BC. 1996. Genetic diversity in the Iberian Peninsula determined from mitochondrial sequence analysis. Ann Hum Gen 60:331-350.

Corruccini RS. 1972. The biological relationships of some prehistoric and historic Pueblo populations. Am J Phys Anthropol 37:373-388.

Corruccini RS, Potter RHY. 1980. Genetic analysis of occlusal variation in twins. Am J Orthodont 78:140-154.

Corruccini RS, Shimada I. 2002. Dental relatedness corresponding to mortuary patterning at Huaca Loro, Peru. Am J Phys Anthropol 117:113-121.

Crisp RP. 2003. Marriage and alliance in the Merovingian Kingdoms, 481-639. Ph.D., The Ohio State University.

Crubézy E. 1988. La place de l'anthropologie dans l'étude des sépultures anciennes. Cahiers Anthropol Paris 1:27-42.

Crubézy E. 1989. Parenté, structures de parenté et societés du passé. Bull Mém Soc Anthropol Paris 1:79-92.

Crubézy E. 1990. Merovingian skull deformations in the southwest of France. In: Austin D, Alcock D., editors. From the Baltic to the Black Sea: studies in medieval archaeology. Hyman: London, p 189-208.

Crubézy E. 2000. L'étude des sepultures ou du monde des morts au monde des vivants: anthropobiologie, archeologie funeraire et anthropologie de terrain. In: Crubezy E, editor. L'Archéologie funéraire. Paris: Errance. p 8-54.

Crubézy E, Sellier P. 1990. Caracteres discrets et organisation des ensembles sépulcraux. Bull Mém Soc Anthropol Paris 2:171-178.

Curta F. 2001. The making of the Slavs: history and archaeology of the Lower Danube Region, ca. 500-700. Cambridge: Cambridge University Press.

Curta F. 2005a. Borders, barriers, and ethnogenesis: frontiers in Late Antiquity and the Middle Ages. Turnhout: Brepols.

Curta F. 2005b. Frontier ethnogenesis in late antiquity: the Danube, the Tervingi, and the Slavs. In: Curta F, editor. Borders, barriers, and ethnogenesis: frontiers in Late Antiquity and the Middle Ages. Turnhout: Brepols. p 173-204.

Dannheimer H. 1966. Der Holzbau am Rande des Reihengraberfelds von Munchen-Aubing. Germania 44.

Darlu P, Bocquet-Appel J-P. 1987. Une méthode de reconnaissance des apparentés basé sur des mésures quantitatives. Bull Mém Soc Anthropol Paris 4:191-200.

Dastugue J. 1978. Contribution de la paléopathologie à la connaissance des civilisations anciennes. Arch Suisses Anthropol Générale 43:319-326.

Dastugue J. 1982. Le pathologiste a-t-il son mot à dire à propos des "Grandes Invasions"? Journée Anthropologique de Valbonne. Notes et Mongraphes Téchniques. CNRS-CRA 12:105-112.

Dastugue J. 1983. État actuel des recherches anthropologiques en Normandie: les population préhistoriques. Bull Mém Soc Anthropol Paris 10:159-167.

Dastugue J. Gervais V. 1992. Paléopathologie du squelette humain. Boubée: Paris.

Dastugue J, Torre S. 1964. Sépultures du IV siècle à Bellengréville (Calvados). Annales de Normandie 14:243-249.

Dastugue J, Torre S. 1965. Étude anthropologique des ossements du cimetière Saint-Martin à Caen. Annales de Normandie 15:329-352.

Dastugue J, Torre S. 1966. Étude anthropologique d'un cimetière de Hallstatt tardif à Ifs (Calvados). Annales de Normandie 17:311-315.

Dastugue J, Torre S. 1971. Le cimetière d'Hérouvillette (VI-VII siècles). Étude anthropologique. Archéol Med 1:127-144.

Dastugue J, Torre S, Buchet L. 1973. Néolithiques de Basse-Normandie. Le deuxième tumulus de Fontenany-le-Marmion, étude anthropologique. L'Anthropologie 77:579-620.

Dastugue J, Torre S, Buchet L. 1974. Néolithiques de Basse-Normandie. Le deuxième tumulus de Fontenany-le-Marmion, étude anthropologique. L'Anthropologie 78:113-164.

Decaens J. 1965. Sépultures franques à Blay (Calvados). Annales Normandie 3:456-460.

Dempsey PJ, Townsend GC, Martin NG, Neale MC. 1995. Genetic covariance structure of incisor crown size in twins. J Dent Res 74:1389-1398.

Derbois M. 2003. Précy-sur-Oise: Rue du Martray. In: Lascour-Rossignol A, editor. Bilan scientifique de la région Picardie. Amiens: DBS. p 85.

Derbois M. 2004. Précy-sur-Oise: Rue du Martray. In: Lascour-Rossignol A, editor. Bilan scientifique de la région Picardie. Amiens: DBS. p 81.

Devor EJ. 1987. Transmission of human craniofacial dimensions. J Craniofac Genet Dev Biol 7:95-106.

de Vos G. 1975. Ethnic pluralism: conflict and accommodation. In: de Vos G, Romanucci-Ross L, editors. Ethnic identity: cultural continuities and change. Chicago: University of Chicago Press. p 5-41.

de Vos G, Romanucci-Ross L. 1975. Ethnic identity: cultural continuities and change. Chicago: University of Chicago Press.

Devroey J-P, Jaubert AN. 2011. Family, income and labour around the North Sea, 500-1000. In: Vanhaute E, Devos I, Lambrecht T, editors. Making a living: family, income and labour. Aarhus: Brepols. p 5-44.

Díaz-Andreu M. 2005. The archaeology of identity. Approaches to gender, age, status, ethnicity, and religion. London: Routledge.

Dixon KR, Southern P. 2014. Late Roman Army. London: Routledge.

Doranlo R. 1921. Crânes francs de Basse-Normandie. Association Française pour l'Avancement des Sciences, Congrès de Rouen. p 742-747.

Dorman JH. 1980. Ethnic groups and ethnicity: some theoretical considerations. J Ethnic Studies 7:23-36.

Droessler J. 1981. Craniometry and biological distance: biocultural continuity and change at the Late-Woodland-Mississippian interface. Evanston: Center for American Archaeology Press.

Dubut V, Chollet L, Murail P, Cartault F, Béraud-Colomb E, Serre M, Mogentale-Profizi N. 2004. mtDNA polymorphisms in five French groups: importance of regional sampling. Euro J Hum Genet 12:293-300.

Durand JD. 1977. Historical estimates of world populations: an evaluation. Pop Develop Rev 3:253-296.

Durand M. 1986. Le terroir médiéval de Champlieu – contribution archéologique. Rev Archéol Picardie 1/2:37-94.

Duvall Y. 1988. Auprès des Saints Corps et Âme. Paris: Château-Gontier.

Duvette L. 2000. Précy-sur-Oise: Rue de Docteur Ch. Andrieu. In: Dubois B, Rossignol A, editors. Bilan scientifique de la région Picardie. Amiens: I. and RG. p 81-82.

Duvette L. 2001. Précy-sur-Oise: Rue de Martray. In: Dubois B, Rossignol A, editors. Bilan scientifique de la région Picardie. Amiens: Yvert – IPC Moulet. p 79-82.

Effros B. 2002. Caring for body and soul. Burial and the afterlife in the Merovingian world. University Park: Pennsylvania State University Press.

Effros B. 2003. Merovingian mortuary archaeology and the making of the early middle ages. Berkeley: University of California Press.

Elton H. 1996. Warfare in Roman Europe. Oxford: Clarendon Press.

Emberling G. 1997. Ethnicity in complex societies: archaeological perspectives. J Arch Res 5: 295-344.

Epstein AL. 1978. Ethos and identity: three studies in ethnicity. London: Tavistock.

Eriksen TH. 1992. Us and them in modern societies: ethnicity and nationalism in Mauritius, Trinidad and beyond. London: Scandinavian University Press.

Eriksen TH. 1993. Ethnicity and nationalism. Anthropologic perspectives. London: Pluto Press.

Escher K. 2005. Genèse et évolution du deuxième royaume burgonde (443-534). Les témoins archéologiques. Oxford: Bar Intl Series 1402.

Escher K. 2006. Les Burgondes, Ier-VIe siècles ap. J.-C. Errance: Paris.

Falconer DS. 1981. Introduction to quantitative genetics. New York: Longman Scientific and Technical.

Fehring GP. 1991. The Archaeology of Medieval Germany: An Introduction. London: Routledge.

Ferembach D, Clément A. 1958. Le cimetière mérovingien de Créteil. Bull Mém Soc Anthropol Paris 9:312-319.

Ferguson RB, Whitehead NL. 1992. The violent edge of empire. In: Ferguson RB, Whitehead NL, editors. War in the tribal zone: expanding states and indigenous warfare. Santa Fe: School of American Research Press. p 1-30.

Fitzgerald CM, Hillson S. 2008. Alternative methods of assessing tooth size in Late Pleistocene and Early Holocene hominids. In: Irish JD, Nelson GC, editors. Technique and application in dental anthropology. Cambridge: Cambridge University Press. p 364-388.

Fowler C. 2004. The archeology of personhood. An anthropological approach. London: Routledge.

Fried MH. 1968. On the concepts of “tribe” and “tribal society”. In: Helm J, editor. Essays on the problem of tribe. Seattle: University of Washington Press. p 3-20.

Gaillard de Semainville H. 1981. Burgondes et Francs. Hist Archéol 56:56-63.

Gaillard de Semainville H. 1993. Les Burgondes. Archeologia 290:50-61.

Gaillard de Semainville H. 1995. Les Burgondes. Apports de l’archéologie. Actes du colloque international de Dijon (5-6 novembre 1992). Dijon: Conseil Régional de Bourgogne et du Ministère de la Culture.

Gaillard de Semainville H., Laugrand R., Perraud R. 1978. Un cas de deformation cranienne artificielle à Briord (Ain). L’Implantation Burgonde au Ve siècle. Rév Période La Physiophile 88:43-49.

Gamba C, Fernándes E, Tirado M, Pastor F, Arroyo-Pardo E. 2011. Brief communication. Ancient nuclear DNA and kinship analysis: the case of a medieval burial

in San Esteban Church in Cuellar (Segovia, Central Spain). Am J Phys Anthropol 144:485-491.

Gamble LW, Walker PL, Russell GS. 2001. An integrative approach to mortuary analysis: social and symbolic dimensions of Chumash burial practices. Am Antiq 66:185-212.

Geary P. 1988. Before France and Germany: the making and transformation of the Merovingian world. Oxford: Oxford University Press.

Geary P. 2002. The myth of nations: The medieval origins of Europe. Princeton: Princeton University Press.

Geller PL, Stockett MK. 2006. Feminist anthropology: past, present, and future. Philadelphia: University of Pennsylvania Press.

Geertz C. 1963. Old societies and new states. New York: The Free Press.

Geertz C. The interpretation of cultures. New York: Basic.

Gibbon E. 1830. The history of the decline and fall of the Roman Empire. London: Joseph Ogle Robinson.

Giddens A. 1984. The constitution of society: outline of the theory of structuration. Cambridge: Polity Press.

Gillet A. 2002a. Introduction: Ethnicity, history, and methodology. In: Gillett A, editor. On barbarian identity. Critical approaches to ethnicity in the Early Middle Ages. Vol. 4. Turnhout: Brepols. p 1-18.

Gillet A. 2002c. On barbarian identity. Critical approaches to ethnicity in the Early Middle Ages. Vol. 4. Turnhout: Brepols.

Gillett A. 2006. Ethnogenesis: a contested model of early medieval Europe. Hist Compass 4:241-260.

Glazer N, Moynihan DP. 1975. Introduction. In: Glazer N, Moynihan DP, editors. Ethnicity theory and experience. Cambridge: Harvard University Press. p 1-26.

Gluckman M. 1971. Tribalism, ruralism, and urbanism in south and central Africa. In: Turner V, editor. Colonialism in Africa 1870-1960 Vol. 3. London: Cambridge University Press. p 127-166.

Goffart W. 1980. Barbarians and Romans: The techniques of accommodation. Princeton: Princeton University Press.

Goffart W. 1988. The narrators of barbarian history (AD 550-800). Jordanes, Gregory of Tours, Bede and Paul the Deacon. Princeton: Princeton University Press.

Goffart W. 1998. The barbarians in Late Antiquity and how they were accommodated in the West. In: Little LK, Rosenwein BH, editors. Debating the Middle Ages: Issues and Readings. Oxford: Blackwell Publishers.

Goffart W. 2002. Does the distant past impinge on the invasion age Germans? In: Gillett A, editor. On barbarian identity. Critical approaches to ethnicity in the Early Middle Ages. Vol. 4. Turnhout: Brepols. p 21-38.

Goffart WA. 2006. Barbarian tides: the migration age and the later Roman Empire. Philadelphia: University of Pennsylvania Press.

Goose DH. 1963. Dental measurement: an assessment of its value in anthropological studies. In: Brothwell DR, editor. Dental Anthropology. New York: Pergamon Press. p 125-148.

Goose DH, Lee GTR. 1971. The mode of inheritance of Carabelli's trait. Hum Biol 43:64-69.

Goosmann E. 2013. Memorable crises: Carolingian historiography and the making of Pippin's reign, 750-900. Ph.D., University of Amsterdam.

Gordon MM. 1975. Toward a general theory of racial and ethnic group relations. In: Glazer N, Moynihan DP, editors. Ethnicity theory and experience. Cambridge: Harvard University Press. p 84-110.

Gower JC. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. Biometrika 53:325-338.

Graham-Campbell J. 2007. The archaeology of medieval Europe. Volume 1. Eighth to twelfth centuries AD. Oakville, Connecticut: Aarhus Univ Press.

Gravlee CC, Bernard HR, Leonard WR. 2003. Heredity, environment, and cranial form: a reanalysis of Boas's immigrant data. Am Anthropol 105:125-138.

Greene K. 1991. The Archaeology of the Roman economy. Berkeley: University of California Press.

Gressier N. 2001. Précy-sur-Oise: Rue du Martray. In: Dubois B, Rossignol A, editors. Bilan scientifique de la région Picardie. Amiens: Yvert – IPC Moulet. p 79.

Grumbkow PV. Frommer S, Kootker L, Davies GR. Mazanec J, Hummel S. 2013. Kinship and mobility in 11th-century A.D. Gammertingen, Germany: an interdisciplinary approach. J Archaeol Sci 40:3768-3776.

Haarnagel 1979. Das Eisenzeitliche Dorf “Feddersen Wierde”. In: Jankuhn H, Wenskus R, editors. Geschichtswissenschaft und Archäologie: Untersuchungen zur Siedlungs-, Wirtschafts- und Kirchengeschicte. Sigmaringen: Thorbecke. p 45-100.

Halfond GI. 2008. Archaeology of Frankish church councils, AD 511-768. Boston: Brill.

Hallgrímsson B, Willmore K, Hall BK. 2002. Canalizatino, developmental stability, and morphological integration in primate limbs. Am J Phys Anthropol 119:131-158.

Halsall G. 2003. Early medieval archaeology and history: Some interdisciplinary problems and potentials for the twenty-first century. In: Goetz H-W, Jarnut J, editors. Mediavistik im 21. Jahrhundert. Stand und Perspektiven der internationalen und interdisziplinaren Mittelalterforschung. Munchen: Fink. p 163-185.

Halsall G. 2007. Barbarian migrations and the Roman West, 376-568. Cambridge: Cambridge University Press.

Halsall G. 2010. Cemeteries and society in Merovingian Gaul. Leiden: Brill.

Hamerow H. 2002. Early medieval settlements: The archaeology of rural communities in northwest Europe, AD 400-900. Oxford: Oxford University Press.

Hammer Ø. 1998. Diffusion and direct signaling models are numerically equivalent. J Theor Biol 192:129-130.

Harpending H, Jenkins T. 1973. Genetic distance among southern African populations. In: Crawford MH, Workman PL, editors. Methods and theories of anthropological genetics. Albuquerque: University of New Mexico Press. p 177-199.

Harpending HC, Ward RH. 1982. Chemical systematics and human populations. In: Nitecki M, editor. Biochemical aspects of evolutionary biology. Chicago: University of Chicago Press. p 213-256.

Harris EF, Smith RJ. A study of occlusion and arch width in families. Am J Orthodont 78:155-163.

Harris EF, Smith RJ. 2009. Accounting for measurement error: a critical but often overlooked process. Archives Oral Biol 54:S107-S117.

Hartl DL, Clark AG, 1989. Principles of population genetics. Sunderland, MA: Sinauer Associates.

Hatton JP, Pooran M, Li CF, Luzzio C, Hughes-Fulford M. 2003. A short pulse of mechanical force induces gene expression and growth in MC3T3-E1 osetoblasts via an ERK 1/2 pathway. J Bone Mineral Res 18:58-66.

Hauser G, DeStefano GF. 1989. Epigenetic variants of the human skull. Stuttgart: Schweizerbart.

Heather PJ. 1991. Goths and Romans 332-489. Oxford: Oxford University Press.

Heather PJ. 1995. The Huns and the end of the Roman Empire in Western Europe. Engl Hist Rev 110:4-41.

Heather PJ. 1997. Foedera and Foederati in the fourth century. In: Pohl W, editor. Kingdoms of the Empire. Leiden: Brill. p 57-75.

Heather PJ. 2008. Ethnicity, group identity, and social status in the Migration Period. In: Garipzanov IH, Geary PJ, Urbańczyk P, editors. Franks, Northmen, and Slavs. Turnhout: Brepols. p 17-50.

Heather PJ. 2010. Empires and barbarians. The fall of Rome and the birth of Europe. Oxford: University Press.

Hechter M. 1975. Review essay. Contemp Sociol 4: 217-222.

Hechter M. 1986. Theories of ethnic relations. In: Stack JF, editor. The primordial challenge: ethnicity in the contemporary world. London: Greenwood Press. p 13-24.

Hedeager L. 1978. A quantitative analysis of Roman imports to Europe north of the limes (0-400AD) and the question of Roman-Germanic exchange. In: Kristiansen K, Paludin-Miller C, editors. New Directions in Scandinavian History. Copenhagen: Aarhus Universitetsforlag. p 191-216.

Hedrick P. 2011. Genetics of populations. Sudbury: Jones and Bartlett Publishers.

Helgason A, Sigurőardóttir S, Nicholson J, Sykes B, Hill EW, Bradley DG, Bosnes V, Gulcher JR, Ward R, Stefánsson K. 2000. Estimating Scandinavian and Gaelic ancestry in the male settlers of Iceland. Am J Hum Genet 67:697-717.

Helgason A, Hickey E, Goodacre V, Stefánsson K, Ward R, Sykes B. 2001. mtDNA and the islands of the North Atlantic: estimating the proportions of Norse and Gaelic ancestry. Am J Hum Genet 68:723-737.

Heuertz M. 1957. Étude des squelettes du cimetière franc d'Ennery (Moselle). Bull Mém Soc Anthropol Paris 8:81-141.

Heuertz M. 1966. Squelettes anciens et du Haut Moyen Âge de la région lorraine franco-luxembourgeoise. Bull Mém Soc Anthropol Paris 9:1-28.

Hickerson NP. 1996. Ethnogenesis in the South Plains: Jumano to Kiowa? In: Hill JD, editor. History, power, and identity. Ethnogenesis in the Americas, 1492-1992. Iowa City: University of Iowa City. p 70-89.

Hill JD. 1996. History, power and identity. Ethnogenesis in the Americas, 1492-1992. Iowa City: University of Iowa City.

Hillgarth JN. 1986. Christianity and paganism, 350-750: the conversion of Western Europe. Philadelphia: University of Pennsylvania Press.

Hillson S. 1996. Dental Anthropology. Cambridge: Cambridge University Press.

Hillson S. 2008. The current state of dental decay. In: Irish JD, Nelson GC, editors. Technique and application in dental anthropology. Cambridge: Cambridge University Press. p 111-135.

Hillson S, Fitzgerald C, Flinn H. 2005. Alternative dental measurements: proposals and relationships with other measurements. Am J Phys Anthropol 126:413-426.

Hodges R. 1982. Dark Age economics. The origins of towns and trade, A.D. 600-1000. New York: St. Martin's Press.

Hodges R. 2001. Towns and trade in the age of Charlemagne. London: Duckbacks.

Hoops J. 1911. Reallexikon der germanischen Altertumskunde. Strasbourg: Trübner.

Howells WW. 1989. Skull shapes and the map: craniometric analyses in the dispersion of modern Homo. Papers of the Peabody Museum of Archaeology and Ethnology, Harvard University, Vol. 79. Cambridge: Peabody Museum of Archaeology and Ethnology, Harvard University.

Howells WW. 1995. Who's who in the skulls. Ethnic identification of crania from measurements. Papers of the Peabody Museum of Archaeology and Ethnology, Vol. 82, Harvard University.

Hickerson NP. 1996. Ethnogenesis in the South Plains: Jumano to Kiowa? In: Hill JD, editor. History, power, and identity: ethnogenesis in the Americas, 1492-1992. Iowa City: University of Iowa City. p 70-89.

Hu D. 2013. Approaches to the archaeology of ethnogenesis: past and emergent perspectives. J Archaeol Res 21: 371-402.

Hudson M. 1999. Ruins of identity: ethnogenesis in the Japanese Islands. Honolulu: University of Hawaii Press.

Hummer HJ. 1998. Franks and Alamanni: a discontinuous ethnogenesis. In: Wood I, editor. Franks and Alamanni in the Merovingian Period: An ethnographic perspective. Woodbridge: Boydell Press. p 9-32.

Hunter JP, Guatelli-Steinberg D, Weston TC, Durner R, Betsinger TK. 2010. Model of tooth morphogenesis predicts Carabelli cusp expression, size, and symmetry in humans. Pub Lib Sci One 5:e11844-e11844.

Huxley JS, Haddon AC. 1935. We Europeans: a survey of 'racial' problems. London: Jonathan Cape.

Innes M. 2007 Introduction to early medieval Western Europe 300-900. London: Routledge.

Insoll T. 2007. The archaeology of identities: a reader. London: Routledge.

Isaacs H. 1974. Basic group identity: idols of the tribe. Ethnicity 1:15-41.

Jakkula E, Rehnströ K, Varilo T, Pietiläinen OPH, Paunio T, Pederson NL, deFaire U, Jäarvelin M-R, Saharinen J, Freimer N, Ripatti S, Purcell S, Collins A, Daly MJ, Palotie A, Peltonen L. Am J Hum Genet 83:787-794.

James E. 1989. Burial and status in the early medieval West. Trans Royal Hist Soc. 39: 23-40.

James E. 2014. Europe's barbarians, AD 200-600. London: Routledge.

Jamison PL, Meier RJ, Thompson-Jacob D. 1989. Meaning of biodistance statistics: a test case using adult monozygotic twins. Am J Phys Anthropol 80:485-492.

Jantz R, Meadows L. 1995. Population structure of Algonquian speakers. Hum Biol 67:375-386.

Jernvall J. 2000. Linking development with generation of novelty in mammalian teeth. Proc Natl Acad Sci 97:2641-2645.

Jernvall J, Jung H-S. 2000. Genotype, phenotype, and developmental biology of molar tooth characters. Yrbk Phys Anthropol 43:171-190.

Jernvall J, Thesleff I. 2000. Reiterative signaling and patterning during mammalian tooth morphogenesis. Mech Develop 92:19-29.

Jernvall J, Åberg T, Kettunen P, Keränen S, Thesleff I. 1998. The life history of an embryonic signaling center: BMP-4 induces p21 and is associated with apoptosis in the mouse tooth enamel knot. Develop 125:161-169.

Jernvall J, Kettunen P, Karavanova I, Martin LB, Thesleff I. 1994. Evidence for the role of the enamel knot as a control center in mammalian tooth cusp formation: non-dividing cells express growth stimulating Fgf-4 gene. Intl J Develop Biol 38:463-469.

Jobling MA, Hurles ME, Tyler-Smith C. 2004. Human evolutionary genetics: origins, peoples, and diseases. New York: Garland.

Jones S. 1997. The archaeology of ethnicity. Constructing identities in the past and present. London: Routledge.

Jouffroy H. 1986. La Construction publique en Italie et dans l'Afrique romaine. Groupe de Recherche d'Histoire romaine de l'Université des Sciences humaines de Strasbourg, Études et Traveaux, II. Strasbourg: AECR.

Joyce RA. 2005. Archaeology of the body. Ann Rev Anthropol 34:139-158.

Jungers WL, Falsetti AB, Wall CE. 1995. Shape, relative size, and size-adjustments in morphometrics. Yrbk Phys Anthropol 38:137-161.

Kayser M, Brauer S, Schädlich H, Prinz M, Batzer MA, Zimmerman PA, Boatin BA, Stoneking M. 2003. Y chromosome STR haplotypes and the genetic structure of U.S. populations of African, European, and Hispanic Ancestry. Genome Res 13:624-634.

Kayser M, Lao O, Anslinger K, Augustín C, Bargel G, Edelmann J, Elias S, Heinrich M, Henke J, Henke L, Hohoff C, Illing A, Jonkisz A, Kuzniar P, Lebioda A, Lessig R, Lewicki S, Maciejewska A, Monies DA, Palowski R, Poetsch M, Schmid D, Schmidt U, Schneider PM, Stradmann-Bellinghausen B, Szibor R, Wegener R, Wozniak M, Zoledziewska M, Roewer L, Dobosz T, Ploski R. 2005. Significant genetic differentiation between Poland and Germany follows present-day political borders, as revealed by Y-chromosome analysis. Hum Genet 117:428-443.

Kavanagh KD, Evans AR, Jernvall J. 2007. Predicting evolutionary patterns of mammalian teeth from development. Nat 449:427-432.

Kellas JG. 1991. The politics of nationalism and ethnicity. London: Macmillan.

Key PJ, Jantz RL. 1990. Statistical measures of intrasample variability. Hum Evol 5:457-469.

Keyes CF. 1976. Towards a new formulation of the concept of ethnic group. Ethnicity 3:202-213.

Keyes CF. 1981. Ethnic change. Seattle: University of Washington Press.

Kieser JA. 1990. Human adult odontometrics: the study of variation in adult tooth size. Cambridge: Cambridge University Press.

Kimura M, Weiss GH. 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. Gentics 49:561-576.

Klaus HD. 2008. Out of light came darkness: bioarchaeology of mortuary ritual, health, and ethnogenesis in the Lambayeque Valley complex, north coast of Peru (AD 900-1750). Ph.D. dissertation, Department of Anthropology, The Ohio State University.

Kohl P. 1998. Nationalism and archaeology: on the constructions of nations and the reconstructions of the remote past. Ann Rev Anthropol 27:223-246.

Konigsberg LW. 1990a. Analysis of prehistoric biological variation under a model of isolation by geographic and temporal distance. Hum Biol 62:49-70.

Konigsberg LW. 1990b. Temporal aspects of biological distance: serial correlation and trend in a prehistoric skeletal lineage. Am J Phys Anthropol 82:45-52.

Konigsberg LW. 2000. Quantitative variation and genetics. In: Stinson S, Bogin B, Huss-Ashmore R, O'Rourke D, editors. Human biology: an evolutionary and biocultural perspective. Hoboken: Wiley-Liss. p 135-162.

Konigsberg LW, Buikstra JE. 1995. Regional approaches to the investigation of past human biocultural structure. In: Beck L, editor. Regional approaches to mortuary analysis. New York: Plenum. p 191-219.

Konigsberg LW, Owsley SD. 1995. Multivariate quantitative genetics of anthropometric traits from the Boas data. Hum Biol 67:481-498.

Konigsberg LW, Algee-Hewitt BFB, Steadman DW. 2009. Estimation and evidence in forensic anthropology: sex and race. Am J Phys Anthropol 139:77-90.

Kopytoff I. 1987. The internal African frontier: the making of African political culture. In: Kopytoff I, editor. The African frontier. The reproduction of traditional African societies. Bloomington: Indiana University Press.

Kossinna G. 1911. Die Herkunft der Germanen: zur Methode der Siedlungsarchäologie. Würzburg: Universitat Leipzig.

Knudson KJ, Stojanowski CM. 2008. New directions in bioarchaeology: recent contributions to the study of human social identities. J Archaeol Res 16:397-432.

Knudson KJ, Stojanowski CM. 2009. Bioarchaeology and identity in the Americas. Gainesville: University Press of Florida.

Knüsel CJ. 2010. Bioarchaeology: a synthetic approach. Bull Mém Soc Anthropol Paris 22:62-73.

Kramar C. 1990. L'étude de l'état sanitaire des populations anciennes est-elle un rêve? Bull Mém Soc Anthropol Paris 2:159-162.

Krawczak M, Lu TT, Willuweit S, Roewer L. 2008. Genetic diversity in the German population. eLibrary Sci.

Kulikowski M. 2005. Ethnicity, rulership, and early medieval frontiers. In: Curta F, editor. Borders, barriers, and ethnogenesis: frontiers in Late Antiquity and the Middle Ages. Turnhout: Brepols. p 249-254.

Kurin DS. 2012. The bioarchaeology of collapse: ethnogenesis and ethnocide in post-imperial Andahuaylas, Peru (AD 900-1250). Ph.D. Dissertation, Vanderbilt University.

Lakens D. 2015. On the challenges of drawing conclusions from *p*-values just below 0.05. PeerJ 3:e1142.

Lane RA, Sublett AJ. 1972. Osteology of social organization: residence pattern. Am Antiq 37:186-201.

Langdon SP. 1995. Biological relationships among the Iroquois. Hum Biol 67:355-374.

Lao O, Lu TT, Nothnagel M, Junge O, Freitag-Wolf S, Caliebe A, Balascakova M, Bertranpetit J, Bindoff LA, Comas D, Holmlund G, Kouvatsi A, Macek M, Mollet I, Parson W, Palo J, Ploski R, Sajantila A, Taglibracci A, Gether U, Werge T, Rivadeneira F, Hofman A, Uitterlinden AG, Gieger C, Wichmann H-E, Rüther A, Schreiber S, Becker C, Nürnberg P, Nelson MR, Krawczak M, Kayser M. 2008. Correlation between genetic and geographic structure in Europe. Curr Biol 18:1241-1248.

Larmuseau MHD, Vanoverbeke J, Gielis G, Vanderheyden N, Larmuseau HFM, Decorte R. 2012. In the name of the migrant father—analysis of surname origins identifies genetic admixture eventus undetectable from genealogical records. Heredity 109:90-95.

Larsen CS. 1983. Deciduous tooth size and subsistence change in prehistoric Georgia coast populations. Curr Anthropol 24:225-226.

Larsen CS. 1997. Bioarchaeology: interpreting behavior from the human skeleton. Cambridge: Cambridge University Press.

Larsen CS. 2010. Description, hypothesis testing, and conceptual advances in physical anthropology: Have we moved on? In: Little MA, Kennedy KAR, editors. Histories of American physical anthropology in the twentieth century. Lanham, Maryland: Rowman and Littlefield. p 233-242.

Laurikkala J, Kassai Y, Pakkasjarvi L, Thesleff I, Itoh N. 2003. Identification of a secreted BMP antagonist, ecotodin, integrating BMP, FGF, and SHH signals from the tooth enamel knot. Devel Biol 264:91-105.

Leach E. 1964. Political systems of highland Burma: a study in Kachin social structure. London: G. Bell and Sons.

Le Jan R. 2001. Convents, violence and competition for power in seventh-century Francia. In: de Jong M, Theuws F, editors. Topographies of power in the Middle Ages. Leiden: Brill. p 243-269.

Lemière J, Levalet D. 1980. Saint-Martin de Verson (Calvados), nécropole des VIIe et VIIIe siècles. Archéol Méd 10:59-104.

Leroi-Gourhan A. 1949. Étude des squelettes recueillis dans la nécropole Saint-Laurent à Lyon. In: Wuilleumier P, Audin A. L'église et la nécropole Saint-Laurent dans le quartier lyonnais de Choulans: étude archéologique et étude anthropologique. Lyon: Audin. p 51-105.

Levy T. 2008. Ethnic identity in Biblical Edom, Israel and Midian: some insights from mortuary contexts in the lowlands of Edom. In: Schloen D, editor. Exploreing the Longue Durée: essays in honor of Lawrence E. Stager. Winona Lake: Eisenbrauns. p 251-261.

Lewis AR. 1976. The dukes of the *Regnum Francorum,* A.D. 550-751. Speculum 51: 381-410.

Lightfoot K, Martinez A. 1995. Frontiers and boundaries in archaeological perspective. Ann Rev Anthropol 24:471-492.

Lorren C. 1989. Le village de St. Martin de Trainecourt à Mondeville (Calvados) de l'Antiquité au Haut Moyen Age. In: Atsma H, editor. La Neustrie : les Pays au Nord de la Loire de 650 à 850: Colloque Historique International. Sigmaringen: Thorbecke. p 439-466.

Loseby ST. 1998. Gregory's cities: urban functions in sixth-century Gaul. In: Wood IN, editor. Franks and Alamanni in the Merovingian Period. An ethnographic perspective. Woodbridge: Boydell Press. p 239-269.

Macchiarelli R, Bondioli L, Mazurier A. 2008. Virtual dentitions: touching the hidden evidence. In: Irish JD, Nelson GC, editors. Technique and application in dental anthropology. Cambridge: Cambridge University Press. p 426-448.

Mafart B-Y. 1996. Rôle de la pathologie dans l'organisation des nécropoles médiévales. Actes du 2e Colloque A.R.C.H.E.A., Orléans. La Simarre:Paris. p 95-103.

Mahalanobis PC. 1936. On the generalized distance in statistics. Proc Nat Inst Sci India 2:49–55.

Malsy, JC. 1972. La nécropole mérovingienne de Chelles (Oise). Saint-Jean-Aux-Bois et le prétendu palais mérovingien dit de Cuise. Rev Archéol Nord-Est Oise 2:75-92.

Manly BFJ. 1995. Multivariate statistical methods: a primer. London: Chapman and Hall.

Mann A. 2012. Vikings, merchants, and pirates at the top of the world: Y-chromosomal signatures of recent and ancient migrations in the Faroe Islands. M.A., University of Louisville.

Mann R. 2008. From ethnogenesis to ethnic segmentation in the Wabash Valley: constructing identity and houses in Great Lakes fur trade society. Intl J Hist Archaeol 12:319-337.

Manouvrier L. 1890. Étude des ossements humains trouvés dans un cimetière de l'époque merovingiènne à Andresy. In: Association Française pour l'Avancement des Sciences, compte rendu de la 19me session, Limoges. Paris: Secrétariat de l'Association. p 573-587.

Manouvrier L. 1897. Étude des squelettes antiques de Collonges, près Remigny (Bourgogne). Bull Soc Anthropol Paris 8:626-654.

Mantel N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res 27:209-220.

Martin R. 1928. Lehrbuch der Anthropologie in systematischer Darstellung, Vol. 2: Kraniologie, Osteologie. Jena: G. Fischer.

Martin R. 1959. Lehrbuch der Anthropologie in systematischer Darstellung mit besonderer Berücksichtigung der anthropologischen Methoden. Vol. 3. Jena: G. Fischer.

Maslow AH. 1954. Motivation and personality. New York: Harper and Brothers.

Masset C. 1973. La démographie des populations inhumée: essai de paléodémographie. L'Homme 13:95-131.

Masset C. 1990. Où en est la paléodémographie. Bull Mém Soc Anthropol Paris 2:109-121.

Masset C. 1994. La paléodémographie. Histoire et Mésure 9:381-394.

Mathisen R. 1989. Ecclesiastical factionalism and religious controversy in fifth century Gaul. Washington DC: Catholic University of America Press.

Matthews C, Leone M, Jordan K. 2002. The political economy of archaeological cultures: Marxism and American historical archaeology. J Soc Archaeol 2:109-134.

Mayhall JT. 2000. Dental morphology: techniques and strategies. In: Katzenberg MA, Saunders SR, editors. Biological anthropology of the human skeleton. New York: Wiley-Liss. p 103-134.

Mayr E. 1997. Evolution and the diversity of life: selected essays. Cambridge: Harvard University Press.

Mays S. 2002. The relationship between molar wear and age in an early 19th century AD archaeological human skeletal series of documented age at death. J Archaeol Sci 29:861-871.

McCollum MA, Sharpe PT. 2001. Developmental genetics and early hominid craniodental evolution. Bioessays 23:481-493.

McGuire RH. 1982. The study of ethnicity in historical archaeology. J Anthropol Archaeol 1:159-178.

McKay J. 1982. An exploratory synthesis of primordial and mobilizationist approaches to ethnic phenomena. Ethnic Racial Studies 5:395-420.

McKitterick R. 1977. The Frankish Church and the Carolingian Reforms, 789-895. London: Royal Historical Society.

McKitterick R. 1983. The Frankish Kingdoms under the Carolingians, 751-987. London: Longman.

McKitterick R. 2004. History and memory in the Carolingian world. Cambridge: Cambridge University Press.

Menin C. 1979. La population gallo-romaine de la nécropole de Maule (France, Yvelines): morphologie cranienne. Bull Mém Soc Anthropol Paris 6:85-110.

Méry A. 1968. La population de Blussangeaux au haut moyen age. Annales Littéraires l'Université Besançon 94:99-112.

Meskell L. 2001. Archaeologies of identity. In: Hodder I, editor. Archaeology theory today. Cambridge: Polity Press.

Metcalf P, Huntington R. 1991. Celebrations of death. The anthropology of mortuary ritual. Cambridge: Cambridge University Press.

Meyran R. 2000. Races et racisme: les ambiguités de l'antiracisme chez les anthropologues de l'entre-deux-guerres. Gradhiva 27:63-76.

Miller D. 1994. Frontier societies and the transition from late antiquity to the early middle ages. In: Mathisen R, Sivan H, editors. Shifting Frontiers in Late Antiquity. Aldershot: Variorium.

Mócsy A. 1974. Pannonia and Upper Moesia. London: Routledge and Paul.

Moerman M. 1965. Ethnic identification in a complex civilization: who are the Lue? Am Anthropol 67:1215-1230.

Moerman M. 1968. Being Lue: uses and abuses of ethnic identification. Berkley: University of California.

Momigliano A. 1963. The conflict between christianity and paganism in the fourth century AD. Oxford: Clarendon Press.

Moormann S, Guatelli-Steinberg D, Hunter J. 2013. Metamerism, morphogenesis, and the expression of carabelli and other dental traits in humans. Am J Phys Anthropol 150:400-408.

Moreland J. 2001. Archaeology and text. London: Duckworth.

Moreland J. 2006. Archaeology and texts: Subservience or enlightenment. Ann Rev Anthropol 35:135-151.

Morita W, Yano W, Nagaoka T, Abe M, Nakatsukasa M. 2014. Size and shape variability in human molars during odontogenesis. J Dent Res 93:275-280.

Morton SG. 1839. Crania Americana; or, a comparative view of the skulls of various aboriginal nations of North and South America: To which is prefixed an essay on the varieties of the human species. Philadelphia: J. Dobson.

Müller-Wille M, Dorfler W, Meier D, Kroll H. 1988. The transformation of rural society, economy, and landscape during the first millennium A.D.: Archaeological and palaeobotanical contributions from northern Germany and southern Scandinavia. Geografiska Annaler 70B:53-68.

Murdoch B, Read M. 2004. Early Germanic literature and culture. Rochester: Camden House.

Murray AC. 1986. The position of the *grafio* in the constitutional history of Merovingian Gaul. Speculum 64: 787-805.

Murray AC. 2002. Reinhard Wenskus on ‘ethnogenesis’, ethnicity and the origin of the Franks. In: Gillett A, editor. On Barbarian Identity. Critical Approaches to Ethnicity in the Early Middle Ages. Vol. 4. Turnhous: Brepols. p 39-68.

Musset L. 1963-1964. Le site mérovingien de Saint-Martin à Mondeville (Calvados). Fouilles du capitaine G. Caillaud (1913-1917). Bull Soc Antiquaires Normandie 57:145-188.

Naji S. 2011. La Granède, Millau. Rapport anthropologique 2011. CNRS-UMR5199, PACEA, Bordeaux 1.

Naroll R. 1964. On ethnic unit classification. Curr Anthrop 5:283-291.

Naroll R. 1968. Who the Lue are. In: Helm J, editor. Essays on the problem of tribe. American Ethnological Society proceedings, 1957-1972. Seattle, University of Washington Press. p 72-79.

Nelis M, Esko T, Mägi R, Zimprich F, Zimprich A, Toncheva D, Karachanak S, Piskáčková T, Balaščák I, Peltonen L, Jakkula E, Rehnström K, Lathrop M, Heath S, Gasparini P, D'Adamo P, Klovins J, Nikitina-Zake L, Kučinskas V, Kasnauskienė J, Lubinski J, Debniak T, Limnorska S, Khrunin A, Estivill X, Rabionet R, Marsal S, Julià A, Antonarakis SE, Deutsch S, Borel C, Attar H, Gagnebin M, Macek M, Krawczak M, Remm M, Metspalu A. 2009. Genetic structure of Europeans: a view from the North-East. PloS One 4:e5472.

Nelson JL. 2008. Frankish identity in Charlemagne's empire. In: Garipzanov IH, Geary PJ, Urbańczyk P, editors. Franks, Northmen, and Slavs: identities and state formation in early medieval Europe. Turnhout: Brepols. p 71-83.

Novelletto A. 2007. Y chromosome variation in Europe: continental and local processes in the formation of the extant gene pool. Annals Hum Biol 34:139-172.

Novembre J, Stephens M. 2008. Interpreting principal component analyses of spatial population genetic variation. Nature Genet 40:646-649.

Nystrom KC. 2006. Late Chachapoya population structure prior to Inka conquest. Am J Phys Anthropol 131:334-342.

Ortman SG. 2010. Genes, language and culture in Tewa ethnogenesis, A.D. 1150-1400. Ph.D., Arizona State University.

Osborn JW. 1978. Morphogenetic gradients: fields versus clones. In: Butler PM, Joysey KA, editors. Development, function and evolution of teeth. London: Academic Press. p 171-201.

Owsley DW, Jantz RL. 1978. Intracemetery morphological variation in Arikara crania from the Sully Site (39SL4), Sully County, South Dakota. Plains Anthropol 23:139-146.

Pálfi G. 1997. Maladies dans l'Antiquité et au Moyen-Âge. Paléopathologie compare des anciens Gallo-Romains et Hongrois. Bull Mém Soc Anthropol Paris 9:1-205.

Palo JU, Ulmanen I, Lukka M, Ellonen P, Sajantila A. 2009. Genetic markers and population history: Finland revisited. Eur J Hum Genet 17:1336-1346.

Parker H. 1965. Feddersen Wierde and Vallhager: a contrast in settlements. Medieval Arch 9:1-10.

Patte E. 1937. Étude anthropologique des crânes barbares recueillis par M. Coquillaud à Savigné (Vienne). Bull Mém Soc Anthropol Paris 8:15-62.

Paxton FS. 1990. Christianizing death. The creation of a ritual process in early medieval Europe. Ithaca: Cornell University Press.

Peck JJ. 2009. The biological impact of culture contact: a bioarchaeological study of Roman colonialism in Britain. PhD dissertation, Department of Anthropology, The Ohio State University.

Peña JA, Garcia-Obregon S, Perez-Miranda AM, De Pancorbo MM, Alfonso-Sanchez MA. 2006. Gene flow in the Iberian Peninsula determined from Y-chromosome STR loci. Am J Human Biol 18:532-539.

Penrose LW. 1953. Distance, size and shape. Ann Eugenics 18:337–343.

Pereira L, Cunha C, Alves C, Amorim A. 2005. African female heritage in Iberia: a reassessment of mtDNA lineage distribution in present times. Hum Biol 77:213-229.

Perry MA. 2007. Is bioarchaeology a handmaiden to history? Developing a historical bioarchaeology. J Anthropol Archaeol 26:486-515.

Perzigian AJ. 1975. Natural selection on the dentition of an Arikara population. Am J Phys Anthropol 42:63-70.

Pétriquin AM, et al. 1980. Le site funéraire de Soyria à Clairvaux-les-Lacs (Jura). Rév Archéol Est Centre-Est 31:157-230.

Peyre E. 1979. La population mérovingienne de la nécropole de Maule (France, Yvelines): analyse anthropologique univariée qualitative et quantitative des crania. Bull Mém Soc Anthropol Paris 6:47-84.

Peyre E. 1980. Analyse multivariée sur le calvarium des mérovingiens de Maule (France, Yvelines). Bull Mém Soc Anthropol Paris 7:233-257.

Pietrusewsky M, Douglas MT. 1992. The skeletal biology of an historic Hawaiian cemetery: familial relationships. Homo 43:245-262.

Pilet C. 1980. La nécropole de Frénouville: étude d'une population de la fin du III du VII siècle. Brit Archaeol Report 83.

Pilet C. 1983. Sannervile (Calvados). Archéol Méd 13: 251-252.

Pilet C, Alduc-Le Bagousse A, Blondiaux J, Buchet L, Grévin G, Pilet-Lemière J. 1990. Les nécropoles de Giberville (Calvados), fin du V siècle – fin du VII siècle après J.-C. Archéol Méd 20:1-140.

Pilet C, Alduc-Le Bagousse A, Blondiaux J, Buchet L, Pilet-Lemiere J. 1992. Le village de Sannerville, "Lirose", fin de la periode gauloise au VII siècle après J.-C. Archeol Med 22:1-189.

Pilet C. 1994. La nécropole de Saint-Martin de Fontenany (Calvados). Recherches sur les peuplement de la plaine de Caen du V siècle avant J.C. au VII siècle après J.C. Gallia 54.

Pohl W. 1998a. Introduction: Strategies of distinction. In: Pohl W, Reimitz H, editors. Strategies of distinction: The construction of ethnic communities, 300-800. Boston: Brill. p 1-16.

Pohl W. 1998b. Telling the difference: signs of ethnic identity. In: Pohl W, Reimitz H, editors. Strategies of distinction: The construction of ethnic communities, 300-800. Boston: Brill. p 17-69.

Pohl W. 2000. Die Germanen. Munchen: Oldenbourg Wissenschaftsverlag GmBH.

Pohl W, Beaupré N. 2005. Aux origines d'une Europe ethnique: transformations d'identité entre Antiquité et Moyen Age. Annales. Histoire, Sciences Sociales 60:183-208.

Polly PD. 2007. Development with a bite. Nat 449:413-415.

Porte P. 1984. Le camp de Larina, forteresse mérovingienne. Dossiers de l'Archéol 78:79-82.

Porte P. 2011. Larina, de l'Antiquité au Moyen Âge. Vol. 2. Biarntz: Séguier.

Potter RHY, Yu PL, Christian JC. 1979. Association of twin zygosity with the mean and variance of tooth size. Acta Genet Med Gemell 28:211-223.

Potter RHY, Corruccini RS, Green LJ. 1981. Variance of occlusion traits in twins. J Craniofac Genet Develop Biol 1:217-227.

Potter RHY, Rice JP, Dahlberg AA, Dahlberg T. 1983. Dental size trait within families : path analysis for first molar and lateral incisor. Am J Phys Anthropol 61:283-289.

Powell JF, Neves WA. 1999. Craniofacial morphology of the First Americans: pattern and process in the peopling of the New World. Yrbk Phys Anthropol 42:153-188.

Prichard JC. 1813. Researchers in the physical history of Man. London: J. and A. Arch.

Radcliffe-Brown AR. 1952. Structure and function in primitive society: essays and addresses. London: Cohen and West.

Ragsdale CS, Edgar HJH. 2015. Cultural interaction and biological distance in postclassic period Mexico. Am J Phys Anthropol 157:121-133.

Ramos-Luis E, Blanco-Verea A, Brión M, Van Huffel V, Sánchez-Diz P, Carracedo A. 2014. Y-chromosomal DNA analysis in French male lineages. Forensic Sci Intl Genet 9:162-168.

Randsborg K. 1980. The Viking Age in Denmark: The Formation of a State. London: Duckworth.

Randsborg K. 1991. The first millennium A.D. in Europe and the Mediterranean. Cambridge: Cambridge University Press.

Rębała K, Martínez-Cruz B, Tönjes A, Kovacs P, Stumvoll M, Lindner I, Büttner A, Wichmann H-E, Siváková D, Soták M, Quintana-Murci L, Szczerkowska Z, Comas D, Genographic Consoritum. 2012. Contemporary paternal genetic landscape of Polish and German populations: from early medieval Slavic expansion to post-World War II resettlements. Eur J Hum Genet 21:415-422.

Redjeb TB, Duvette L, Quérel P, Chaidron C, Lepetz S, Matterne V, Maréchal D. 2005. Les campagnes antiques: bilans et perspectives. Rev Archéol Picardie 3-4: 177-222.

Reid C, Van Reenen JF, Groeneveld HT. 1991. Tooth size and Carabelli trait. Am J Phys Anthropol 84:427-432.

Reimitz H. 2008. *Omnes Franci*: Identifications and identities of the early medieval Franks. In: Garipzanov IH, Geary PJ, Urbańczyk P, editors. Franks, Northmen, and Slavs. Turnhout: Brepols. p 51-70.

Relethford JH. 1991a. Effect of population size on marital migration distance. Hum Biol 63:95-98.

Relethford JH. 1991b. Genetic drift and anthropometic variation in Ireland. Hum Biol 63:155-165.

Relethford JH. 1994. Craniometric variation among modern human populations. Am J Phys Anthropol 95:53-62.

Relethford JH. 1996. Genetic drift can obscure population history: problem and solution. Hum Biol 68:29-44.

Relethford JH. 2003. Anthropometric data and population history. In: Herring DA, Swedlund AC, editors. Human biologists in the archives: demography, health, nutrition, and genetics in historical populations. Cambridge: Cambridge University Press. p 32-52.

Relethford JH. 2004. Boas and beyond: migration and craniometric variation. Am J Hum Biol 16:379-386.

Relethford JH, Blangero J. 1990. Detection of differential gene flow from patterns of quantitative variation. Hum Biol 62:5-25.

Relethford JH, Lees FC. 1982. The use of quantitative traits in the study of human population structure. Yrbk Phys Anthropol 25:113–132.

Relethford JH, Crawford MH, Blangero J. 1997. Genetic drift and gene flow in post-famine Ireland. Hum Biol 69:443-465.

Reuter T. 1985. Plunder and tribute in the Carolingian Empire. Trans Roy Hist Soc 35:75-94.

Reynolds S. 1998. Our forefathers? Tribes, peoples, and nations in the historiography of the Age of Migrations. In: Murray AC, editor. After Rome's fall: narrators and sources of early medieval history. Toronto: University of Toronto Press. p 17-36.

Rice P, Rice D. 2005. The final frontier of the Maya: Central Petén, Guatemala, 1450-1700 CE. In: Parker B, Rodseth L, editors. Untaming the frontier in anthropology, archaeology, and history. Tucson: University of Arizona Press. p 147-173.

Richard C, Pennarun E, Kivisild T, Tambets K, Tolk H-V, Metspalu E, Reidla M, Chevalier S, Giraudet S, Lauc LB, Peričić M, Rudan P, Claustres M, Journel H, Dorval I, Müller C, Villems R, Chaventré A, Moisan J-P. 2007. An mtDNA perspective of French genetic variation. Annals Hum Biol 34:68-79.

Rizk OT, Amugongo SK, Mahaney MC, Hlusko LJ. 2008. The quantitative genetic analysis of primate dental variation: history of the approach and prospects for the future. In: Irish JD, Nelson GC, editors. Technique and application in dental anthropology. Cambridge: Cambridge University Press. p 317-346.

Roberts CA. 2006. A view from afar: bioarchaeology in Britain. In: Buikstra JE, Beck LA, (editors). Bioarchaeology: the contextual analysis of human remains. New York: Academic Press. p 417-439.

Roewer L, Kayser M, Dieltjes P, Nagy M, Bakker E, Krawczak M, de Knijff P. 1996. Analysis of molecular variance (AMOVA) of Y-chromosome-specific microsatellites in two closely related human populations. Hum Mol Gen 5:1029-1033.

Rogers AR, Harpending HC. 1983. Population structure and quantitative characters. Genetics 105:985-1002.

Roosens EE. 1989. Creating ethnicity. The process of ethnogenesis. Newbury Park: Sage.

Roseman CC, Weaver TD. 2004. Multivariate apportionment of global human craniometric diversity. Am J Phys Anthropol 125:257-263.

Rothe J, Melisch C, Powers N, Geppert M, Zander J, Purps J, Spors B, Nagy M. 2015. Genetic research at a fivefold children's burial from medieval Berlin. Forensic Sci Intl Genet 15:90-97.

Royce A. 1982. Ethnicity identity: strategies of diversity. Bloomington: Indiana University Press.

Riquet R. 1951. Les néolithiques du tumulus de Fontenay-le-Marmion. Bull Mém Soc Anthropol Paris 2:105-118.

Russell JC. 1958. Late ancient and medieval populations. Trans Am Phil Soc 48:1-152.

Russell JC. 1972. Population in Europe 500-1500. In: Cipolla CM, editor. The Fontana economic history of Europe. Glasgow: Collins.

Saint-Pierre C, Naji S, Scrinzi M, Legendre S, Laguarrigue P, Marty G. 2011. La Granède (Millau, Aveyron). Église paléochrétienne et espace funéraire. Unpublished report, submitted to Direction Régionale des Affaires Culturelles Midi-Pyrénées.

Salmela E, Lappalainen T, Fransson I, Andersen PM, Dahlman-Wright K, Fiebig A, Sistonen P Savontaus M-L, Schreiber S, Kere J, Lahermo P. 2008. Genome-wide analysis of single nucleotide polymorphisms uncovers population structure in Northern Europe. PLoS One 3:e3519.

Sauter M-R. 1939. Quelques cas de déformation crânienne artificielle de l'époque barbare dans la région de Genève. Archives Suisses Anthropol Genève 8:355-360.

Sauter M-R. 1961. Quelques contributions de l'anthropologie à la connaissance du Haut Moyen-Âge. Mém Doc Soc Hist Archéol Genève 40:1-18.

Sauter M-R, Moeschler P. 1960. Caractères dentaires mongoloides chez des Burgondes de la Suisse occidentale (Saint-Préx, Vaud). Archives des Sci 13:387-426.

Sazzini M, Sarno S, Luiselli D. 2014. The Mediterranean human population: an anthropological genetics perspective. In: Goffredo S, Dubinsky Z, editors. The Mediterranean Sea. Its history and present challenges. New York: Springer. p 529-551.

Schillaci MA, Stojanowski CM. 2003. Postmarital residence and biological variation at Pueblo Bonito. Am J Phys Anthropol 120:1-15.

Sciulli PW, Janini C, Giesen M. 1988. Phenotypic selection on the dentition in a Late Archaic population of Ohio. Am J Phys Anthropol 76:527-533.

Scott GR, Potter RHY. 1984. The analysis of tooth crown morphology in American white twins. Anthropol 22:223-231.

Scott GR, Turner CG. 1997. The anthropology of modern human teeth. Cambridge: Cambridge University Press.

Scuvée F. 1973. Le cimetière barbare de Réville (Manche) (VIe et VIIe siècles). Caen: Caron.

Serafin S, Peraza Lope C, Gonzalez EU, Ku PD. 2014. Odontometric investigation of the origin of freestanding shrine ossuaries at Mayapan. In: Wrobel GD, editor. The bioarchaeology of space and place. New York: Springer. p 141-167.

Sharpe PT. 1995. Homeobox genes and orofacial development. Connect Tissue Res 32:17-25.

Sharrock SR. 1974. Crees, Cree-Assiniboines, and Assiniboines: interethnic social organization on the far northern plains. Ethnohist 21:95-122.

Shils EA. 1957. Center and periphery: essays in macrosociology. Selected papers of Edward Shils. Chicago: Chicago University Press.

Simmer A. 1993. La nécropole mérovingienne d'Énnery (Moselle). Thionville: Association Française d'Archéologie Mérovingienne.

Simon C. 1979. La déformation artificielle de la nécropole de Sézégnin (GE). Archéol Suisse 2:186-188.

Simon C. 1982. Nécropole de Sézégnin (Avusy, Genève). Nécropole de Thoiry (Ain, France). Étude anthropologique et paléodémographique. Archives Suisses Anthropol Gen 46:77-175.

Simon C. 1990. Quelques réflexions sur la paléodémographie. Bull Mém Soc Anthropol Paris 2:123-132.

Simon C. 1995. La déformation cranienne artificielle dans le basin du Leman: État de la question. In: Gaillard de Semainville H., editor. Les Burgondes. Apports de l'archéologie. Actes du colloque international de Dijon (5-6 novembre 1992). Dijon: Conseil Régional de Bourgogne et du Ministère de la Culture. p 205-215.

Singer M. 1968. The concept of culture. In: Sills DL, editor. International encyclopedia of the social sciences. London: Macmillan and Free Press. p 527-543.

Sjøvold T. 1984. A report on the heritability of some cranial measurements and non metric traits. In: van Vark GN, Howells WW, editors. Multivariate statistical methods in physical anthropology. Dordrecht: D. Reidel. p 223-246.

Skinner M. 2002. Enamel-dentine junction morphology of extant hominoid and fossil hominin lower molars. Ph.D. Dissertation, George Washington University.

Smith BH. 1984. Patterns of molar wear in hunter-gatherers and agriculturalists. Am J Phys Anthropol 63:39-56.

Smith CAB. 1972. Coefficients of biological distance (Review). Annals Hum Genet 36:241-245.

Smouse PE, Long JC, Sokal RR. 1986. Multiple regression and correlation extensions of the Mantel Test of matrix correspondence. System Zool 35:627-632.

Sofaer JR. 2006. The body as material culture: a theoretical osteoarchaeology. Cambridge: Cambridge University Press.

Sokal RR, Harding RM, Oden NL. 1989. Spatial patterns of human gene frequencies in Europe. Am J Phys Anthropol 80:267-294.

Sparks CS, Jantz RL. 2002. A reassessment of human cranial plasticity: Boas revisited. Proc Natl Acad Sci USA 99:14636-14639.

Spence MW. 1974. The study of residential practices among prehistoric hunters and gatherers. World Archaeol 5:346-357.

Steadman DW. 2001. Mississippians in motion? A population genetic analysis of interregional gene flow in west-central Illinois. Am J Phys Anthropol 114:61-73.

Steuer 1982. Frühgeschichtliche Sozialstrukturen in Mitteleurope: Eine Analyse der Auswertungsmethoden des archäologischen Quellenmaterials. Göttingen: Abhandlungen der Akademie der Wissenschaften.

Stojanowski CM. 2001. Cemetery structure, population aggregation, and phenotypic variability in the mission cemeteries of La Florida. Ph.D. dissertation, Department of Anthropology, University of New Mexico.

Stojanowski CM. 2004. Population history of native groups in pre- and postcontact Spanish Florida: aggregation, gene flow, and genetic drift on the southeastern U.S. Atlantic coast. Am J Phys Anthropol 123:316-322.

Stojanowski CM. 2005a. The bioarchaeology of identity in Spanish colonial Florida: Social and evolutionary transformation before, during, and after demographic collapse. Am Anthropol 107:417–431.

Stojanowski CM. 2005b. Biocultural histories in La Florida: A bioarchaeological perspective. Tuscaloosa: University of Alabama Press.

Stojanowski CM. 2009. Bridging histories: the bioarchaeology of identity in postcontact Florida. In: Knudson KJ, Stojanowski CM, editors. Bioarchaeology and identity in the Americas. Gainesville: University Press of Florida. p 59-81.

Stojanowski CM. 2010. Bioarchaeology of ethnogenesis in the colonial Southeast. Gainesville: University Press of Florida.

Stojanowski CM, Buikstra JE. 2004. Biodistance analysis, a biocultural enterprise: A rejoinder to Armelagos and Van Gerven (2003). Am Anthropol 106:430-431.

Stojanowski CM, Buikstra JE. 2005. Research trends in human osteology: a content analysis of papers published in the American Journal of Physical Anthropology. Am J Phys Anthropol 128:98-109.

Stojanowski CM, Schillaci MA. 2006. Phenotypic approaches for understanding patterns of intracemetery biological variation. Yrbk Phys Anthropol 49:49-88.

Stork I. 1991. Neues aus Lauchheim, Ostalbkreis. Archaeologische Augrabungen in Baden-Wurttemberg. p 209-215.

Sturtevant W. 1971. Creek into Seminole. In: Leacock E, Lurie N, editors. North American Indians in historical perspective. New York: Random House. p 92-128.

Susanne C. 1975. Genetic and environmental influences on morphological characteristics. Annals Hum Biol 2:279-287.

Susanne C. 1977. Heritability of anthropological characters. Hum Biol 49:573-580.

Tacitus C. 1840 [AD 83]. Germaniae Libellus. London: Taylor and Walton.

Talbert RJA. 2010. Rome’s world: the Peutinger Map reconsidered. Cambridge: Cambridge University Press.

Tatarek NE, Sciulli PW. 2000. Comparison of population structure in Ohio's Late Archaic and Late Prehistoric periods. Am J Phys Anthropol 112:363-376.

Teaford MF, Ungar PS. 2006. Dental adaptations of African apes. In: Henke W, Tattersall I, Hardt T, editors. Handbook of Paleoanthropology. Berlin: Springer. p 1107-1132.

Theuws F. 2009. Grave goods, ethnicity, and the rhetoric of burial rites in Late Antiquity northern Gaul. In: Derks T, Roymans N, editors. Ethnic constructs in Antiquity. Amsterdam: Amsterdam University Press. p 283-320.

Thompson EA. 1996. The Huns. Oxford: Blackwell.

Todd M. 2004. The Early Germans. Oxford: Blackwell Publishing.

Topf AL, Gilbert MTP, Dumbacher JP, Hoelzel AR. 2006. Tracing the phylogeography of human populations in Britain based on 4^{th}-11^{th} century mtDNA genotypes. Mol Biol Evol 23:152-161.

Torroni A, Bandelt H-J, Macauley V, Richards M, Cruciani F, Rengo C, Martinez-Cabrera V, Villems R, Kivisild T, Metspalu E, Parik J, Tolk H-V, Tambets K, Forster P, Karger B, Francalacci P, Rudan P, Janicijevic B, Rickards O, Savontaus M-L, Huopenen K, Laitinen V, Koivumäki S, Sykes B, Hickey E, Novelletoo A, Moral P, Sellitto D, Coppa A, Al-Zaheri N. 2001. A signal, from human mtDNA, of postglacial recolonization in Europe. Am J Hum Gen 69:844-852.

Townsend GC. 1992. Genetic and environmental contributions to morphometric dental variation. J Hum Ecol 2:61-72.

Townsend GC, Brown T. 1978. Heritability of permanent tooth size. Am J Phys Anthropol 49:497-504.

Townsend GC, Brown T, Richards LC, Rogers JR, Pinkerton SK, Travan GR, Burgess VB. 1986. Metric analyses of the teeth and faces of South Australian twins. Acta Genet Med Gemellol (Roma) 35:179-192.

Townsend G, Harris EF, Lesot H, Clauss F, Brook A. 2009. Morphogenetic fields within the human dentition: a new clinically relevant synthesis of an old concept. Arch Oral Biol 54:S34-S44.

Townsend G, Richards L, Hughes T. 2003. Molar intercuspal dimensions: genetic input to phenotypic variation. J Dent Res 82:350-355.

Townsend G, Bockmann M, Hughes T, Brook A. 2012. Genetic, environmental and epigenetic influences on variation in human tooth number, size and shape. Odontol 100:1-9.

Tucker A, Sharpe P. 2004. The cutting-edge of mammalian development: how the embryo makes teeth. Nature Rev Genet 5:499-508.

Turner CG. 1986. The first Americans: the dental evidence. Natl Geogr Res 2:37-46.

Turner VW. 1969. The ritual process: structure and anti-structure. Aldine Transaction: London.

Tylor EB. 1873. Primitive culture. London: John Murray.

Tyrell A. 2000. Skeletal non-metric traits and the assessment of inter- and intra-population diversity: past problems and future potential. In: Cox M, Mays S, editors. Human osteology in archaeology and forensic science. London: Greeenwich Medical Media Ltd. p 289-306.

Ungar PS. 2010. Mammal teeth: origin, evolution, and diversity. Baltimore: Johns Hopkins University Press.

Utermohle CJ, Zegura SL. 1982. Intra- and interobserver error in craniometry: a cautionary tale. Am J Phys Anthropol 57:303-310.

Utermohle CJ, Zegura SL, Heathcote GM. 1983. Multiple observers, humidity, and choice of precision statistics: factors influencing craniometric data quality. Am J Phys Anthropol 61:85-95.

Vallois H. 1925. Étude des ossements franco-mérovingiens de Baye (Marne). Bull Mém Soc Anthropol Paris 7:180-217.

Vallois HV. 1943. Anthropologie de la population française. Didier: Paris.

van Es WA. 1967. Wijster: a native village beyond the imperial frontier. Palaeohistoria 11.

van Gennep A. 1909. Les rites de passage. Emile Nourry: Paris.

van Ossel P, Ouzoulias P. 2000. Rural settlement economy in northern Gaul in the late Empire. J Roman Arch 13:133-160.

Van Reenen JF. 1982. The effects of attrition on tooth dimensions of San (Bushmen). In: Kurtén B, editor. Teeth: form, function and evolution. New York: Columbia University Press. p 182-203.

Varela HH, Cocilovo JA. 2002. Genetic drift and gene flow in a prehistoric population of the Azapa Valley and Coast, Chile. Am J Phys Anthropol 118:259-267.

Varoqueaux C. 1966. Fouille d'un cimetière du Hallstatt final à Ifs (Calvados). Annales de Normandie 16:295-321.

Varzari A. 2006. Population history of the Dniester-Carpathian evidence from Alu insertion and Y-chromosome polymorphisms. Ph.D., Ludwig-Maximilians-Universität München.

Vatteoni S. 1989. La recherche des liens de parenté par l'anthropologie physique. D.E.A. Université de Caen.

Verneau R, Ripoche O. 1898. Les sépultures gallo-romaines et mérovingiennes de Mareuil-sur-Ourcq (Oise). Anthropol 19:497-530.

Vidoli, GM. 2012. Shifting borders: population movement and the geopolitical landscape of the Middle Cumberland Region during the Mississippian period. Ph.D. State University of New York at Binghamton.

Viollet le Duc E. 1860. Ruines de Champlieu (Oise). Rev Archéol 1:44-54.

Vitzthum VJ. 2003. A number no greater than the sum of its parts: the use and abuse of heritability. Hum Biol 75:539-558.

von Cramon-Taubadel N. 2014. Evolutionary insights into global patterns of human cranial diversity: population history, climatic and dietary effects. J Anthropol Sci 92:43-77.

Voss BL. 2005. From casta to Californio: social identity and the archaeology of culture contact. Am Anthrop 107:461-474.

Voss BL. 2008. The archaeology of ethnogenesis: race and sexuality in colonial San Francisco. Berkeley: University of California Press.

Wallace-Hadrill JM. 1983. The Frankish Church. Oxford: Oxford University Press.

Weale ME, Weiss DA, Jager RF, Bradman N, Thomas MG. 2002. Y chromosome evidence for Anglo-Saxon mass migration. Mol Biol Evol 19:1008-1021.

Weaver TD, Roseman CC, Stringer CB. 2007. Were neandertal and modern human cranial differences produced by natural selection or genetic drift. J Hum Evol 53:135-145.

Weiss KM, Stock D, Zhao Z. 1998. Dynamic interactions and the evolutionary genetics of dental patterning. Crit Rev Oral Biol Med 9:369-398.

Wells P. 1999. The barbarians speak: How the conquered peoples shaped Roman Europe. Princeton: Princeton University Press.

Wenskus R. 1961. Stammesbildung und Verfassung: das Werden der fruehmittelalterlichen gentes. Böhlau: Koln and Graz.

Werner J. 1964. Frankish royal tombs in the cathedrals of Cologne and St-Denis. Antiquity 38: 201-216.

Wickham C. 1984. The other transition: From the ancient world to feudalism. Past and Present 103:3-36.

Wickham C. 2005. Framing the Early Middle Ages. Oxford: Oxford University Press.

Wilkie L, Farnsworth P. 2005. Sampling many pots: an archaeology of memory and tradition at a Bahamian plantation. Gainesville: University Press of Florida.

Williams-Blangero S. 1989. Clan-structured migration and phenotypic differentiation in the Jirels of Nepal. Hum Biol 61:143-157.

Williams-Blangero S, Blangero J. 1989. Anthropometric variation and the genetic structure of the Jirels of Nepal. Hum Biol 61:1-12.

Williams-Blangero S, Blangero J. 1990. Effects of population structure on within-group variation in the Jirels of Nepal. Hum Biol 62:131-146.

Willems W. 1989. Rome and its frontier in the north: the role of the periphery. In: Randsborg K, editor. The birth of Europe: archaeology and social development in the first millennium AD. Rome: Analecta Romana Instituti Danici. p 33-45.

Wolfram H. 1988. History of the Goths. Berkeley: University of California Press.

Wolfram H. 1990. Die Goten von der Anfängen bis zur Mitte des sechsten Jahrhunderts: Entwurf einer historischen Ethnographie, 3rd edition. Munich: Verlag.

Wood IN. 1993. The Merovingian kingdoms, 481-751. London: Longman.

Wright S. 1943. Isolation by distance. Genetics 28:114-138.

Wright S. 1951. The genetical structure of populations. Ann Eugen 15:323-354.

Wright S. 1969. Evolution and the genetics of populations. Vol. 2. The theory of gene frequencies. Chicago: University of Chicago Press.

Yelvington KA. 1991. Ethnicity as practice? A comment on Bentley. Comp Studies Soc Hist 33:158-168.

Young B. 1977. Paganisme, christianisation et rites funéraires mérovingiens. Archéologie Médiévale VII: 5-81.

Zammit J. 1990. Nouvelles perspectives en anthropologie des populations anciennes: paléoépidemiologie et approche de l'état sanitaire. Bull Mém Soc Anthropol Paris 2: 149-158.

Zimmerman A, Hilpert J, Wendt KP. 2009. Estimations of population density for selected periods between the Neolthic and AD 1800. Hum Biol 81: 357-380.

Zschocke J, Hoffman GF. 1999. Phenylketonuria mutations in Germany. Hum Genet 104:390-398.