Developing an Infrastructure for Biodistance Research

Using Deciduous Dental Phenotypes

by

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ABSTRACT

Bioarchaeologists often use dental data and spatial analysis of cemeteries to infer the biological and social structure of ancient communities. This approach is commonly referred to as biological distance ("biodistance") analysis. While permanent crown data feature prominently in these efforts, few studies have verified the accuracy of biodistance methods for recognizing *child* relatives using *deciduous* teeth. Thus, as subadults comprise an essential demographic subset of mortuary assemblages, deciduous phenotypes may represent a critical but underutilized source of information on the underlying genetic structure of past populations. The goal of the dissertation is to quantitatively analyze the developmental program underlying deciduous phenotypes and to evaluate their performance in accurately reconstructing known genealogical relationships. This project quantifies morphological variation of deciduous and permanent tooth crowns from stone dental casts representing individuals of known pedigree deriving from three distinct populations: European Canadians, European Australians, and Aboriginal Australians.

To address the paucity of deciduous-focused validation research, phenotypic distances generated from the dental data are subjected to performance analyses (biodistance simulations) and compared to genetic distances between individuals. While family-specific results vary, crown morphology performs moderately well in distinguishing relatives from non-relatives. Comparisons between deciduous and permanent results (i.e., Euclidean distances, Mantel tests, multidimensional scaling output) indicate that deciduous crown variation provides a more direct reflection of the underlying genetic structure of pedigreed samples. The morphology data are then analyzed within a quantitative genetic framework using maximum likelihood variance components analysis. Novel narrow-sense heritability and pleiotropy estimates are generated for the complete suite of deciduous and permanent crown characters, which facilitates comparisons between samples, traits, dentitions, arcades, antimeres, metameres, scoring standards, and dichotomization breakpoints. Results indicate wide-ranging but moderate heritability estimates for morphological traits, as well as low to moderate integration for characters within (deciduous-deciduous; permanent-permanent) and between (deciduous-permanent) dentitions. On average, deciduous and permanent homologues are more strongly genetically correlated than characters within the same tooth row. Results are interpreted with respect to dental development and biodistance methodology. Ultimately, the dissertation empirically validates the use of dental morphology as a proxy for underlying genetic information, including deciduous characters.

This dissertation is dedicated to my family: my parents, Chuck and Peggy Paul, and my sisters and best friends, Maddie and Colleen Paul. Thank you for providing me strong roots and able wings.

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CHAPTER 1

INTRODUCTION

Both today and in the distant past, kinship identities have shaped human behaviors and worldviews. Bioarchaeology expands our understanding of kinship by contributing deep time perspectives (Gowland and Knüsel, 2006; Knudson and Stojanowski, 2008, 2009; Johnson and Paul, 2016) and often turns to intrasite or intracemetery biological distance analyses (biodistance analyses) to explore the intersection of biological and social affinity as manifested in mortuary behavior (see Corruccini and Shimada, 2002; Stojanowski and Schillaci, 2006; Meyer et al., 2012; Paul et al., 2013; Duncan, 2015; Miller, 2015; Prevedorou and Stojanowski, 2017), especially where genetic material is degraded or unavailable. Unfortunately, researchers tend to exclude subadult biological material from these studies, leaving children underrepresented in contextual examinations of population structure, kinship (as a dimension of collective social identity), and kin-centered (bio)social phenomena (but see Pilloud, 2009; Pilloud and Larsen, 2011; Sciulli and Cook, 2016; Sutter and Chhatiawala, 2016). This dissertation addresses the standard omission of subadults—and specifically deciduous dental datasets—from biodistance studies by using modern pedigreed samples to explore the foundations of deciduous crown variation and its potential to contribute to bioarchaeological kinship research. The dissertation's ultimate aim is to generate a knowledge-based infrastructure for incorporating deciduous dental data into biodistance research.

Biodistance: Theory, Assumptions, and Multiscalar Analytical Frameworks

Buikstra et al. (1990) defined biological distance (biodistance) as "a measurement of population divergence based on polygenic traits . . . [that] can reflect both genetic and environmental differentiation between populations" (1). Systematic, if not also typological or descriptive, studies of phenotypic variation have a long history (e.g., Morton, 1839; Hrdlička, 1907, 1918a, 1920; Boas, 1912; Hooton, 1930), yet it was in the spirit of Washburn's New Physical Anthropology (Washburn, 1951, 1953) that contextualized, population-focused biodistance research proliferated (for historical discussions of typology, race, and biodistance research see Adams et al., 1978; Armelagos et al., 1982; Armelagos and Van Gerven, 2003; Stojanowski and Buikstra, 2005). Even before bioarchaeology emerged as an autonomous field championing theoretically-grounded and problem-oriented research (Buikstra, 1977; Buikstra and Beck, 2006; Agarwal and Glencross, 2011; Martin et al., 2013; Larsen, 2015), phenotypic data were used to explore relationships between regional populations (e.g., Neumann, 1952; Laughling and Jorgensen, 1956; Brothwell, 1959; Berry and Berry, 1967; Wilkinson, 1971; Corruccini, 1972; Howells, 1973, 1989; Pietrusewsky, 1973; Turner, 1985a, 1986) and to detect microevolutionary change over time (e.g., Ossenberg, 1969; Turner, 1969; Jantz, 1972, 1973). In these efforts, osteological and dental phenotypic variation were interpreted as quantifiable reflections of a sample's (or group of samples') underlying genotypic structure, the reasoning being that closely related individuals are expected to be more phenotypically similar than non-relatives (Buikstra et al., 1990; Pietrusewsky, 2013; Hefner et al., 2016).

In this way, biodistance research has been founded upon theoretical expectations informed by an understanding of the effects of specific evolutionary processes on allele frequencies and population variation (Konigsberg, 2006; Stojanowski and Schillaci, 2006; Relethford, 2016). These processes include mutation, gene flow, genetic drift, and selection (Hartl and Clark, 1997). The rates of change in biological variation caused by these evolutionary processes depend on demographic parameters, such as effective population size (Relethford, 1980, 1986, 1991; 2007; Rogers and Harpending, 1986; Chakraborty, 1990; Hartl and Clark, 1997), but their impact is considered detectable within time spans typifying archaeological investigation (Relethford et al., 1997; Relethford, 2016; Stojanowski and Schillaci, 2006). Though theorists laid the foundation for modern population genetics during the first half of the 20th century (e.g.; Wright, 1922, 1932, 1951, 1965; Fisher, 1930, 1953; Haldane, 1937, 1949, 1954, 1956), it was not until the 1970's that bioarchaeologists began to directly engage population genetics theory. Konigsberg (2006) cites two foundational projects responsible for this integration: Cadien et al. (1974) and the dissertation work of Rebecca Lane (Lane, 1977; see also Lane and Sublett, 1972). Cadien et al. (1974) drew upon genetic models and theory in order to present an essential critique: skeletal samples represent lineages and not true biological (breeding) populations (Cadien et al., 1974). Lane's work, meanwhile, focused on biological variation in Alleghany Seneca cemeteries (Lane and Sublett, 1972; Lane, 1977). With reference to genealogical information and cranial non-metric traits, Lane examined the correspondence of phenotypic distances and estimated kinship measures (Lane and Sublett, 1972; Lane, 1977; Konigsberg, 2006). This research was innovative in its direct comparison of genetic and phenotypic affinity, and it was among the first studies to “distinguish quantitatively genetic relationships *within* a single [skeletal] population” (Lane and Sublett, 1972:186).

In biodistance analysis, phenotypes are most commonly quantified as cranial non-metric and dental morphological trait frequencies, as well as cranial metrics and odontometrics (i.e., metrical trait means/variance) (Buikstra et al., 1990; Stojanowski and Schillaci, 2006). Thus, biodistance approaches the same questions addressed by anthropological genetic research but with a distinct dataset that *approximates* the behavior of genetics (Buikstra et al., 1990; Stojanowski and Schillaci, 2006; Hefner et al., 2016). This approximation (i.e., non-equivalence) weds biodistance analysis to a number of inherent assumptions and limitations: 1) changes in allele frequencies are observable and quantifiable by reference to phenotype (Relethford, 2007; Konigsberg, 2012), and 2) biological affines will be more phenotypically similar than individuals that share no biological affinity (Stojanowski and Schillaci, 2006; Konigsberg, 2012; Relethford, 2016). Biodistance also functions under the assumption that 3) mutation rates and selection are held constant and that environmental effects are minimal and/or provide randomly distributed input into population-wide phenotypic variation (Buikstra et al., 1990; Stojanowski and Schillaci, 2006). Advances in quantitative trait research and modeling (e.g., Crawford and Workman, 1973; Relethford and Lees, 1982; Williams-Blangero, 1987, 1989a, 1989b; Relethford and Blangero, 1990; Relethford 1991, 1996, 2001, 2003, 2004, 2007; Lande, 2000; Konigsberg, 2006, 2012) have been useful in addressing these assumptions, enabling more direct integration of population genetic models into biodistance research (e.g., Stefan, 1999; González-José et al., 2001, 2002; Steadman, 2001; Stojanowski, 2004, 2005c; Byrd, 2014; Irish, 2015). The final assumption relates to a pervasive complication in bioarchaeological and paleodemographic research: 4) skeletal samples are not equivalent to natural biological populations (Cadien et al., 1974; Kennedy, 1981; Wood et al., 1992; DeWitte and Stojanowski, 2015). Bioarchaeological samples, instead, represent an accumulation of skeletal remains within a specific location or site (Cadien et al., 1974; Kennedy, 1981; Konigsberg, 1987, 1990a; Wood et al. 1992) or "temporal aggregates or lineages" (Stojanowski and Schillaci, 2006:51). Advances in modern dating techniques have somewhat ameliorated this concern, as has the fluorescence of bioarchaeology. As an anthropological subfield, bioarchaeology advocates a biocultural approach to research and emphasizes context as essential to analytical interpretation (Buikstra, 1977; Buikstra et al., 1990; Zuckerman and Armelagos, 2011; Martin et al., 2013).

Researchers apply biodistance analyses at various scales, examining patterns of biological variation at the global, regional, site, or cemetery level (Konigsberg, 1987, 2006; Buikstra et al., 1990; Konigsberg and Buikstra, 1995; Stojanowski and Schillaci, 2006; Hefner et al., 2016). Biodistance is most visible in its application at an interregional or interpopulation scale; such analyses approach questions of significance at the species-level, addressing population origins, migrations, and interactions. The most prominent of interregional biodistance research has focused on patterns and timing of human migrations. Hrdlička's cranio-dental (1907, 1918a, 1918b, 1920, 1942) and Turner's dental (Turner and Bird, 1981; Turner, 1983, 1985a, 1986, 1990, 2002; Haeussler and Turner, 1992; Turner and Scott, 2007; Scott et al., 2016) research focused primarily on the peopling of the New World. Howells' (1969, 1973, 1989, 1995) research on interregional cranial variation represents another highly visible broad-scale biodistance initiative. More recent studies continue to focus on the origins and migration patterns of groups inhabiting specific geographic contexts (e.g., Neves and Pucciarelli, 1991; Haydenblit, 1996; Pietrusewksy, 2003, 2005, 2006, 2010; Hallgrímsson et al., 2004; Sutter, 2005a, 2006; Hanihara and Ishida, 2009; Bernal et al., 2010; Alsup, 2012; Nikita et al., 2012; Stojanowski et al., 2013a, 2013b; Willermet et al., 2013; Scott et al., 2016), often incorporating advanced models, data collection techniques, and analytical approaches to examine past migration events and broad-scale variation (González-José et al., 2001, 2002; Relethford, 2001, 2002, 2004; Edgar, 2002; Hanihara and Ishida, 2005; Hanihara, 2008; Hubbe et al., 2010; Galland and Friess, 2016).

Biodistance research at the intraregional/microevolutionary scale addresses a variety of geographically localized questions, most concerning (sub)regional affinity. Intraregional studies typically focus on quantifying biological affinity between ethnic, linguistic, cultural, or religious collectives or on reconstructing population history within a distinct area (Stojanowski and Schillaci, 2006; Larsen, 2015). Noteworthy work is best categorized by geographic region, for example: *Africa and Middle/Near East* (Irish, 2005, 2006; Zakrzewski, 2007; Schillaci et al., 2009; Soltysiak and Bialon, 2013; Irish et al., 2014; Hubbard et al., 2015), *Central America and the Maya Region* (Wroble, 2003; Scherer, 2004, 2007; Cucina et al., 2015; Cucina, 2016), *Central and Eastern Europe* (Budnik et al., 2004; Khudaverdyan, 2011, 2012, 2013a, 2013b, 2014; Pawn, 2012; McIlvaine et al., 2014; Triantaphyllou et al., 2015; Movsesian and Bakholdina, 2017), *prehistoric and colonial Florida* (Griffin et al., 2001; Stojanowski, 2001, 2003a, 2004, 2010; Seasons, 2010), *Lower Illinois Valley* (Buikstra 1972, 1976, 1980; Droessler, 1981; Konigsberg, 1987, 1988; Konigsberg and Buikstra, 1995; Steadman, 1998, 2001), *Mexico*

(Christensen, 1997, 1998a, 1998b, 2001; Aubry, 2009; Ragsdale and Edgar, 2015; Cucina et al., 2016), *Peru and the Andes* (Blom et al., 1998; Blom, 1999; Sutter, 2000; Sutter and Mertz, 2004; Varela et al., 2008, 2013; Nystrom and Malcom, 2010; Bethard, 2013; Torres-Rouff et al., 2013; Johnson, 2016), and *the Southwestern United States* (Schillaci et al., 2001; Schillaci and Stojanowski, 2002, 2003; Schillaci, 2003; Durand et al., 2010; Byrd, 2014; Ragsdale and Edgar, 2014). Intraregional analyses examine aspects of demography at a relatively localized scale, such as population size, distribution, residential mobility, migration, or replacement (Stojanowski and Schillaci, 2006; Hefner et al., 2016). Each factor plays an important role in directing genetic and phenotypic patterning across a region or through time (Relethford and Lees, 1982; Relethford and Blangero, 1990; Hartl and Clark, 1997; Konigsberg, 2006, 2012; Relethford, 2007).

These "scales" of biodistance research face unique complications. Interregional biodistance research focuses on entire populations or regional aggregates as units of analysis (Stojanowski and Schillaci, 2006). Generally, theoretical assumptions are more easily violated at this broad scale because the studies span broad temporal and geographic ranges and often reference samples that are unrepresentative of "true" breeding populations (Cadien et al., 1974; Konigsberg, 1987, 1990a; Stojanowski and Schillaci, 2006). Similarly, intraregional biodistance research requires temporal or site/cemetery samples that are representative of the (sub)populations of interest. Obtaining such a sample is particularly difficult in bioarchaeological research, because mortuary contexts can differentially represent subpopulations (Bocquet-Appel and Masset, 1982; Konigsberg, 1987; 1990a; Stojanowski and Schillaci, 2006). In addition to duration of use (Konigsberg, 1990a, 1990b), mortuary contexts vary in their inclusivity depending on their size and location. A single cemetery might exclusively represent individuals of a particular socioeconomic status, sex, age demographic, kin-collective, ethnic affiliation, or disease/pathology status (Stojanowski and Schillaci, 2006; DeWitte and Stojanowski, 2015). Biases based in biology (i.e., differential frailty, survivorship, size, preservation) strongly affect cemetery composition, potentially leading to fewer/more than expected individuals of particular demographic subsets represented in an assemblage (Binford, 1971; Bocquet-Appel and Masset, 1982; Henderson, 1987; Wood et al., 1992; Waldron, 1994; Buckberry, 2000; Jackes, 2000, 2011; Wright and Yoder, 2003; DeWitte and Stojanowski, 2015). Small-scale biodistance analysis, though not immune to the complications of sample bias, is unique in its ability to directly approach these issues (Stojanowski and Schillaci, 2006; DeWitte and Stojanowski, 2015).

Small-scale biodistance research: kinship analysis. Small-scale (intracemetery or intrasite) biodistance analysis examines biological variation within a single mortuary or settlement area (Konigsberg, 1987; Stojanowski and Schillaci, 2006; Hefner et al., 2016). Thus, small-scale biodistance research focuses on individuals, discrete burials, or discrete burial areas within broader mortuary contexts as units of analysis (Stojanowski and Schillaci, 2006). Small-scale biodistance analyses can have one of several aims: a) to examine postmarital residence and mating practices, b) to detect micro-chronological trends, c) to detect differential frailty and selection processes within a population, d) to investigate overall phenotypic variability encompassed within a cemetery sample, and e) to identify kin collectives within a mortuary context (*kinship analysis*) (Konigsberg, 1987; Stojanowski and Schillaci, 2006). In his dissertation work involving site-specific biodistance analyses, Konigsberg recognized only categories a, b, and e as analytical types (Konigsberg, 1987). In a 2006 review of small-scale biodistance research, Stojanowski and Schillaci identified a number of additional analytical types, including categories c and d listed above, which they termed "age-structured phenotypic variation" analyses and "variance comparison" methods (Stojanowski and Schillaci, 2006). This dissertation deals most directly with kinship analysis (category e).

The goal of kinship analysis is to detect potential biological relatives within a mortuary context, usually with reference to some aspect of spatial or material structure (Konigsberg, 1987; Buikstra et al., 1990; Stojanowski and Schillaci, 2006; Hefner et al., 2016). Spatially and/or archaeologically defined subgroups, however, are not prerequisites for kinship analysis (Alt and Vach, 1991, 1992 1995; Vach and Alt, 1993; Case, 2003; Stojanowski and Schillaci, 2006). Depending on the size and inclusivity of a particular cemetery, one can extend kinship analyses to distinguish broader biosocial collectives interred within a single mortuary space (Goldstein, 1980; Birkby, 1982; Stojanowski and Schillaci, 2006; Pilloud and Larsen, 2011; Paul et al., 2013; Johnson and Paul, 2016; Hefner et al., 2016). This may include detecting distinct clans, for example (Goldstein, 1980; Birkby, 1982; Byrd and Jantz, 1994). Yet, due to the inherent limitations of phenotypic data (discussed above), exact genetic relationships are rarely established or verified through intracemetery biodistance analysis (Sjøvold, 1975, 1976-1977; Stojanowski and Schillaci, 2006; Johnson and Paul, 2016). The exception is kinship analysis within a historical context, for which genealogical information is available in headstones, family annals, or ecclesiastical/site records (e.g., Spence, 1996; Usher and Weets, 2001; Usher, 2005; Velemínský and Dobisíková, 2005; Usher and Polmateer, 2007). More commonly the result of intracemetery kinship analysis is the identification of individuals who are likely to be relatively closely related when compared to the other individuals interred within the same context (Sjøvold, 1975, 1976-1977; Stojanowski and Schillaci, 2006; Johnson and Paul, 2016).

Kinship analysis is founded on the theoretical premise that close relatives are more likely than distant or non-relatives to possess genes that are identical due to inheritance from a shared ancestor ("identical by descent") (Thompson, 1986; Blouin, 2003; Konigsberg, 2012). As such, family members share greater phenotypic similarity than non-relatives (Stojanowski and Schillaci, 2006). Kinship analyses are plagued by the same assumptions and limitations as those at play in broader scale biodistance research. Detecting potential genealogical relationships between individuals in bioarchaeological contexts is complicated by reduced temporal control as compared to modern genetic analyses (Buikstra, 1972, 1980; Konigsberg, 1987, 1990a; Stojanowski and Schillaci, 2006). Often, it is unclear whether skeletal individuals were members of the same age cohort or separated by several generations, except for within highly temporally contextualized cemeteries, a requirement for successful kinship analysis (Stojanowski and Schillaci, 2006). Further, most demographic parameters, such as effective population size, are unknown (Cadien et al., 1974; Rogers and Harpending, 1986; Konigsberg, 1987; Chakraborty, 1990; Stojanowski and Schillaci, 2006; Relethford, 2007).

Importantly, kinship analysis—like all biodistance analysis—is inherently limited in resolution due to the nature of phenotypic data. Traditionally, selectively neutral traits with high narrow-sense heritability estimates have been considered desirable for reconstructing evolutionary and biological relationships (Sjøvold, 1984; Devor, 1987;

Buikstra et al., 1990; Tyrrell, 2000; Relethford, 2002; Roseman, 2004; Roseman and Weaver, 2004, 2007; Relethford, 2007; Konigsberg, 2012; Pilloud and Hefner, 2016). There are, however, issues with using heritability estimates as the sole measure of trait utility for biodistance analysis (Rösing, 1986; Eades and Desideri, 2003; Vitzthum, 2003; Stojanowski and Schillaci, 2006; Paul and Stojanowski, 2015). For example, the small sample sizes involved in intrasite and intracemetery studies necessitate maximization of phenotypic variation in order to distinguish relatives from non-relatives, potentially making highly variable traits more desirable for small-scale analyses than traits associated with high heritability estimates (Stojanowski and Schillaci, 2006). In addition, phenotypic characters with low heritability values are not necessarily "overly environmental" but may reflect diminished genetic variability within a population as a result of separate evolutionary processes (e.g., natural selection or genetic drift) (Buikstra et al., 1990; Vitzthum, 2003; Visscher et al., 2008). Though rarely explicitly stated, narrow-sense heritability (h^2) captures the *additive* contribution of genes to a phenotypic character; estimates of this value can be inflated in cases of genetic interaction (epistasis), dominance, and shared environment among relatives (Falconer and Mackay, 1996; Visscher et al., 2008; Manolio et al., 2009; Zuk et al., 2012; Liu et al., 2015). For this reason, an understanding of the underlying genetic architecture of phenotypes can be more informative than heritability, alone (Zuk et al., 2012). Finally, heritability is population specific and not necessarily constant (Vitzthum, 2003; Visscher et al., 2008), which complicates the application of this measure to bioarchaeological and paleoanthropological contexts.

Modeling approaches have shown that even a completely heritable, additive, and selectively neutral quantitative trait is limited in its power to reconstruct biological relationships (Rogers and Harpending, 1983; Edge and Rosenberg, 2015a, 2015b). A neutral phenotypic trait is expected to relay the same amount of information about (sub)population membership as a single neutral biallelic locus (Rogers and Harpending, 1983; Edge and Rosenberg, 2015a, 2015b), regardless of the number of genetic loci influencing that character (Chakraborty and Nei, 1982; Rogers and Harpending, 1983; Lande, 1992; Edge and Rosenberg, 2015a, 2015b). These expectations have informed studies of hominin variation, most focusing on the influence of drift and selection on craniofacial dimensions (Relethford, 2002; Roseman, 2004; Roseman and Weaver, 2004; Weaver et al., 2007; Relethford, 2010; Roseman, 2016). Kinship analysis is particularly hindered by this limitation. Due to their focus on small-scale biological relationships these studies demand a high degree of resolution from phenotypic datasets, which may represent only the amount genetic information provided by a small number of polymorphic loci (Rogers and Harpending, 1983; Edge and Rosenberg, 2015a, 2015b). Considering also the ways in which skeletal/dental variation is quantified (i.e., as minimally-variable dimensions, ordinal expression grades, or dichotomized presence/absence scores), a considerable amount of underlying genetic information is lost through the use of phenotypic traits (Roseman, 2016; for biodistance examples see Ricaut et al., 2010; Meyer et al., 2012; Hubbard et al., 2015). For this reason, kinship analysis relies heavily on multivariate analytical techniques to explore large phenotypic datasets that include numerous (presumably informative) traits (Stojanowski and Scillachi, 2006; see also Chapters 3-5). The issue of trait selection is central to the dissertation and is discussed (along with heritability as both a measure and concept) in greater depth throughout Chapters 3-5.

The pioneers of intracemetery kinship analysis outlined its basic principles (Acsadi and Nemeskéri, 1957; Nemeskéri, 1962) as well as probabilistic methods that examine the co-occurrence of rare and discrete traits in potential kin (Ullrich, 1962, 1969a, 1969b; Sjøvold, 1975, 1976-1977, 1984). Since this initial push, the foci of kinship analyses have ranged from methodological to contextualized and problem-oriented. Method-oriented studies investigate the performance of particular phenotypic characters or statistical tests in successful genealogy reconstruction; the prevalence of these studies peaked in the 1980s and 1990s, though their presence in the literature rightly persists (e.g., *non-metric/morphological traits*: Rösing, 1982, 1986; Alt and Vach, 1991, 1992, 1994, 1995; Vach and Alt, 1993; Alt et al., 1996; Paul and Stojanowski, 2015; *metric traits*: Hanihara et al., 1983; Doi et al.; 1986; Corruccini and Shimada, 2002; Adachi et al., 2003). Kinship analyses can also draw upon rich contextual information to answer site or region-specific questions about the intersection of social structure and mortuary practice, while often (secondarily) expanding upon methodological queries (e.g., Bondioli et al., 1986; Jacobi, 1997, 2000; Christensen, 1998c; Case, 2003; Stojanowski, 2005a, 2005b; Stojanowski et al., 2007; Duncan, 2011; Pilloud and Larsen, 2011; Harper and Tung, 2012; Meyer et al., 2012; Paul et al., 2013; Stojanowski, 2013; Alt et al., 2015; Prevedorou and Stojanowski, 2017). Small-scale (intracemetery) biodistance analysis is dynamic, because it facilitates direct examination of localized phenomena often considered “noise” (or held-constant) in broader-scale analyses (Stojanowski and Schillaci, 2006; DeWitte and Stojanowski, 2015).

Deciduous Teeth: Applications in Biological Anthropology

Complications of phenotypic data aside, continuous (metric) and discrete (non-metric/morphological) traits of the cranium (De Stefano et al., 1984; Hauser and De Stefano, 1989; Howells, 1989; Buikstra and Ubelaker, 1994) and dentition (Kieser, 1990; Turner et al., 1991; Buikstra and Ubelaker, 1994; Hillson, 1996; Alt, 1997; Scott and Turner, 1997; Hillson et al., 2005; Stojanowski, 2007) represent the most common lines of evidence upon which biodistance research is based. Yet rarely do researchers incorporate craniodentally immature individuals into biodistance analyses, especially in small-scale or intracemetery contexts. This is partially due to preservation biases (Henderson, 1987; Waldron, 1994; Buckberry, 2000; Jackes, 2011) but also due to the nature of subadult phenotypic data. The plasticity of the cranium prior to skeletal maturity compromises the effectiveness of using craniometrics and possibly cranial non-metric data, although Wood (2012) found subadult non-metric traits to reflect ancestry with fidelity. Unlike immature crania, deciduous teeth are early forming, robust in developmental timing, and unchanging in dimension and morphology post-mineralization (Kronfeld, 1935; Garn et al., 1959; Kraus, 1959; Moorrees et al., 1963; Kraus and Jordan, 1965; Smith, 1991; Liversidge and Molleson, 2004; Cardoso, 2007). Thus, they represent an underexplored source of biodistance data.

The vast majority of physical and dental anthropological research focuses on the permanent dentition, because the deciduous elements have thinner enamel that is more susceptible to wear (Grine, 2005; Mahoney, 2010), are shed early in life and incrementally (Moorrees et al., 1963), and are less consistently represented in the archaeological/fossil record. Yet, deciduous teeth do receive attention independent of their later-forming counterparts. A number of these studies are descriptive, defining phenotypic variability within and across populations. These include population-focused discussions of deciduous crown dimensions (including asymmetry and dimorphism) in living and prehistoric samples (e.g., *Aboriginal and European Australia:* Hanihara, 1976; Margetts and Brown, 1978; Townsend and Brown, 1979; Farmer and Townsend, 1993; Townsend and Farmer, 1998; *African and European America*: Vaughn and Harris, 1992; Harris, 1994; Heikkinen et al., 2016; *the Caribbean*: García-Godoy and Townsend, 1984; García-Godoy et al., 1985; *England*: Foster et al., 1969; Foster and Hamilton, 1969; Liversidge and Molleson, 1999; *Iceland:* Axelsson and Kirveskari, 1984; *India/Pakistan:* Lukacs, 1981, 1986; Lukacs et al., 1983; Kaul and Prakash, 1984; Shankar, 2013; Eswara et al., 2014; *Indonesia*: Kuswandari and Nishino, 2003; *Japan:* Brace and Nagai, 1982; Mizoguchi, 1998; *Jordan*: Hattab et al., 1999; *Liberia*: Moss and Chase, 1966; *Ohio Valley*: Sciulli, 1977, 1990, 2001; *Spain/Portugal:* Cardoso, 2010; Viciano et al., 2013; *South Africa*: Grine, 1986; *South America:* Sawyer et al., 1982; Anfe et al., 2012). Select multi-population surveys and comparative studies have synthesized this literature (see Kramer and Ireland, 1959; Harris, 2001; Harris and Lease, 2005; Hanihara and Ishida, 2005; Eigboo et al., 2010), including one publication that surveyed spatio-temporal variability in ten deciduous crown dimensions (Harris and Lease, 2005). Harris and Lease (2005) concluded that the strongest population distinction is between those with relatively large anterior teeth (Europeans) and relatively large postcanine elements (Africans and Asians), while Amerindian deciduous dimensions are highly variable (Harris and Lease, 2005: 603). Their results also support the commonly reported trend in dental reduction through time, generally associated with shifts in subsistence patterns (e.g., Brace and Mahler, 1972; Brace, 1978; Frayer, 1979; Larsen, 1983; Calcagno, 1989; Brace et al., 1991; Christensen, 1998d; Sciulli, 2001; Hill, 2004; cf., Perzigian, 1975; Smith, 1978), although rates of decrease in deciduous tooth size vary between groups (Harris and Lease, 2005:604). Also common are descriptions of primary dental development and emergence patterns (e.g., Roche et al., 1964; Friedlaender and Bailit, 1969; Malcolm, 1973; Nyström, 1977; Baghdady and Ghose, 1981; Hitchcock et al., 1984; Holman and Jones, 1991, 1998, 2003; Nyström et al., 2001; Mahoney, 2012), as well as discussions of common developmental defects (e.g., Skinner, 1986; Lukacs and Walimbe, 1998; Stojanowski and Carver, 2011; Kar et al., 2014).

Comparatively, the treatment of deciduous dental morphology is less visible. Population-specific descriptive studies dominate the literature on deciduous crown morphology (e.g., *Africa*: Grine, 1986, 1990; *Ohio Valley*: Sciulli, 1977, 1990, 1998; *Australia:* Adler and Donlon, 2010; *America/Canada*: Saunders and Mayhall 1982a; Lease, 2003; Lease and Sciulli, 2005 Sciulli and Lease, 2005;; Harris and Barcroft, 2010; *Colombia*: Aguirre et al., 2006; Delgado-Burbano, 2008; Díaz et al., 2014; *Denmark*: Jørgensen, 1956; *India*: Joshi, 1975; *Japan/Japanese-Americans*: Hanihara, 1956, 1965, 1966, 1967, 1968; 1970; Yagi, 1973; Kitagawa et al., 1992, 1995; Kitagawa, 2000; *Middle/Near East*: Salako and Bello, 1998; *Pacific Islands*: Suzuki and Sakai, 1973; *Pima/Southwest United States*: Tocheri, 2002; *Poland*: Szlachetko, 1959; *South/Southeast Asia:* Lukacs and Walimbe, 1984; Lukacs and Kuswandari, 2013). Select morphological anomalies have also been described (e.g., *fused/double elements:* Brook and Winter, 1970; Benazzi et al., 2010; Marinelli et al., 2012; *three-rooted mandibular molars:*

Sugiyama et al., 1976; Mayhall, 1981; *delta-form molars*: Dahlberg, 1949; Butler and Hughes, 1984; Kitagawa et al., 1996). Among the most prolific contributors to the study of deciduous morphology is Kazuro Hanihara, who described deciduous morphological variation across European, African, and Japanese Americans (Hanihara, 1956, 1963) and, most famously, outlined the highly derived "Mongoloid" morphological complex in Japanese children (Hanihara, 1961, 1965, 1966, 1967, 1970). Paul Sciulli and Loren Lease's research is also noteworthy. Their work described changes in Ohio Amerindian deciduous crown traits through time (Sciulli, 1977, 1990, 1998) as well as differences in deciduous postcanine morphology between European and African Americans (Sciulli, 1998; Lease, 2003; Sciulli and Lease, 2005). In early descriptive research, both Hanihara and Sciulli found European Americans to exhibit stronger expression of maxillary incisor shoveling and Carabelli's trait, while African Americans exhibited higher frequencies of accessory cusp features (e.g., Cusp 6, deflecting wrinkle, protostylid) and more complex postcanine crowns (Hanihara, 1963, 1967; Sciulli, 1998). These findings corroborate those of other researchers who examined western European and African populations (e.g., Jørgensen, 1956; Grine, 1986), although Grine (1986) found stronger expression of maxillary incisor shoveling in African Americans and South African Blacks.

Morphological trait definitions and scoring standards. Early descriptive research yielded conflicting within-population frequencies for certain deciduous morphological features. For example Hanihara (1961, 1963) reported relatively high protostylid frequencies in individuals of European background and elevated frequencies of deflecting wrinkle expression in individuals of African background, contradicting Jørgensen's (1956) and Grine's (1986) findings, respectively (Lease, 2003; Lease and Sciulli, 2005).

Researchers attribute these disparities to the use of variable scoring criteria between researchers (Lease, 2003; Edgar and Lease, 2007). Deciduous trait descriptions are scattered throughout individual publications, some based on features originally described in the permanent dentition (e.g., *canine mesial ridge*: Irish and Morris, 1996; *Carabelli's trait/protoconulid*: Grine, 1986). Dahlberg and Hanihara took initial strides toward standardizing deciduous morphological trait recording (see Dahlberg, 1951, 1956; Hanihara, 1961, 1963). Hanihara's represented the most comprehensive suite of scoring standards for over thirty years, until Sciulli (1998) incorporated additional characters as part of his work with Ohio Amerindians. Sciulli ultimately compiled a set of 57 morphological traits: 33 crown and 24 root features (see Sciulli, 1998:192-196). Lease, drawing upon Sciulli's work, amassed a comprehensive deciduous morphological scoring system in her 2003 dissertation, adding recording standards for mandibular molar cusp number (Lease, 2003:153-159). Appendix A of Lease's dissertation includes standards originally presented in other publications, most described in Hanihara (1961, 1963), Sciulli (1998), or augmented from Turner et al. (1991) and the Arizona State University Dental Anthropology System (ASUDAS) that was originally designed for use in permanent teeth (Lease, 2003:153-159).

Unfortunately, published standards for deciduous morphological trait scoring have not shared the same popularity as their permanent counterparts (Turner et al., 1991). The ASUDAS is commonly applied to bioarchaeological research and, with some controversy, to paleoanthropological investigations (e.g., Smith, 1978; Bailey, 2002, 2006; Irish et al., 2013; 2014; Kimbel, 2013). This is partially an artifact of the underrepresentation of deciduous teeth in anthropological research generally. Still lacking from the literature is a highly visible, comprehensive publication akin to Turner et al. (1991) presenting deciduous trait definitions and gradients of expression. As it stands, deciduous morphological traits have not been unified under a single system; indeed, the most current compilation of traits lacks a title (Lease, 2003). In contrast to ASUDAS, only a subset of trait expression grades are captured in reference plaques. These plaques, created by Dahlberg and Hanihara, are rare and out-of-production, leaving most researchers only the written standards by which to adhere during data collection (Dahlberg, 1951, 1956; Hanihara, 1961, 1963). Thus, standardization marks an important "next step" in the development of deciduous dental anthropology. This dissertation approaches the topic of morphological scoring standards and "best practices" in biodistance research by directly comparing distinct scoring systems (see Chapters 3-5).

Comparative analyses: deciduous and permanent teeth. Studies that compare deciduous and permanent crown phenotypes within the same individual or sample are highly visible in the physical anthropology literature. Intra-individual comparisons of deciduous and permanent phenotypes require longitudinal samples and are often conducted using clinical collections (e.g., Seipel, 1946; Dahlberg and Mikkelsen, 1947; Barrett, 1957; Moorrees et al., 1957; Moorrees and Chadha, 1962; Barrett et al., 1964; Thompson and Popovich, 1977; Brown et al., 1980; Scott et al., 1983; Yuen et al., 1996, 1997; Kondo et al., 1999; Kondo and Townsend, 2004; Edgar and Lease, 2007) or in mixed-age samples/children possessing mixed dentition (e.g., Joshi, 1975; Kieser, 1984; Thomas et al., 1986; Smith et al., 1987, 1997; Kondo et al., 1996; Aguirre et al., 2006; Paul et al., 2017). Studies comparing deciduous and permanent odontometrics have found moderate to strong correlation between corresponding elements (Moorrees et al., 1957;

Brown et al., 1980; Yuen et al., 1996; Bravo et al., 2010; Hussain et al., 2016) indicating that deciduous crown size is a somewhat reliable predictor of successive crown dimensions within individuals (Yuen et al., 1996, 1997; Bravo et al., 2010; Hussain et al., 2016). Studies comparing morphological traits within individuals yield variable results. For example, Saunders and Mayhall (1982a) examined differential morphological trait expression in the maxillary deciduous and permanent molars. They found high concordance between deciduous and permanent molar characters and suggested that the second deciduous molar is, in fact, a member of the broader molar tooth "district" (Saunders and Mayhall, 1982a:45). However, they observed trait discordance between successive incisors and a "gradient" of diminishing expression for certain molar features moving distally from the dm2[1], which they attributed to disparate developmental trajectories between elements (Saunders and Mayhall, 1982a). In a more recent survey, Edgar and Lease (2007) quantified correspondence between deciduous and permanent tooth morphology and found week correlations between deciduous and permanent anterior dental features but strong correlations between certain molar characters, including Carabelli's trait and deflecting wrinkle (Edgar and Lease, 2007:732).

Researchers have also compared successive tooth crowns in their degree of fluctuating asymmetry (e.g., Bailit et al., 1970; DiBennardo and Bailit, 1978; Townsend,

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[1] Throughout the dissertation, individual dental elements are denoted by the following abbreviations: "d"=deciduous; "x"=maxillary or upper; "n"=mandibular or lower; "i/I"=incisor; "c/C"=canine; "PM"=premolar; "m/M"=molar. Throughout, deciduous teeth are represented by lowercase type and permanent teeth are represented by upper case type. In certain instances, the dental arcade is not indicated by "x" or "n", but instead by numbered superscripts or subscripts. For morphological abbreviations see Appendix C.

1981; Saunders and Mayhall, 1982b; Guatelli-Steinberg et al., 2006). Saunders and Mayhall (1982b) examined morphological fluctuating asymmetry in successive dental elements, focusing on Carabelli's trait and protostylid. They found asymmetry to increase distally along the molar row from the dm2 to the M3 (Saunders and Mayhall, 1982b). Guatelli-Steinberg et al. (2006) compared fluctuating asymmetry between deciduous and permanent (post)canine dimensions in a South Carolina Gullah sample, interpreting fluctuating asymmetry as an indicator of developmental instability. They found successive crowns to significantly differ in fluctuating asymmetry in only 25 percent of the focal elements. Deciduous elements exhibited greater asymmetry in most cases of incongruity (Guatelli-Steinberg et al., 2006). Both studies concluded that fluctuating asymmetry reflects not only susceptibility to environmental stressors but aspects of developmental programming/timing, as well (Saunders and Mayhall, 1982b; Guatelli-Steinberg et al., 2006).

Where permanent and deciduous data conflict, researchers often invoke explanations related to differences in their distinct developmental environments/trajectories. Deciduous teeth begin enamel formation in-utero, with primary dental development spanning two to three years, while permanent dental development lasts between eight and fourteen years (Schour and Massler, 1940; Fanning and Moorrees, 1969; Smith, 1991; Liversidge and Molleson, 2004). Due to their early and rapid developmental trajectory that affords them an "environmental shield", researchers have postulated that deciduous phenotypes provide a relatively faithful reflection of underlying genotype (Saunders and Mayhall, 1982a; Smith and Tillier, 1989; Paul and Stojanowski, 2015; Paul et al., 2017). Thus, accurate genealogy reconstruction may rely upon the integration of deciduous dental data into small-scale biodistance research. This dissertation provides an indirect assessment of this hypothesis by presenting intra-individual comparisons of the performance of deciduous and permanent dental datasets in their ability to reliably reconstruct documented pedigrees (see Chapters 3-4).

Deciduous crown variation and reconstructing biological relationships. A subset of deciduous dental research includes studies that test the performance of deciduous elements in determining an individual's taxonomic status or ancestry. Recent paleoanthropological studies have used deciduous crown morphology, shape, and outline to distinguish between hominin taxa. Bailey et al. (2014a, 2016) found the crown shape of deciduous molars to significantly differ between *Homo sapiens* and *Homo neanderthalensis* (see also Benazzi et al., 2011a; Harvati et al., 2015; Fornai et al., 2016; as well as Benazzi et al., 2014; Fabbri et al., 2016 for treatment of lateral incisors/enamel thickness). Additional studies have found dm2 to distinguish *Homo sapiens* from *Homo erectus* (Souday, 2008; Souday and Bailey, 2011; Bailey et al., 2014b). Benazzi et al. (2011b, 2012) found cervical as well as crown outlines of dm2s to be effective in assigning taxonomic status in *H. sapiens* and *H. neanderthalensis*. These studies are essential to paleoanthropological research in contexts where deciduous teeth are among the only or best-preserved fossil elements recovered (e.g., Dean, 1987; Smith and Tillier, 1989; Dean et al., 1993; Moggi-Cecchi et al., 1998; Alemseged et al., 2006; Dean and Smith, 2009; Toussaint et al., 2010; Zanolli et al., 2012, 2015; Benazzi et al., 2014; Arnaud et al., 2016).

Within modern humans, methodological research centers on the utility of deciduous elements to establish bioregional affiliation and population history (e.g., Sciulli, 1977, 1980; Lukacs and Walimbe, 1984; Kitagawa et al., 1992, 1995; Kitagawa, 2000; Harris et al., 2001; Lease, 2003; Lease and Sciulli, 2005; Lukacs and Kuswandari, 2013; Malik et al., 2014). Noteworthy is the work of Loren Lease, whose dissertation employed both deciduous metrics and morphology in discriminating between African and European Americans (Lease, 2003). Two discriminant function analyses based on primary odontometrics yielded accurate assignment in 89 percent of cases, while 250 out of 785 logistic discriminant functions based on two, three, or four morphological trait complexes yielded accurate assignment in 70 percent of cases (Lease, 2003). Lease derived the discriminant functions used to test modern American samples from documented or archaeological samples of known European or African origin (Lease, 2003). In a more critical examination of specific phenotypic characters, Lease and Sciulli (2005) combined deciduous odontometrics (mesiodistal dimensions of dc, dm1, and dm2) with one or more morphological feature(s) (most commonly, cusp number of the maxillary molars) to discriminate between European and African American children. Results showed correct allocation in approximately 91 percent of cases. Importantly, they found that combined deciduous morphological and metric data were more successful than a single data type in determining ancestry in American children (Lease and Sciulli, 2005).

In certain cases, bioarchaeologists focus on deciduous phenotypic variation to resolve questions of biological affinity, microevolution, and subsistence/behavior (e.g., Smith 1976, 1978; Sciulli, 1977, 1990, 1998; Lukacs and Walimbe, 1984, 2005; Kitagawa et al., 1995; Kitagawa, 2000; Lease, 2003; Lease and Sciulli, 2005;

McClelland, 2003; Stojanowski and Carver, 2011; Lukacs and Kuswandari, 2013). However, highly uncommon are contextual, small-scale kinship studies based on deciduous phenotypes. One exception is a study by Pilloud and Larsen (2011) that used both deciduous and permanent teeth to examine spatial-structure and kinship at Çatalhöyük, Turkey (see also Pilloud, 2009). Additionally, Sciulli and Cook (2016) used both deciduous and permanent buccolingual crown diameters to explore biological variation at the Fort Ancient SunWatch village cemetery. They found the cemetery to be kin structured and to contain a limited number of non-local individuals (Sciulli and Cook, 2016). In a recent chapter, Sutter and Chhatiawala (2016) used both deciduous and permanent dental crown morphology to examine population structure (R-matrix and F_{ST}) across three temporal samples from the Moche site of San José de Morro. They found strong concordance between the permanent and deciduous results, and cite a "paucity of remains relative to adults" to explain a lack of statistical significance for the deciduous-derived F_{ST} values (Sutter and Chhatiawala, 2016:358). A major conclusion of this chapter is that population structure analyses based on deciduous morphological data corroborate those based on permanent morphological data (Sutter and Chhatiawala, 2016). While the latter two studies bode well for the integration of deciduous phenotypic data into site-level and cemetery-level biodistance research, to date, deciduous teeth mark an underexploited line of evidence in problem-oriented biodistance research.

RESEARCH ORIENTATION

This dissertation provides a critical synthesis of formative literature and recent trends in anthropological kinship research, small-scale biodistance analysis, and deciduous heritability/quantitative genetic research. Foundational knowledge of these areas of inquiry is essential to approaching the question of whether deciduous dental data can meaningfully enhance “small scale” biodistance analyses, specifically in detecting relatedness between individuals who died prior to adulthood.

This dissertation focuses on quantitative genetics and kinship reconstruction in archaeological and forensic contexts, with the aim of developing an infrastructure for identifying child relatives based on the size and shape of deciduous (baby) teeth. Essential to these efforts is an understanding of the determinants of deciduous dental phenotypes and delineating relationships between latent genetic, developmental, and environmental factors and the observable dental traits with which we approach anthropological questions. Pedigreed dental samples have long played a key role in establishing this baseline knowledge for the permanent dentition, while genealogy-based studies involving deciduous teeth have been limited by comparison. This dissertation focuses on deciduous crown morphology collected from dental casts representing individuals of known genetic relation in three pedigreed samples: 1) the Australian Twin Study sample (University of Adelaide); 2) the Yuendumu Aboriginal Growth Study sample (University of Adelaide); and 3) the Burlington Growth Study sample (University of Toronto).

DISSERTATION STRUCTURE

This dissertation has been organized into six chapters[2]. Chapter 2 provides theoretical and historical context for the dissertation, reviewing kinship as a topic of anthropological inquiry, broadly, and bioarchaeological approaches to kinship, specifically. The chapter reviews recent theoretical advances arising from sociocultural anthropology, emphasizing major paradigm shifts and critiques occurring throughout the twentieth century, most importantly the prioritization of social conceptions of relatedness over genealogy and biology (e.g., Schneider 1968, 1972, 1984). Bioarchaeological kinship research is reviewed with an emphasis on social identity theory and differential treatment and interpretation of, often, conflicting lines of evidence. The chapter also presents the results of a quantitative and qualitative literature review aimed at gauging the degree to which sociocultural theoretical developments have impacted bioarchaeological kinship studies over the last six decades. The chapter presents a framework for approaching kinship as a mid/multiscalar dimension of social identity and closes with a discussion of productive directions for future bioarchaeological kinship research.

Chapter 3 presents a performance analysis assessing the utility of deciduous dental morphology for reconstructing biological relationships in the Burlington Growth Study sample. Background on the application of dental data to bioarchaeological and biodistance research is presented. The chapter presents heritability estimation as a traditional avenue for evaluating trait utility for reconstructing biological relationships

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[2] Three of the dissertation chapters have been published as coauthored journal articles. All coauthors have approved the use of augmented versions of these papers as dissertation chapters. See Appendix A for a full author contribution statement.

and reviews recent literature that highlights the limitations of heritability as both a concept and measure. “Performance” is offered as an alternative to heritability, and is defined as “reflecting the ability of phenotypic traits to reconstruct known genealogical relationships at the inter-individual scale” (Chapter 3:148). Performance of the Burlington Growth Study deciduous morphology sample is then assessed from two perspectives, 1) from a general comparative perspective referencing distances generated from a multivariate dataset, and 2) from a simulated bioarchaeological perspective with reference to pattern-recognition and visualization procedures (e.g., multidimensional scaling). Results indicate that deciduous crown morphology performs well in identifying pairs of biological relatives within a broader sample. However, performance varies considerably at the family level. The results are discussed with respect to bioarchaeological kinship research, and opportunities for incorporating children into studies of past biosocial phenomena.

Chapter 4 presents a comparative performance analysis focused on the utility of permanent dental morphology for reconstructing biological relationships in a matched set of individuals from the Burlington Growth Study sample. The longitudinal nature of the sample makes it possible to directly compare the deciduous data’s (Chapter 3) and permanent data’s utility for reconstructing biological relationships among a single group of documented families. Performance is gauged using the same informal metrics presented in Chapter 2 and via a Mantel test which quantifies correlations between a proxy genetic distance matrix (i.e., based on relatedness coefficients) and 1) a phenotypic distance matrix based on deciduous morphology data, and 2) a phenotypic distance matrix based on permanent morphology data. Correlations between homologous deciduous and permanent trait expression are also presented. Results indicate that permanent crown morphology performs moderately well in distinguishing biological relatives from unrelated individuals in a broader sample, although performance varies greatly by family. All performance metrics indicate deciduous morphology outperforms permanent morphology in identifying biological relatives. Further, family-specific performance varies greatly depending upon the dental morphological dataset employed. Results are discussed with respect to biodistance "best practices" and current data collection standards.

Chapter 5 presents a heritability study focused on deciduous and permanent crown morphology across three pedigreed dental cast samples: 1) the Burlington Growth Study sample, 2) the University of Adelaide Twin Study sample, and 3) the University of Adelaide Yuendumu Aboriginal Growth Study sample. The chapter presents novel heritability and pleiotropy estimates for phenotypic characters generated via maximum likelihood variance components analysis in SOLAR v. 8.1.1 (Blangero et al., 1995-2016; Almasy and Blangero, 1998). Heritability estimates and genetic correlations are compared between homologous deciduous and permanent dental traits, between samples, between scoring systems (for deciduous characters), and between dichotomization breakpoints for select traits. Results are discussed within the framework of data collection practices, biodistance research, and the human diphyodont dental complex. The chapter discusses potential application of the results, namely for understanding broader patterns of genetic integration and the evolution of mammalian dentitions.

In Chapter 6, the dissertation and its conclusions are summarized. The chapter evaluates whether the overarching aim of the dissertation—to develop an infrastructure for incorporating deciduous phenotypic data into biodistance research—was achieved. Chapter 6 also discusses the potential contribution of deciduous crown data to various (social)scientific fields and to exploring biosocial phenomena in deep time. The dissertation closes with a consideration of questions that arise in light of the presented results, as well as future research directions.

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CHAPTER 2

BIOARCHAEOLOGY AND KINSHIP: INTEGRATING THEORY, SOCIAL RELATEDNESS, AND BIOLOGY IN ANCIENT FAMILY RESEARCH

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Family is a fundamental human institution that forms the basic social units of collective action beyond the individual agent. Families instill social roles and values in children, influence mate choices, and organize subsistence activities. Whereas family relationships are a near universal aspect of the human experience, conceptions of relatedness vary among societies past and present. In an era where the definition of "family" grows increasingly flexible and biosocial in nature, it is important that we place current conceptions of kinship within an expansive temporal perspective. The variable nature of family composition through time and space has important social and legal implications in our society in terms of who has the right to marry, to raise children, or to inherit material wealth. Investigating family-based social organization and social relatedness in the past helps highlight their fluid natures and, in turn, can help educate against general misperceptions and discrimination based on ideas about the naturalness of the nuclear family within human evolutionary history.

Why kinship? At a time when funding for the social sciences faces the constant threat of dissolution, it is imperative that social scientists communicate the relevance of their work. Why is it that we "care" about kinship? What are the practical applications of ancient family research? In Western academia, the resurgence of kinship studies, in part, reflects increasing politicization and popularization of "the family" as projected through public media (Farber, 1981; Carsten, 2000, 2004; Stone, 2001). In recent years, legislation, news outlets, and even television programs have dedicated their attention to the “crisis of the family.” This is not surprising considering that the past several decades have witnessed scientific advances in reproductive technologies and sociopolitical movements that have challenged the “typical” Western family structure (see Weston, 1991; Strathern, 1992c; Hayden, 1995; Ragoné, 1996; Edwards et al., 1999; Franklin, 2001; Thompson, 2001; Butler, 2002; Levine, 2003, 2008; Blackwood, 2005).

The public’s fascination with ancient “family” burials and the importance of engaging broader audiences in (bio)archaeological research must also be acknowledged (Stojanowski and Duncan, 2015). Images of small group burials containing individuals interpreted as family members tend to capture the public imagination due to their propensity to invoke sentiments of empathy and commonality between modern and past peoples (e.g., Cohen, 2015:35). It is for this reason, too, that we must continue to develop methods and theory aimed at more nuanced understandings of relatedness.

The study of kinship was a staple of ethnographic research for much of anthropology’s history as a discipline (e.g., Morgan, 1871; Malinowski, 1913; Rivers, 1914; Radcliffe-Brown and Forde, 1950; Radcliffe-Brown, 1952; Evans-Pritchard, 1951; Lévi-Strauss, 1969). Rivers’ (1910) genealogical method of fieldwork was a cornerstone of British social anthropology for decades (Bouquet, 1993). Envisioned as a “natural” system for recording relationships, genealogies have a complicated history within Western society (Klapish-Zuber, 1991, 2000; Bouquet, 1993; Bamford and Leach, 2009). Genealogical models of relatedness based on inheritance of shared biogenetic substance have served as the normative paradigm for conceptualizing kinship in Western society as far back as the Middle Ages. Drawing from traditions dating to classic antiquity, 11th-century Christian scholars formalized the genealogy depicted as a family tree in order to represent Jesus Christ's ancestors (Klapish-Zuber, 1991, 2000), and by the 16th century family genealogies were popular across Europe (Connerton, 1989). Although Euro-Americans tend to take the language and symbols of genealogies as naturally constitutive aspects of kinship, genealogies were produced through experiments with different visual tools and organizing metaphors (Klapish-Zuber, 2000). Thus, the normative Western conception of relatedness emerged around the same time as Western conceptions of the body (Giddens, 1991; Burkitt, 1999), two critical components of modern Euro-American ontology.

Beginning in the 1960s, kinship research met considerable resistance from scholars who identified the concept as "biologistic" and at the root of anthropology's Eurocentric perspectives on social structure, broadly, and gender and "relatedness," specifically (see Schneider, 1968, 1972, 1984; MacCormack and Strathern, 1980; Collier and Yanagisako, 1987). In response, kinship within sociocultural anthropology has largely been reconceptualized as a social process, and studies of kinship increasingly embrace more complex and culturally relativistic conceptions of relatedness (e.g., Carsten, 2000, 2004; Franklin and McKinnon, 2000, 2001). For example, Lévi-Strauss' "house society" model – in which social relatedness is primarily organized around shared space, practice, and (im)material property – emphasizes affinal relations over genealogical relations and has been applied as an alternative to biologically-structured kin systems in anthropological research over the past four decades (Lévi-Strauss, 1983a, 1983b, 1984, 1987, 1991). More recently, Sahlins (2013:2) has defined kinship as "'mutuality of being': people who are intrinsic to one another's existence…," a definition that may prioritize social aspects of relatedness but accommodates genealogical or biological aspects of kinship relevant in many cultural contexts past and present, even though Sahlins ultimately considers these fundamentally social as well.

As sociocultural anthropologists began turning away from biological and genealogical approaches to kinship, biological anthropologists seized on genealogical kinship as a viable approach to understanding human origins and humankind's relationship with other primates. Since the mid-20th century, evolutionary scholarship has cited genetic relatedness as a vehicle for the rise of "behavioral modernism" and various human social behaviors (e.g., Silk, 1987; Hewlett, 2001; Salter, 2008; Silk and House, 2011). Most famously, Hamilton's Rule outlines a potential explanation for the practice of altruistic behavior among social organisms (Hamilton, 1964). This rule claims that altruism (i.e., an act that enhances another's fitness at the expense of the actor's) is selected for when the cost of performance is eclipsed by the benefit to the other individual, as weighted by their degree of genetic affinity to the actor (i.e., coefficient of relatedness) (Hamilton, 1964; Salter, 2002, 2008). Thus, biological affinity is thought to drive the behaviors of social actors (Hamilton, 1964; Trivers, 1971; Silk, 1987). Some have examined Hamilton's Rule as a means of understanding individual versus collective fitness within primate communities and evolutionary settings (e.g., Silk, 2002); other scholars have explored how genetic relatedness influences the actions of humans across various contexts (e.g., Hewlett, 2001).

Building on this theoretical framework, empirical ethnographic research on modern foraging societies also provides insights into the role of kinship in structuring social group composition and interaction (e.g., Hill et al., 2011; Bailey et al., 2014). Kin co-residence, for example, has been found to have strong impacts on reproductive success and/or parenting investment (Sear and Mace, 2008; Ellsworth et al., 2014), marriage practices (Walker et al., 2013), social inequality or distribution of material wealth (Smith et al., 2010), and cooperative foraging and group size (Smith, 1985). Additional developments within evolutionary and/or biological anthropological approaches to kinship include kin recognition (e.g., Langergraber et al., 2007b; Lieberman et al., 2007; Pfefferle et al., 2014), the origins of human and non-human primate kin formations and the social and environmental landscapes in which they emerged (e.g., Jones, 2003, 2011; Chapais, 2008, 2013, 2014; Wood and Marlowe, 2011; Hill et al., 2014), and relationships between kin-based social organization and other adaptive collective behaviors (e.g., altruism, cooperation, and the evolution of language) (e.g., Langergraber et al., 2007a, 2011; Shenk and Mattison, 2011; Milicic, 2013; Boyd et al., 2014).

Within anthropology there have been recent attempts to bridge the rift between sociocultural and biological approaches to kinship. For example, Chapais (2014) uses a comparative phylogenetic approach to demonstrate that the suite of complex social traits relating to kinship, what Chapais refers to as the “human kinship configuration”, has a deep evolutionary history and, thus, a biological foundation. Although Chapais (2014:754) makes a compelling case for the dual nature of human kinship as “biological and cultural,” the comments made by kinship scholars on Chapais’ article demonstrate the extent to which Chapais’ approach unfortunately characterizes social aspects of kinship as secondary byproducts of a set of universal behaviors and reflect the extent to which evolutionary and sociocultural approaches to kinship continue to diverge. Developing a holistic approach to kinship that incorporates biological and cultural aspects requires capturing the complexities of biocultural behaviors without reducing either the biological or social factors (McKinnon and Silverman, 2005).

As a synthetic field championing “biocultural” and problem-oriented research, bioarchaeology is well positioned to embrace novel conceptions of kinship and use diverse sets of data (i.e., biological and cultural) to undertake the challenge of reconstructing ancient kin relations (Meyer et al., 2012). Yet, intracemetery biodistance methods commonly employed in bioarchaeological investigations of “relatedness” are often focused on methodological improvement or generate inferences that are quite narrow in scope: reconstructing site formation processes, identifying kin-structured cemeteries, or assessing relatedness among skeletons interred within a collective grave, for example (Stojanowski and Schillaci, 2006). Although bioarchaeologists recognize the potential of kinship studies for addressing scales of sociopolitical organization relevant to broader anthropological questions (e.g., Alt and Vach, 1998; Case, 2003; Stojanowski and Schillaci, 2006), this potential remains relatively undeveloped, presenting a challenging but fruitful direction for future research (Stojanowski and Schillaci, 2006; Meyer et al., 2012). Of special promise is the use of social identity frameworks to address broader questions of human social organization in the past through kin-based social identity. To date, bioarchaeological studies of identity have concentrated on individual (e.g., osteobiographies) and community/population (e.g., age, gender, status, and ethnic identities) levels of analysis, while mid-or multiscale kin-based identity remains underexplored.

In this chapter, I critically review recent developments among anthropological approaches to kinship, emphasizing consideration of relatedness as “mutuality of being” following Sahlins (2013) and how this perspective can be applied to the bioarchaeological record. Next, I present a brief historical overview of bioarchaeological kinship research. Results from a formal literature review of kinship studies in bioarchaeology are used to assess overall trends with regard to data types and conceptualizations of kinship. Then I present a broader review of bioarchaeological kinship literature and discuss how kinship is being defined and reconstructed from complex datasets, focusing on developments over the past 10 years. I highlight studies that consider non-biological forms of kinship, go beyond the mere identification of relatives within mortuary contexts, and make broader inferences about social organization and the ways in which family relations were constituted. I identify important methodological developments but note the overall lack of theoretical development compared to ethnographic considerations of social relatedness.

In the second half of the chapter, I present a new vision for bioarchaeological approaches to relatedness that builds on social identity theory, and I consider the strengths and limitations of its utility as a conceptual framework for interpreting bioarchaeological data. This approach to kinship diverges from recent archaeological efforts to revitalize the investigation of kinship in past societies (Ensor, 2011, 2013a, 2013b) and is a unique and timely contribution to anthropological discussions of relatedness. Finally, I highlight potentially fruitful directions for future research by identifying critical issues to be addressed in order to establish kinship and family as vibrant topics of inquiry within bioarchaeology.

Recent Developments in Sociocultural Approaches to Kinship

The title of Sahlins' recent book *What Kinship Is – And Is Not* (2013) captures one of the fundamental questions addressed by anthropological kinship research: to what extent does biology influence kin structure and family-centered behaviors? Biological relatedness is a universal reality – every person is a progeny of other human beings (Godelier, 2011) – but its social significance varies widely, and thus kinship cannot be equated with biological affinity. Durkheim (1898) was among the first social theorists to take this stance, claiming that kinship is dynamic and malleable and requires participation beyond biological reproduction. He cited acts of marriage, adoption, and parent-offspring emancipation as evidence of the schism between predetermined relatedness and social affinity (Durkheim, 1898).

In this section, I review recent developments in anthropological kinship research of greatest relevance to bioarchaeological approaches to kinship. I briefly trace currents of theoretical development that arose amid the initial wave of responses to Schneider's critiques; in doing so, I contextualize developments over the past 10 years. Due to constraints of space and the dense nature of this literature, I omit from this discussion recent developments in formal (i.e., quantitative) kinship analysis (e.g., Read, 2007, 2011, 2012; Leaf, 2013), historical linguistics (e.g., Jones, 2010; Ehret, 2011; Fortunato, 2011a, 2011b; Jones and Milicic, 2011), and isonymy (e.g., King and Jobling, 2009;

Darlu et al., 2012; Larmuseau et al., 2012). Readers interested in developments within these approaches to kinship should consult the preceding citations.

The 1960s and 1970s marked a transitional phase in kinship research. As evolutionary anthropologists and primatologists embraced kinship as a subject for comparative investigation, sociocultural anthropologists began questioning the genealogical method and the presumptive biological nature of kin relatedness prevalent in kinship studies from their inception (e.g., Leach, 1961, 1971; Beattie, 1964; Needham, 1971; Southwold, 1971). David Schneider (1968, 1972) published several critiques during this period, denouncing kinship as a cross-cultural system. He insisted that previous research reinforced Western preoccupation with “natural kinship” and prioritized classification of kin systems over consideration of social experience. Schneider’s critique focused on the genealogical model as a Western cultural construct. Schneider (1968, 1972, 1984) argued that seemingly biological objects such as blood are social constructs that convey biological affinity (see also Strong and Van Winkle, 1996; Carsten, 2001, 2011, 2013; Marks, 2002; Tallbear, 2013). Kin are ultimately connected by an ‘enduring solidarity’ produced and maintained through social interactions and expressed as ‘blood ties’ (Schneider, 1968; see also Baumann, 1995). Thus, rather than reflecting a naturalistic human universal (i.e., a “biological fact”), the genealogical basis underlying Euro-American conceptions of kinship – and therefore anthropological kinship theory – is a culturally constituted symbolic system unique to Western societies (Schneider, 1968). In other words, the cross-cultural study of kinship, which had been one of anthropology’s major contributions to the social sciences, was invalid (Schneider, 1984). Several in depth explorations of Schneider’s lasting contributions to the field and critiques of his approach are available to readers looking for additional details of his work and its impact (e.g., Yanagisako, 1978; Carsten, 1995; Ottenheimer, 1995; Peletz, 1995; Holy, 1996; Feinberg and Ottenheimer, 2001; Leaf, 2001; McKinley, 2001).

Instead of signaling the end of kinship studies, Schneider's deconstruction of kinship research precipitated a variety of reactions and responses, including explorations of alternatives to heteronormative models of kinship and family (Collier and Yanagisako, 1987; Weston, 1991; Borneman, 1992, 2001; Strathern, 1992a, 2001; Lewin, 1993; Modell, 1994; Hayden, 1995; Franklin and Ragoné, 1998), new emphasis on previously unchallenged assumptions about gender relations that permeate earlier models of kinship (e.g., Rosaldo, 1974; Rubin, 1975; Yanagisako, 1979; MacCormack and Strathern, 1980; Leacock, 1981; Collier et al., 1982; Collier and Yanagisako, 1987; Scheffler, 1991; Blackwood, 1995, 2000; Yanagisako and Delaney, 1995), and development of constructivist approaches to kinship within a variety of cultural contexts (e.g., Carsten, 1995, 1997; Rival, 1998; Bodenhorn, 2000; Leach, 2003).

To emphasize the shift away from genealogical approaches to kinship, researchers began framing kinship as "relatedness." An effort was made to disentangle biological relationships based on reproduction (i.e., genitrix and genitor) from kinship as social relationships (i.e., mother and father) (e.g., Ottenheimer, 1995). Constructivists argued that there is no pretheoretical, prediscursive "intractable core" to human relatedness (Astuti, 2009:229). Rather than a universal "biological fact," relatedness is a "process of becoming" generated and maintained by purposeful action (Carsten, 1995:223). Viewed in this light, kinship as social relatedness can be based on any number of shared experiences, practices, and commonalities – including commensality, co-residence, shared knowledge, shared status, shared labor, shared connections to "place" and landscape, and naming rituals or name sharing – that establish a "mutuality of being" between people who see themselves as "intrinsic to one another's existence" (Sahlins, 2013:2; see also Strathern, 1973; Merlan and Rumsey, 1991; Weismantel, 1995; Carsten, 1997; Bodenhorn, 2000; Nuttall, 2000).

Kinship manifested as "household" or "residence" emerged as yet another productive area of post-Schneiderian scholarship (see Carsten and Hugh-Jones, 1995; Joyce and Gillespie, 2000). Drawn from and expanding the concept of "house societies" developed by Lévi-Strauss (1983a, 1983b, 1984, 1987, 1991), the social house was developed as a non-biological manifestation of relatedness. The house is considered a meaningful space that serves as a nexus for social memory formation and the transgenerational regulation of resources particular to domestic collectives (or kin) (Gillespie, 2000b, 2001, 2002; Joyce, 2000, 2001a, 2008; Chesson, 2001; Hodder and Cessford, 2004). One advantage of this model is that the material correlates of the social group (social house) can be readily identified in the archaeological record (e.g., the material remains of the physical house and objects that symbolize the house), thus facilitating considerations of kinship and relatedness in prehistory (Gillespie, 2000a; Joyce, 2000; Marshall, 2000; cf. Ensor, 2011, 2013a, 2013b; Carleton et al., 2013). House society approaches to kinship have been used to explore small-scale, kin-based social organization within a variety of archaeological and ethnographic contexts (e.g., McKinnon, 1991; Carsten and Hugh-Jones, 1995; Carsten, 1997; Joyce and Gillespie, 2000).

Within the past 10 years, another wave of kinship research has emerged in sociocultural anthropology. Many of the research foci developed following Schneider's critiques – including gender inequality within families, kinship and power, non-normative family formations, and non-biological bases of relatedness – persist as vibrant areas of research (e.g., Lamphere, 2001, 2005; Lancaster, 2005; Van Vleet, 2008; Bamford, 2009; Howell, 2009; see also Kakaliouras, 2006). Additionally, scholars continue to explore how kinship intersects with broader social issues. Kinship is no longer conceptually isolated as a separate "domain" of human behavior (Collier and Yanagisako, 1987); it is considered interrelated with – and critical to understanding – human impact on the environment, interpersonal violence, socioeconomic behavior, political organization, patient care, and ideology (e.g., Kelly, 2011; Bodenhorn, 2013; Lambek, 2013; McKinnon and Cannell, 2013; Rutherford, 2013; Shever, 2013; Yanagisako, 2013).

A growing number of scholars have directed critical focus at constructivist approaches to family. The constructivist model has been described as a "reactive inversion" of the genealogical model, but it has had little effect in terms of displacing biological relatedness as the basis of kinship in anthropology (Viveiros de Castro, 2009; Sahlins, 2013). This is, in part, because the influence of genealogical discourse permeates Western worldview (e.g., Bamford, 2009; Bamford and Leach, 2009; Holmes, 2009; Ingold, 2009; Leach, 2009). Although shared biological substances are less valued within constructivist approaches, biology is still present – often implicitly – as what is given or immutable within constructions of relatedness (Astuti, 2009; Bamford and Leach, 2009; Ingold, 2009; Viveiros de Castro, 2009; Sahlins, 2013). The genealogical model continues to play a prominent role in anthropological kinship studies in general (see

Holy, 1996; Godelier, 2011; Shenk and Mattison, 2011; Trautman and Whitley, 2012; Ensor, 2013a, 2013b) and implicitly underlies and informs constructivist approaches to relatedness (Astuti, 2009; Leach, 2009; Viveiros de Castro, 2009). Thus, despite appearances or claims otherwise, "the outcome of the focus on kinship as Western cultural construction has perversely resulted in a reinscription of the notion that human beings are everywhere biological beings with the capacity for culture…. People may share culture, but it never makes them *kin*" (Leach, 2009:185, emphasis original).

There also is increased awareness that other aspects of Western worldview permeate constructivist approaches to kinship. A view of kinship in which individuals create their own kin connections using potentially flexible forms of relatedness may represent "the final hegemony of consumptive individualism" (Viveiros de Castro, 2009:261; see also Strathern, 1992a, 1992b; Leach, 2009). Therefore, even recent anthropological approaches to kinship are ill-suited for analyzing social relatedness in non-Western contexts where their application can obscure differences in the way family relatedness is understood and experienced (Schneider, 1984; Astuti, 2009; Holmes, 2009; Lambek, 2011; Viveiros de Castro, 2009). To apply Western notions of kinship – genealogical or constructivist – to non-Western contexts is to impose "alien ontological categories" on non-Western peoples (Astuti, 2009:216).

A key to moving beyond Western understandings of kinship is to adopt conceptions of relatedness suitable to different contexts. Ethnographers are attempting to convey non-Western ontologies of relatedness and truly explore what kinship means in different cultural contexts (Leach, 2003, 2009; Bamford, 2004, 2009; Viveiros de Castro, 2009; Kelly, 2011). For example, according to Viveiros de Castro (2009:241), Amazonian kinship is based on a "nonbiological theory of life." Within Amazonian worldview, the soul or spirit is a shared substance that connects all persons (human or non-human), whereas a person's body is constructed through interactions with others. Those interactions with other bodies form the basis of Amazonian kinship and reveal that within Amazonian ontology, affinity is "given, internal and constitutive," whereas consanguinity is "constructed, external and regulative" (Viveiros de Castro, 2009:258–259). In Papua New Guinea, the Kamea conceptualize the parent–child bond as an "inherently disembodied one"; social relatedness is based on relationships formed through interactions with other persons within an engaged landscape (Bamford, 2009:160). Similarly, the Reite of Papua New Guinea have a non-genealogical understanding of relatedness wherein knowledge of and interaction with an engaged landscape is a shared substance that forms the basis of relatedness (Leach, 2009). The Vezo in Madagascar make an ontological distinction between biological inheritance/genealogical relatedness and social relatedness, but they emphasize non-biological parent-child relationships as critical to family life (Astuti, 2009).

These ethnographic examples represent fundamentally different ways of conceptualizing personhood, family, and relatedness compared to the normative ontologies found in Western sociocultural contexts (Ingold, 2000, 2009, 2013; Oliver, 2009; Viveiros de Castro, 2009; Robertson, 2011; Descola, 2013; Palsson, 2013). Conveying non-Western forms of relatedness requires consideration of non-Western ontologies of gender, personhood, and human/non-human animal/landscape interactions (Ingold, 2000, 2009, 2013; Descola, 2013). However, one must exercise caution when drawing distinctions between Western and non-Western ideologies, as preconceived notions of innate differences can result in over-simplistic and “othering” representations of non-Western forms of kinship.

More generally, researchers are trying to develop alternatives to genealogical thinking. Genealogies are a particular way of thinking about and establishing the parameters of possible relationships within a very narrow perspective (Klapish-Zuber, 1991, 2000; Ingold, 2000). Depictions of genealogies (i.e., family trees or kinship diagrams) restrict the potential to recognize other conceptualizations of relatedness and forms of kin-based organization (Bouquet, 1996, 2001; Bamford and Leach, 2009; Ingold, 2009; Leach, 2009). Researchers have employed alternative models to the tree analogy for genealogical relationships, with many favoring a rhizome model, a web, or an interwoven “meshwork” of relatedness in which “everything is potentially interconnected with everything else” (Pálsson, 2009:107; see also Deleuze and Guattari, 1988; Holmes, 2009; Ingold, 2009). In sum, kinship remains a flourishing field of study in sociocultural anthropology. Ongoing theoretical debates have produced new insights into relatedness in Western and non-Western contexts, many of which involve non-biological or non-genetic conceptions of kinship.

Bioarchaeological Kinship Research

In this section, I provide a brief historical overview of bioarchaeological kinship research, focusing on approaches used to explore family organization in the past, conceptions of kinship and relatedness applied to ancient contexts, and the types of inferences or observations drawn from data on kinship. Because the focus is on theoretical developments, I only briefly discuss data and analytical methods. The diverse types of data and analytical methods used to investigate postmarital residence practices and to identify closely related individuals in archaeological contexts are reviewed in detail elsewhere (see Konigsberg, 1987, 1988; Hauser and DeStefano, 1989; Alt and Vach, 1998; Stojanowski and Schillaci, 2006). I also present the results of a formal literature review to evaluate publishing trends for bioarchaeological kinship studies.

The origins of bioarchaeological kinship research are difficult to pinpoint (Stojanowski and Schillaci, 2006), but by the 1970s two distinct areas of inquiry emerged in bioarchaeological family research: (1) the identification of kin or family groups within mortuary contexts, and (2) the investigation of postmarital residence patterns. In the bioarchaeological literature, the former is referred to as "kinship analysis" (Stojanowski and Schillaci, 2006). Rather than place a singular emphasis on consanguineal relationships accessed via kinship analysis, I discuss both kinship and postmarital residence analysis; each uniquely contributes to more holistic understandings of relatedness in the past, providing greater opportunities to generate broad inferences about social organization and sociocultural practices.

The study of postmarital residence practices using skeletal and dental data from archaeological samples began in earnest in the 1970s (e.g., Corruccini, 1972; Lane and Sublett, 1972; Spence, 1974a, 1974b; Lane, 1977). Collectively, scholars established methods for identifying postmarital residence practices using biodistance analysis of within-group and between-group biological distance and variance. The assumption is that the more mobile sex will exhibit greater intrasite skeletal/dental variation, and the non-mobile sex will exhibit greater intersite variation and biodistance. Konigsberg (1987, 1988) provided formal justification of postmarital residence studies by using population genetics models to demonstrate that the differential movement of females or males into a settlement results in measurable distinctions in phenotypes that persist through time as long as the predominant pattern remains stable. Drawing on socioeconomic and political correlates of particular postmarital residence patterns documented in ethnographic contexts (e.g., Murdock, 1967; Ember and Ember, 1971; Divale, 1977; Korotayev, 2003; Porčić, 2010; cf. Allen and Richardson, 1971), bioarchaeologists use postmarital residence practices to make inferences about changes in subsistence, the formation of descent groups, gendered divisions of labor, resource control, and the nature and extent of intergroup hostility or warfare (e.g., Schillaci and Stojanowski, 2002, 2003; Tomczak and Powell, 2003).

Kinship analyses use phenotypic (e.g., skeletal and dental discrete trait frequencies or metric values) or genetic data to identify close biological relatives in mortuary contexts. Alt and Vach (1998) describe three types of research contexts that affect the methodology used and the expected outcome in kinship analyses: small grave analyses, structured spatial analyses, and unstructured spatial analyses. In small grave analyses, the objective is to infer whether a group of individuals within a clearly delimited mortuary context (e.g., a tomb, a cave, or under a house floor) are close biological relatives (e.g., Sjøvold, 1976/1977; Bondioli et al., 1986; Alt and Vach, 1998). Structured kinship analysis quantifies (non)correspondence of cemetery spatial structure (e.g., distinct sectors or “family plots” within a cemetery), cultural attributes (e.g., grave structure, body treatment), and patterns of biological variability in order to identify mortuary behavior with potential familial bases (e.g., Strouhal and Jungwirth, 1979; Bondioli et al., 1986; Howell and Kintigh, 1996; Jacobi, 1997, 2000; Shimada et al., 2004). Unstructured spatial analysis attempts to identify members of kin groups without a priori reference to spatial structure or cultural attributes within larger cemeteries. A non-random distribution of phenotypic (e.g., Vach and Alt, 1993; Alt and Vach, 1995a, 1995b) or genetic (Stone and Stoneking, 1993; Stone, 1996; Dudar et al., 2003) data suggests some underlying factor(s) influenced the burial program. Alt and Vach (1995b) refer to identified clusters as "hypothetical families" and recommend verifying these groupings with additional data including archaeological and demographic evidence (i.e., skeletal age and sex).

Identification of close biological relatives in mortuary contexts and the development and refining of research methodologies for doing so are often the primary goals of bioarchaeological kinship analysis (Alt and Vach, 1998; Case, 2003; Stojanowski and Schillaci, 2006). Some studies have evaluated the probability of familial relationship using phenotypic data (e.g., Hanihara et al., 1983; Doi et al., 1986; Alt and Vach, 1995a, 1995b; Matsumura and Nishimoto, 1996; Alt et al., 1997) and genetic data (e.g., Shinoda and Kunisada, 1994; Hummel and Herrmann, 1996; Gerstenberger et al., 1999; Shinoda and Kanai, 1999; Keyser-Tracqui et al., 2003; Scholz et al., 2001), while others have attempted to reconstruct pedigrees among individuals (e.g., Rösing, 1986; Spence, 1996). Studies also have explored the goodness of fit between results obtained from genetic and phenotypic data and the relative effectiveness of different types of phenotypic traits in reconstructing biological relatedness (e.g., Shinoda et al., 1998; Corruccini and Shimada, 2002; Adachi et al., 2003; Shimada et al., 2004).

By drawing on ethnographic data suggestive of broad patterns of correlation between kin-based mortuary practices and other sociocultural phenomena (see Goldstein, 1976, 1980; Carr, 1995; Parker Pearson, 1999; Saxe, 1970), bioarchaeologists can use the identification of kin groups within mortuary contexts to make inferences regarding the inheritance of wealth, social status, and sociopolitical organization. Unfortunately, many studies remain focused on methodological improvement and do not attempt to use kinship data to make inferences about broader anthropological issues (Alt and Vach, 1998; Case, 2003; Stojanowski and Schillaci, 2006). Alt and Vach (1998) note the potential for kinship studies to contribute to reconstructions of higher scale issues regarding social organization, including the "constitution of social families" and the role of heredity in ascribed social inequality. Case (2003) comments on the potential for kinship studies to elucidate the development of multigenerational political and economic inequality within communities (see also Stager, 1985).

This broader potential remains unrealized, a tendency that may be linked to underlying Western notions of relatedness that influence the ways in which kinship is studied. Indeed, throughout the first three decades of bioarchaeological research, kinship was almost ubiquitously reduced to close biological affinity. It remains unclear, though, whether recent theoretical developments in sociocultural approaches to relatedness have influenced contemporary bioarchaeological studies of kinship and family. To address this unknown I conducted a formal literature review to empirically assess theoretical and analytical trends in bioarchaeological kinship research.

MATERIALS AND METHODS

Quantitative Literature Review

The goals for the quantitative literature review were to assess broad temporal patterns in the terminology and types of anthropological data employed in bioarchaeological kinship studies, as well as the dimensions or forms of relatedness that these studies considered. I administered keyword searches of nine terms relevant to kinship or family-centered research using the digital archives of 13 English-language academic journals in which bioarchaeological studies are commonly published (Table 1). I included only studies set within bioarchaeological contexts; that is to say, I counted only those studies that included, at a minimum, data generated from non-contemporary human remains or their surrounding mortuary contexts.

Results were tallied as decadal publication counts of relevant keyword hits between 1950 and 2013. Counts from 2010–2013 were used to project trends throughout the current decade; the same was done to obtain decadal counts for journals that were first published after 1950 and whose inaugural issue fell between the first and tenth year of a decade. As a requirement for generating keyword-based counts, terms of interest were always identified (at a minimum) within the body of the text of a publication. Decadal counts also were recorded for types of anthropological data employed in bioarchaeological kinship/family studies (i.e., archaeological, bioarchaeological, linguistic, sociocultural). Finally, I noted whether individual articles addressed biological relatedness, social relatedness, or some combination of the two. To examine trends over time, counts were standardized by the number of journals monitored per decade. I made no adjustment for overall increase in the number of issues and/or articles published by journals through time; I have considered this limitation in the interpretation of the results. Ultimately, the *International Journal of Paleopathology* yielded a zero count for publications containing any of the monitored keywords during the period surveyed; thus, I do not present results for this journal.

Though informative, journal-based literature reviews have limitations. They may unintentionally exclude those sources most likely to report research that incorporates emerging data or theoretical models: dissertations. Single author books and edited volumes have also emerged as important media for presenting bioarchaeological research, and their contribution is not measured by the quantitative review. Additionally, the quantitative literature review was limited to English-language journals.

Qualitative Literature Review

To address the limitations of the quantitative literature review, a more inclusive, qualitative review of bioarchaeological literature from the past 10 years was performed. This review is designed to assess whether developments identified in the quantitative literature review reflect meaningful changes in the way kinship and relatedness are conceptualized in bioarchaeology. The qualitative literature review facilitated the identification of general topical, methodological, and interpretive trends in recent bioarchaeological kinship research. Although English-language publications are emphasized, a sampling of non-English sources is cited below.

RESULTS

Quantitative Literature Review

The quantitative literature review revealed increasing variability in published family/kin terminology through time (Fig. 1). There are zero articles from the 1950s referencing any of the nine monitored terms, but the 2000s and 2010s (projected) boast bodies of bioarchaeological kinship literature that reference all nine keywords (Table 2). This pattern underscores the growing diversity of contexts, questions, and theoretical frameworks with which bioarchaeologists are engaging during the 21st century. Across the last six decades, diversity in the lines of evidence utilized to examine kinship increased. In the 1960s, bioarchaeological family research drew heavily on ethnohistoric and ethnographic data; biological and archaeological data grew more prevalent in the following decades (Table 3). The 2000s and 2010s (projected) have been marked by almost equal prevalence of sociocultural, biological, and archaeological data, whereas the use of linguistic (surname) data was minimal during the same period.

A concordant temporal trend was identified in the form(s) of relatedness considered. Throughout the 1960s, publications featuring bioarchaeological explorations of kinship primarily dealt with issues of biological or biosocial relatedness (Table 4). The 2000s were the first to approach a balance between the volume of bioarchaeological papers discussing biological relatedness, social relatedness, and both biological and social relatedness within the same paper (Table 4). Since the start of the 21st century, the field has witnessed considerable intensification in the publication of bioarchaeological studies of all kinship types, with biosocial kinship investigations enjoying the greatest relative increase in publication frequency. This trend may reflect the progressively interdisciplinary nature of bioarchaeological research in recent years, or possibly a greater integration of contemporary social theory into what would otherwise be more biologically oriented considerations of affinity.

In sum, the volume of published bioarchaeological research focusing on kinship has increased over the last several decades, especially since the start of the 21st century, and this trend is projected to continue throughout the near future (Fig. 1). These results highlight sustained growth in academic curiosity surrounding relatedness and family in the past. These trends also are likely influenced, in part, by the emergence of bioarchaeology as a distinct subdiscipline during the late 20th century and the (variably) expanding volume of articles published within journals annually, often associated with the increased prevalence of online publishing, both generally and for bioarchaeology specifically.

Qualitative Literature Review

The types of inferences generated in recent bioarchaeological kinship research exhibit a similar pattern as seen in theoretical developments in kinship studies – a mixture of "business as usual" and novel efforts. Scholars continue to make important methodological contributions to the study of kinship by identifying traits potentially useful as indicators of genetic relatedness within skeletal samples (e.g., Villotte et al., 2011; Offenbecker and Case, 2012; Paul and Stojanowski, 2015), comparing the effectiveness of different types of data for identifying biological relatedness (e.g., Velemínský and Dobisíková, 2005; Adachi et al., 2006; Ricaut et al., 2010), and incorporating new analytical techniques (e.g., Usher and Allen, 2005; Ricaut et al., 2006; Gamba et al., 2011; Usher and Weets, 2014). Identification of close biological relatives in small grave and cemetery contexts continues to be the primary objective of many studies (e.g., Gamba et al., 2011; Baca et al., 2012; Perego, 2012; Lull et al., 2013; Deguilloux et al., 2014; Lee et al., 2014). Criteria for positively identifying probable nuclear families vary widely between studies; the most effective efforts establish (and sometimes meet) rigorous criteria that yield more nuanced interpretations of social aspects of family organization in the past (e.g., Simón et al., 2011; Meyer et al., 2012; Bentley, 2013; Grumbkow et al., 2013; Mata-Míguez et al., 2014). Initial excitement about the potential of ancient DNA (aDNA) to directly test hypotheses regarding systems of inheritance, postmarital residence patterns, and kinship systems (Stoneking, 1995; Shinoda and Kanai, 1999; Kaestle and Horsburgh, 2002; Williams et al., 2002; Usher et al., 2003) have been tempered in recent years. The more precise identification of genetically related individuals afforded by analysis of autosomal, mitochondrial, and Y-chromosomal genetic markers, or some combination of the three, has contributed inferential power to studies of kin-based social organization in the past (e.g., Haak et al., 2008). However, inferences made using aDNA data are subject to the same conceptual issues as other indicators of biological or genetic relatedness (Deguilloux et al., 2011; Meyer et al., 2012).

Analysis of postmarital residence practices in archaeological contexts continues to yield important insights into sociopolitical organization, population migrations, and subsistence practices (e.g., Bentley et al., 2012; Bentley, 2013). In their diachronic analysis of postmarital residence practices in the Middle Ohio Valley, Cook and Aubry

Table 1. Journals and variables included in the formal literature review monitoring trends in bioarchaeological kinship research.

Journals [a] (Years Monitored)	Key Words[b]	Data Types	Kinship “Type”[c]
American Anthropologist (1950-2013)	Affine/Affinal	Archaeological	Biological
American Antiquity (1950-2013)	Family	Biological	Biological and Social
American Journal of Physical Anthropology (1950-2013)	House/household	Linguistic	Social
Anthropological Science (1993-2013)	Intracemetery	Sociocultural	
Archaeological Papers of the American Anthropological Association (1989-2013)	Kin/Kinship		
Current Anthropology (1950-2013)	Mate Exchange		
HOMO- Journal of Comparative Human Biology (2000-2013[d])	Matrilocal/Matrilineal		
Human Biology (1950-2013)	Patrilocal/Patrilineal		
International Journal of Osteoarchaeology (1991-2013)	Postmarital Residence		
International Journal of Paleopathology (2011-2013)			
Journal of Archaeological Sciences (1974-2013)			
Journal of Human Evolution (1972-2013)			
Latin American Antiquity (1990-2013)			

[a] Only bioarchaeological publications (i.e., those involving archaeological skeletal/dental or mortuary data) were included. [b] Publications were only included in keyword counts if the keyword appeared in the body of the article. [c] Kinship “type” was categorized as follows: biological, biological, and social, or social. [d] Search dates reflect limitations to journal access, not publication duration.

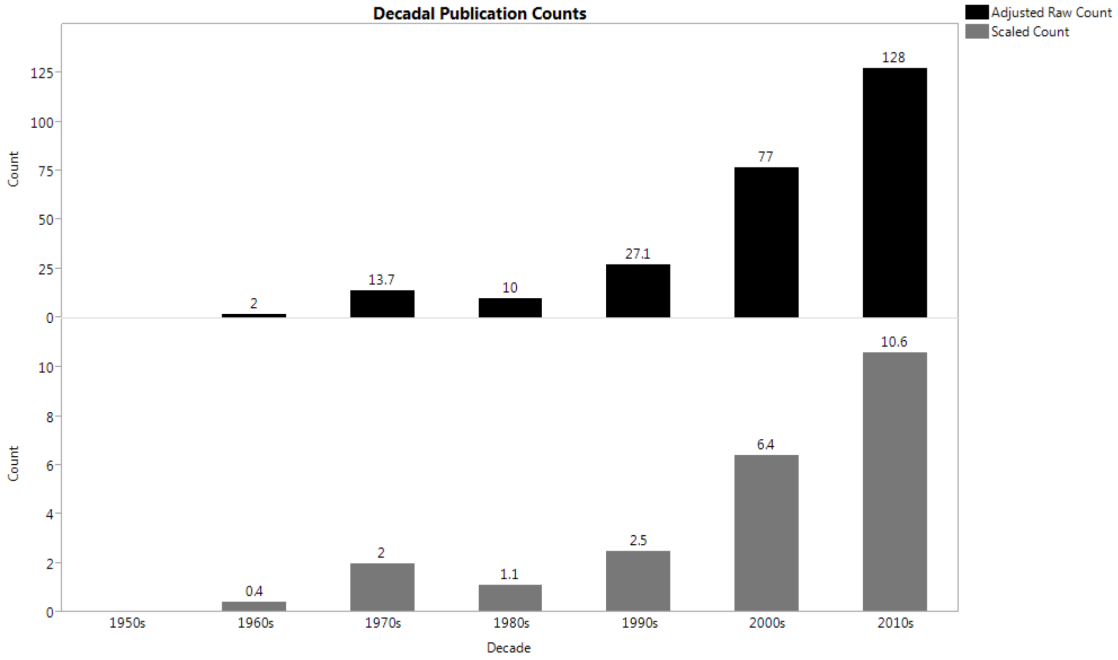

Figure 1. Counts of bioarchaeological kinship studies published across decades. Adjusted raw counts incorporate projected counts for those journals whose inaugural issues were published mid-decade, as well as projections for the 2010s as based on raw counts from 2010–2013. Scaled decadal counts are equivalent to the adjusted raw counts divided by the number of journals monitored during each 10-year span.

(2014) identify matrilocal, patrilocal, and "multilocal" residential patterns. They suggest that people likely connected with kin on either side of the family in an opportunistic fashion (see Ember and Ember, 1972). In another example, Nystrom and Malcom (2010) identify two different postmarital residence patterns within the Chiribaya polity on the south coast of Peru: non-elite patrilocality combined with elite male mobility.

Methodological refinements are welcome and necessary contributions to the field, but it is important that bioarchaeological kinship research connects understandings of family organization with issues of broader anthropological (and societal) interest.

Bioarchaeologists have recently begun to consider non-biological forms of relatedness in archaeological contexts (e.g., Lozada, 2011b; Pilloud and Larsen, 2011; Gregoricka, 2013). Interpretive work of this kind creates space for alternative family structures such as fictive kin, households, residence groups, or *ayllus* within bioarchaeological kinship research. *Ayllus* are multiscalar social groups in contemporary Andean highland societies (and described in ethnohistoric sources) as based on nested levels of affiliation ranging from household kin groups (minimal *ayllu*) to the ethnic community (maximal *ayllu*) (Bastien, 1978; Isbell, 1978; Allen, 1988; Albarracín-Jordán, 1996b; Abercrombie, 1998). Through careful application of *ayllu* organization to archaeological contexts, bioarchaeological research in the Andes has used more flexible, non-biological conceptions of relatedness to interpret data and make inferences regarding social organization and social identity (e.g., Blom, 1999; Knudson and Blom, 2009; Torres-Rouff et al., 2013).

Bioarchaeologists often cite interment with symbolic “inalienable possessions” or within residence areas as behaviors tied to the direct or indirect generation of social memory; such acts are often viewed as ancestor veneration or as reflecting traditional or “alternative” forms of relatedness (Christensen, 1998a,c; Hutchinson and Aragon, 2002; González-Ruibal, 2006; King, 2006, 2010; Laneri, 2010). The house model and ancestor veneration have been discussed in detail by Mesoamericanists, particularly for the Maya (e.g., Gillespie, 2000b, 2001, 2002; Joyce, 2001b; Watanabe, 2004; Duncan and Hageman, 2015; Miller, 2015; Novotny, 2013), and by archaeologists working in Southeast Asia (e.g., White and Eyre, 2010).

Table 2. Raw and adjusted keyword count values[a] and keyword percentage values[a] across monitored decades.

	Affine/ Affinal	Family	House/ Household	Intra-cemetery	Kin/ Kinship	Mate Exchange	Matrilocal/ local/-lineal	Patrilocal/ Patrilineal	Post-marital
1950s	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*
1960s	0.0	2.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0
	0.0	*50.0*	*0.0*	*0.0*	*50.0*	*0.0*	*0.0*	*0.0*	*0.0*
1970s	1.0	8.0(8.5)	5.0	1.0	4.0	0.0	4.0	4.0	1.0
	3.6	*28.6*	*17.9*	*3.6*	*14.3*	*0.0*	*14.3*	*14.3*	*3.6*
1980s	0.0	9.0	4.0	1.0	7.0	1.0	1.0	2.0	2.0
	0.0	*33.3*	*14.8*	*3.7*	*25.9*	*3.7*	*3.7*	*7.4*	*7.4*
1990s	0.0	21.0(22.1)	11.0	2.0(2.4)	20.0(20.8)	0.0	4.0(4.1)	2.0	3.0
	0.0	*33.3*	*17.5*	*3.2*	*31.7*	*0.0*	*6.3*	*3.2*	*4.8*
2000s	4.0	55.0	36.0	6.0	54.0	8.0	14.0	21.0	19.0
	1.8	*25.3*	*16.6*	*2.8*	*24.9*	*3.7*	*6.5*	*9.7*	*8.8*
2010s[b]	3.0(7.5)	40.0(100.0)	26.0(65.0)	5.0(12.5)	41.0(102.5)	2.0(5.0)	9.0(22.5)	11.0(27.5)	7.0(17.5)
	2.1	*27.8*	*18.1*	*3.5*	*28.5*	*1.4*	*6.3*	*7.6*	*4.9*

[a]Percentages of total raw counts are italicized. [b]Raw counts were adjusted to incorporate projections for those decades in which a journal was not in print throughout all 10 years. Where raw and adjusted counts do not correspond, the adjusted count is enclosed by parentheses. Raw counts for 2010-2013 were adjusted for all journals in order to project trends for the current decade (2010s).

Table 3. Data types used in published bioarchaeology kinship studies by decade[a].

	Biological	Archaeological	Sociocultural	Linguistic
1950s	0.0	0.0	0.0	0.0
	0.0	*0.0*	*0.0*	*0.0*
1960s	1.0	1.0	2.0	0.0
	25.0	*25.0*	*50.0*	*0.0*
1970s	13.7	12.7	2.0	0.0
	48.2	*44.7*	*7.1*	*0.0*
1980s	9.0	3.0	2.0	0.0
	64.3	*21.4*	*14.3*	*0.0*
1990s	15.1	21.0	5.0	0.0
	36.7	*51.1*	*12.2*	*0.0*
2000s	51.0	64.0	30.0	1.0
	34.9	*43.9*	*20.5*	*0.7*
2010s	95.0	92.5	35.0	0.0
	42.7	*41.6*	*15.7*	*0.0*

[a] Percentages of total raw counts are italicized.

A critical aspect of implementing broader conceptions (i.e., non-Western, non-biological) of kin relatedness is establishing criteria for identifying families in archaeological contexts when there is little or no biological evidence of distinct genealogical groupings (Duncan, 2005). Thus, studies that operationalize alternative (i.e., non-genealogical) conceptions of relatedness are required. Researchers in the Near East have explored the role of fictive kinship in socioeconomic organization. Pilloud and Larsen (2011) borrow the concept of “practical” kin from Bourdieu (1977) to interpret data patterns that indicate biological affinity did not influence residential burial practices

Table 4. Kinship “types” considered in published bioarchaeological studies by decade[a].

	Biological	Social	Biological and Social
1950s	0.0 *0.0*	0.0 *0.0*	0.0 *0.0*
1960s	1.0 *50.0*	0.0 *0.0*	1.0 *50.0*
1970s	10.7 *78.1*	0.0 *0.0*	3.0 *21.9*
1980s	6.0 *60.0*	2.0 *20.0*	2.0 *20.0*
1990s	14.1 *52.0*	5.0 *18.5*	8.0 *29.5*
2000s	31.0 *40.4*	13.0 *16.9*	33.0 *42.9*
2010s	47.5 37.3	20.0 *15.7*	60.0 *47.0*

[a]Percentages of total raw counts are italicized.

at the Neolithic site of Çatalhöyük. Pilloud and Larsen suggest that practical kin relationships were established to facilitate large-scale economic activities requiring cooperative labor or were potentially related to issues of inheritance or religious practices. Gregoricka (2013) uses strontium isotope signatures to identify three non-local individuals buried in six monumental Umm an-Nar tombs. These “non-local” individuals are otherwise indistinguishable from burials of local individuals based on mortuary practices. Gregoricka suggests this pattern may reflect fictive kinship relations established to foster exchange as interregional economic activity became more important.

These considerations of flexible kin identities make a valuable contribution to the literature and underscore the importance of rigorous hypothesis testing or evaluation of alternative explanatory models before inferring fictive kinship in archaeological contexts.

Overall, there is a marked lack of precision in the use of the term "kinship." Sometimes kinship is used – explicitly or implicitly – to mean biological, genetic, or molecular relatedness, and other times (even within the same study) kinship is differentiated from biological affinity and used more broadly to incorporate social aspects of relatedness (e.g., Scott, 2006; Česnys and Tutkuvienė, 2007; Gamba et al., 2011; Kurin, 2012; Miller, 2013). Even studies that implement broader conceptualizations of relatedness can reduce kinship to biology either through data analysis or interpretations of results (e.g., Ricaut et al., 2006; Scott, 2006; Harper and Tung, 2012; Matney et al., 2012). This may reflect the complexity of kinship and its manifold nature and perhaps indicates disciplinary growing pains as scholars attempt to push conceptual boundaries (e.g., Pilloud and Larsen, 2011; Gregoricka, 2013; Paul et al., 2013).

Bioarchaeologists are using investigations of family-based social organization to make inferences about major subsistence transitions (i.e., foraging to agriculture), differential access to land, and health (e.g., Alzualde et al., 2007; Bentley et al., 2009, 2012; Harper and Tung, 2012; Alt et al., 2013). Expanding on a strong European tradition of methodological and interpretive intracemetery kinship research (e.g., Alt et al., 1997, 2005; Haak et al., 2008), Meyer et al. (2012) use molecular genetic data to determine whether past peoples structured mortuary contexts based on biological lineage, but they integrate this information with archaeological and osteological data, including information on paleopathology and trauma, to examine intra-familial relationships and their manifestation within the funerary space. This approach yields highly detailed kinship reconstruction, exposing potential sibships, parent–offspring relationships, and marital partnerships. Here, genetic relationships reveal dimensions of personhood and kinship at the individual scale but also "scale up" to inform understandings of mortuary practice, exogamy, and postmarital residence systems at the community level.

In a holistic research program that marks a productive direction for spatially structured kinship research, Stojanowski (2013) integrates data from mortuary practices, age-structured phenotypic variation, and paleopathology to access hidden heterogeneity and differential frailty of a familial nature. Building on the identification—using archaeological data—of distinct kin-based burial programs in two different mission period cemeteries in La Florida, Stojanowski suggests that the Native American communities associated with the cemeteries had different experiences within the sociopolitical climate of the Spanish colony (Stojanowski, 2005c, 2013b). Stojanowski's (2013b) novel integration of family, community, and environmental factors in the exploration of differential stress and frailty provides a fruitful avenue for engaging with the Osteological Paradox, a fundamentally important, yet often overlooked conceptual issue that affects interpretations of health in past populations (Wood et al., 1992; Wright and Yoder, 2003; DeWitte and Stojanowski, 2015). Furthermore, this study realizes the potential for bioarchaeological research to elucidate interrelations between family social organization and intergenerational socioeconomic inequality (Alt and Vach, 1998; Case, 2003; Stojanowski and Schillaci, 2006).

In sum, bioarchaeological kinship research continues to have a methodological focus. Although methodological improvements are critical to advancing the field, the identification of genetically related individuals in archaeological contexts is merely one component of what should be a multifaceted effort to understand how kin-based relations were established and maintained within specific cultural contexts in the past. It appears that progress in the ethnographic and theoretical realms are, to some extent, influencing the ways in which bioarchaeologists are tackling the ancient family experience. The use of multiple lines of evidence – including molecular, phenotypic, body modification, isotopic, and myriad types of archaeological data – is becoming more common. Analysis of complex datasets and subsequent interpretation of results can be complicated, but such approaches can produce more nuanced reconstructions of relatedness in the past (e.g., Haak et al., 2008; Meyer et al., 2012; Alt et al., 2013; Paul et al., 2013; Stojanowski, 2013b). In some cases, kinship is incorporated as a post hoc interpretation (e.g., Scott, 2006; Zvelebil and Pettitt, 2013), rather than included as an integral component of the research design (e.g., Harper and Tung, 2012; Huffer, 2012; Miller, 2013; Stojanowski, 2013b). Although there are exceptions, it appears that Stojanowski and Schillaci's (2006) assessment stands: the potential of bioarchaeological kinship studies to contribute to broader anthropological questions remains unrealized.

Part of the problem is an imbalance between the incorporation of diverse types of data used to investigate kinship within the past. Many bioarchaeological studies are not fully integrating archaeological data or theory into their research design but instead do so in an ad hoc or post hoc fashion. Rather than prioritizing one line of evidence over another, different kinds of data should be brought to bear on a question either simultaneously through advanced modeling methods or separately but within a framework where each is equally weighted and not granted greater value a priori. I am not suggesting a devaluing of biological evidence in lieu of other data. Biological data will continue to play an integral role in past explorations of relatedness. As Geller (2008:130) notes, the balance of sociocultural and biological data in bioarchaeology offers a “welcome counterpoint to social constructivists’ scholarship” not only in terms of conceptualizing the body “strictly in terms of the late modern individual” but also with regard to the nature of relatedness.

DISCUSSION

Bioarchaeology has developed into a theoretically-oriented field that incorporates data from human skeletal remains and associated mortuary settings into highly contextualized, smaller scale regional- and site-based archaeological investigations (see Buikstra and Beck, 2006; Agarwal and Glencross, 2011; Martin et al., 2013; Larsen, 2015). I agree with Geller’s (2008:129) assessment that bioarchaeologists, in general, have “exercised caution with respect to their theoretical engagement” and support her call for a more theoretically informed bioarchaeology. One way to develop a more theoretically oriented bioarchaeological approach to family is to consider kinship using social identity theory. Kinship has been identified in the bioarchaeological literature as a potentially informative aspect of social identity in the lives of past peoples (e.g., Scott, 2006; Temple et al., 2011; Gregoricka, 2013), but it has not been fully developed within a social identity framework (cf. Paul et al., 2013).

Kinship as Social Identity

The concept of identity describes a universal experience of human sociality. Social identity marks an integration of an individual’s diverse statuses, roles, and experiences into a coherent image of self (Epstein, 1978; Holland et al., 1998) and involves the negotiation of self-identification(s) with and external ascriptions to multiple social groups (e.g., Shennan, 1989; Jenkins, 2008). Social identities can be individual or collective; collective identities, specifically, are founded on an individual’s sentiments of belonging within a broader group and others’ recognition of the individual’s affiliation with that collective (Jenkins, 2008).

Social identities are dynamic and continuously altered or reaffirmed through signifying behaviors and practices (Jones, 1997; Díaz-Andreu et al., 2005; Insoll, 2007). Of importance to archaeologists, these behaviors often involve recognizable, physical correlates rendering social identities materially substantiated (Giddens, 1979; Stein, 1999a; Díaz-Andreu and Lucy, 2005; Sofaer, 2006; Jenkins, 2008; Voss, 2008). Expressions of identity can be visible in the archaeological record in various forms: material remnants of funerary ritual and habitual practices, body modification, and patterns of mate exchange genetically and phenotypically encoded within individual bodies, to name a few (e.g., Blom et al., 1998; Hamilakis et al., 2002; Joyce, 2005; Sofaer, 2006; Stojanowski, 2010; Sharratt, 2011).

In concert with these lines of physical evidence, the application of social identity theory to bioarchaeological research has provided a means for examining dimensions of the lived experience in ancient contexts. Indeed, over the past decade, “bioarchaeology of identities" has grown in popularity as an area of research and as a topic of numerous edited volumes (e.g., Knudson and Stojanowski, 2008, 2009; Agarwal and Glencross, 2011; Amundsen-Meyer et al., 2011; Baadsgaard et al., 2011). Since their advent, bioarchaeological investigations of social identity have focused on broad-scale collective identities such as ethnicity, gender, social or socioeconomic status, religion, and age (Meskell, 2001; Gowland and Knüsel, 2006; Buikstra and Scott, 2009; Hollimon, 2011). Another subset of identities research has focused on the individual, using social theory and osteobiographical data to access facets of personhood and to examine a single life course (e.g., Hawkey, 1998; Gilchrist, 2000; Robb, 2002; Boutin, 2011, 2012; Knudson et al., 2012; Stodder and Palkovich, 2012). These studies tend to invert analytical approaches that use population or sample averages, instead starting from an individual to emphasize variation rather than some postulated norm (Zvelebil and Weber, 2013). By comparison, mid-scale (e.g., neighborhoods, parishes, sodalities, etc.) and multiscalar collective identities (e.g., kin groups) remain largely underinvestigated despite representing key spheres of social interaction and identification (cf. Pilloud and Larsen, 2011; Paul et al., 2013).

Kin identity is both personal and interpersonal, but it is ultimately based on commonality and shared experience (e.g., ancestry, domestic space) and, therefore, is collective in nature (McKinnon, 1991). Kinship/family represents a critical multiscalar collective identity for which bioarchaeology can offer deep time perspectives. Approaching kinship as a multilevel form of social identity provides a yet undeveloped scale of analysis to explore connections between individual-, small group-, and community-level identities to address broader questions of human social organization in the past (Meyer et al., 2012).

Operationalizing this approach will be challenging. Limited to often incomplete ethnohistoric records and/or material manifestations of identity that survive taphonomic processes, bioarchaeologists must fully engage archaeological and biological data to make informed inferences on past social behaviors and practices. Traditional practice has been to employ mortuary analysis in combination with complementary biological methods. By acknowledging that burial reflects social memory of the deceased and that it is the living who bury the dead, the contextualized extrapolation of social information from mortuary contexts is often an essential aspect of bioarchaeological identities research (Goodenough, 1965, 1968; Hodder, 1980, 1982, 1987; Parker Pearson, 1982, 1999; Hodder and Cessford, 2004; Thomas et al., 2006). More recently, the physical body has emerged as an essential source of data on identity, one integrated into the overall funerary context (see Parker Pearson, 1999; Rakita et al., 2005; Sofaer, 2006; Geller, 2009b; Duncan and Hofling, 2011; Duncan and Schwarz, 2014).

Bioarchaeological work that examines the corporeal correlates of social relatedness (e.g., isotopic patterning, body modifications, patterned activity markers, or stress indicators) permits inferences regarding kin practices and principles of social organization, both in cases of biological kinship as well as those of “alternative” or “fictive” kin (Pilloud and Larsen, 2011; Meyer et al., 2012; Gregoricka, 2013). In fact, in an effort to avoid biologically deterministic or primordialist interpretations of relatedness, archaeologists have grown increasingly cognizant that genotypic/phenotypic variability and behavioral/cultural variability are not directly related (Díaz-Andreu, 2005; Stojanowski, 2005a, 2005b; see also Barth, 1969). Collective identities are often founded on non-biological factors; notions of relatedness – like ethnic identity – can be borne out of fictive ancestry or fictive notions of shared origin (Barth, 1969; Jones, 1997; see also Bourdieu (1977) and Pilloud and Larsen (2011) for a discussion of "official" versus "practical" kin). Additionally, genetic relatives do not always affiliate with a bounded social collective (i.e., families) (Stojanowski, 2005b). Thus, biological and mortuary evidence are mutually informative but not inherently linked. For example, renegotiation of corporate membership and kin/residence identity need not preclude the possibility for reactive exclusion (Barth, 1969; Bawden, 2005)

In addition to further developing conceptions of what constitutes relatedness and identifying types of data that can be used to evaluate kin identity in different contexts, it is equally important to think about ways to differentiate kinship from other forms of social identity within archaeological contexts. What distinguishes kin-based identities from other social identities? Specifically, without reference to small-scale biological relationships, how is kinship to be disentangled from community and ethnicity? What are the material correlates of each? What lines of evidence might be effective in distinguishing between them? There is unlikely to be an analytical panacea or highly diagnostic line of evidence for isolating kinship identity in the past. Rather, effective interpretations will rely on attenuated readings of patterns (along with consideration of multiple analytical scales) within different archaeological contexts combined with analogic reasoning (e.g., incorporation of ethnographic and ethnohistoric data and cross-cultural comparisons) when appropriate.

Future Directions

Approaching relatedness as a multiscalar form of social identity provides a holistic approach to family organization that is flexible enough to be sensitive to salient aspects of relatedness in diverse archaeological contexts and sufficiently generalizable to permit cross-cultural explorations of family life. There are a number of conceptual lacunae that need to be addressed as bioarchaeologists explore aspects of relatedness in the past. These include expanding conceptions of relatedness associated with Western-derived models of kinship by focusing more attention on sibling relationships and non-normative (i.e., non-genealogical, non-biological) family models. Bioarchaeological investigations of family organization and kin-based social identity can both draw on and inform considerations of other aspects of social organization and worldview, including relatedness and power, and how family relations structure and are structured by locally-salient conceptions of gender, age, and the life course, for example.

Alternative models of families and conceptions of relatedness. Anthropology has struggled with the study of kinship in part because it "deals with a biological process culturally defined and a cultural process with biological consequences" (Ottenheimer, 1995:65). Kin-based relations are universal (Lancaster, 2005; Godelier, 2011), but the content of kinship – the way that people marry or raise children, whatever it is that establishes a mutuality of being – is "multivocal," meaning it varies between and within societies (Ottenheimer, 1995; Lancaster, 2005; Sahlins, 2013). Further, what constitutes kinship, what kinship does, and what kinship means are not static but have varied over the vast temporal spans subject to anthropological investigation. Therefore, perhaps the only flawed approach to investigating kinship is a monistic one (Ottenheimer, 1995). There is room for many different conceptions of kinship and different (bio)archaeological approaches to kinship (e.g., Ensor, 2013a, 2013b). To effectively explore the biocultural underpinnings of kin-based behavior, theoretical approaches to kinship, whether rooted in evolutionary or sociocultural perspectives, should be able to accommodate – or at a minimum not preclude – approaches from either subdiscipline (Chapais, 2014).

Undeniably, human reproduction is necessary for the perpetuation of the species. This does not mean that physical relationships that produce offspring necessarily form the basis of social relatedness in the present or in the past (Sahlins, 2013). Surrogacy and adoption could have enabled same-sex spouses the opportunity to raise children in the past just as they do today. The notion that husband-wife and parent-child relationships – cornerstones of "nuclear" or "conjugal" family units – are paramount to understanding kinship is flawed, biased, and prohibits a more complete understanding of relatedness (Weston, 1991; Hayden, 1995; Blackwood, 2005; Dowson, 2006; Geller, 2009a). Even within biological or consanguineal models of kinship, the focus on genealogical (i.e., intergenerational) relationships marginalizes siblingship, a potentially significant aspect of relatedness in many contexts (see Marshall, 1983; Carsten, 1995; Gibson, 1995; Paul and Stojanowski, 2015). Alternative, non-heteronormative models of family units are needed to foster different considerations of relatedness.

Bioarchaeologists are attempting to accommodate non-biological forms of relatedness in their studies of family-based social organization in the past. These contributions are noteworthy for expanding beyond genealogical conceptions of relatedness, but they are still predominantly situated within a Western conception of kinship wherein biology is the de facto characteristic that defines family relations and alternative forms of relations are supplemental (Viveiros de Castro, 2009). To develop alternative (i.e., non-biological/non-Western) forms of relatedness, bioarchaeologists need to develop conceptual models for evaluating non-biological forms of social relatedness in the archaeological record. Although this will be challenging in application – with or without ethnographic/ethnohistoric analogs – it is critical to consider alternative models of relatedness when reconstructing kinship in the past (Watanabe, 2004).

This is not to suggest a post-biological era of kinship research. Cross-culturally, a common aspect of mutuality of being is sharing common biogenetic substance (Sahlins, 2013), and in many contexts performative or process-based kin relations are modeled on procreative ones (Holy, 1996; Shapiro, 2014). Although kinship is not simply reducible to genealogy, consideration of genetic relatedness will continue to play an important role in the future of kinship studies. The use of biodistance and genetic analysis in combination with contextually relevant cultural indicators of relatedness can help disentangle kin-based affiliations from other mid-level and larger scales of social identities including neighborhood, community, and ethnic affiliations.

There is a need, for example, to develop and evaluate alternative interpretive models when individuals buried in close spatial proximity within a cemetery are not close genetic relatives (Rudbeck et al., 2005; Deguilloux et al., 2011). Additionally, the absence of evidence of genetic relatedness in cases where other types of data (e.g., mortuary, isotopic, etc.) are suggestive of a family-based relationship could be an indication of kinship based (at least in part) on social relatedness or, minimally, a non-genealogical conception of kinship (Deguilloux et al., 2011). Alternatively, these data could be indicators of a shared social identity based on something other than kinship (e.g., community, status, etc.).

Postmarital residence patterns. Postmarital residence analyses involve several (often implicit) assumptions (Stojanowski and Schillaci, 2006; Nystrom and Malcom, 2010) that must be carefully considered in terms of potential limitations on the inferences drawn from such studies as currently configured. First, for studies using skeletal samples, it is assumed that skeletons are correctly sexed. This is treated as primarily a methodological concern, although greater consideration of the influence of heteronormative bias in sexing techniques should be considered (Geller, 2005, 2008, 2009b; Hollimon, 1997). In some contexts, it may be more appropriate to group individuals for analysis using culturally salient gendered identities, including any potential "third gender" categories (e.g., Hollimon, 1997; Geller, 2005) rather than using biological sex estimated from the skeleton.

Second, there is an implicit assumption that postmarital residence practices in life are correlated with burial location at death or "postmortem residence" (Ensor, 2013b:63). Ethnographic (Matney et al., 2012) and archaeological (Keegan, 2009) examples describe mortuary practices wherein individuals who were mobile during life were returned to their natal family for burial. Such practices create "interpretational problems" for investigations of postmarital residence practices using biological data from archaeological contexts (Ensor, 2013b:62). Bioarchaeologists need to explicitly state the assumptions underlying their analyses and interpretations and actively build on current conceptual frameworks to address these issues.

To the extent to which contemporary horticulturalist and foraging groups provide acceptable models of social group interaction and behavior in the past, bioarchaeologists might draw on ethnographic evidence to formulate both expectations and inferences about kinship in ancient contexts. Information on postmarital residence and social group composition in modern hunter-gatherer societies (e.g., Hill et al., 2011; Walker et al., 2013; 2014) might inform expectations of intracemetery analyses, where the proportion of co-residing (and co-interred) kin is otherwise indeterminable. These studies also might shed light on complex kin dynamics of which archaeologists must be cognizant while reconstructing past social relationships; for example, co-parenting and partible paternity, in which more than one male is thought to be essential to offspring conception (see Ellsworth et al., 2014).

In some archaeological contexts social relatedness may have been more significant in determining burial location within cemeteries than genetic relatedness, rendering biologically-based interpretations of postmarital residence problematic. The modeling and simulation research of Usher and colleagues marks a promising avenue for explicitly testing the correspondence of conscious mortuary behavior (i.e., cemetery composition) and kin/community structure observable in the archaeological record (see Usher et al., 2003; Usher and Allen, 2005; Usher and Weets, 2014). Related endeavors referencing simulated data or conducted in highly controlled archaeological contexts will shed light on the life and death manifestation of kinship identity, as well as our ability to recover dimensions of relatedness from mortuary data.

Family, childhood, and life course. Developments in life-course theory highlight the influence of age-dependent facets of social identity and status in structuring social interactions (e.g., Gilchrist, 2000, 2004; Robb, 2002; Prowse, 2011; Zvelebil and Weber, 2013). Bioarchaeological investigations of family and relatedness will benefit from incorporating life-course and life-history perspectives. For example, Robb (2002) describes the ways in which individuals' life histories influence social group histories. As posited by Robb (2002:159), "'linear biographies' are interwoven via age-status identity and interage relations to form a cyclical history of the group as a whole." As cyclical histories are dependent on reproduction and regeneration of the collective, it is reasonable to consider families and children essential to this circuit. Bioarchaeologists may, for example, identify mortuary treatments corresponding to interwoven patterns of skeletal age and relatedness, indicating socially meaningful transitions in the life course that correspond to shifts in kin identity.

Explorations of childhood, in particular, might be effectively conducted within a research framework centered on collective kin identity. For most individuals, their earliest and most formative social interactions are shared with relatives (Carsten, 2000; Jenkins, 2008). And, relevant to Robb's (2002) conception of time and the life course, children both physically and symbolically perpetuate and eternalize family identities (Carsten, 2000; Stafford, 2000). The intersection of childhood and family represents a potentially rewarding direction for theoretical bioarchaeological research.

Bioarchaeological approaches to childhood already constitute a developing sector of social identities research (e.g., Perry, 2005; Sofaer, 2006; Lewis, 2007). Yet to date, these research programs are rarely integrated into more comprehensive investigations of archaeological kinship.

King's (2006) study of age-centered mortuary behavior at Early Postclassic Río Viejo, Oaxaca, provides an example of bioarchaeology's potential to access the intersection of childhood and kinship. King's research centers on mortuary contexts and asks why subadults were excluded from burials beneath house floors, a common mortuary context for adults at Early Postclassic Río Viejo (King, 2006, 2010). Instead of interpreting the absence of child burials as evidence for the exclusion of children from household or kin collectives, King references childhood imagery in ceramic figurines to construct an alternative interpretation. Children were not simply "nonmembers" of houses; they occupied fluid social positions (King, 2006). Affiliation with specific households (and/or biological kin collectives) remained fluid until an individual passed through a socially significant stage of the life course. In this way, the experiential time of the individual child was "interwoven via age-status identity" into the non-linear history of the corporate residence (family) (Robb, 2002:159; King, 2006, 2010). Studies of this kind, especially if both biological and social models of relatedness are integrated, would make a strong addition to bioarchaeological approaches to kinship.

Kinship and power. Kinship conceptualized as mutuality of being does not imply that relationships are inherently beneficent practices (cf. Fortes, 1949). Kinship relations are as likely to be characterized by enmity as by amity (e.g., Freeman, 1973; Franklin and

McKinnon, 2001; Peletz, 2001; Strong, 2001, 2002; Van Vleet, 2008). Family dynamics can include acts of violence and establish relationships enmeshed with power hierarchies, what Van Vleet (2008:195) calls the "micropolitics of interactions." Skeletal evidence of trauma consistent with familial or "domestic" violence is well documented in the bioarchaeological literature (e.g., Martin, 1997; Walker, 1997; Wilkenson, 1997; Novak, 2006; Martin et al., 2012). However, despite an increase in theoretical approaches to violence in the past (e.g., Martin et al., 2012; Tung, 2012), a disconnect between bioarchaeological investigations of domestic trauma and family-based social organization remains. The integration of evidence for familial violence with social relatedness, gender relations, and embodiment theory could generate new insights on individual experience and social organization in past societies. In addition, the antiquity of modern behavioral phenomena like interpersonal (or kin-structured) violence is a topic of contemporary social importance and public interest.

CONCLUSION

Kinship is currently a vibrant topic of research across the humanities, social sciences, and life sciences, with applications to diverse fields including modern human origins (e.g., Chapais, 2014), social inequality (e.g., Smith et al., 2010; Cohen, 2015), and genetic counseling (e.g., Atkinson et al., 2013). Kinship remains an active area of research within all anthropological subdisciplines. In particular, Ensor (2011, 2013a, 2013b) has recently pushed to make kinship a focus within archaeological research. Bioarchaeology, too, has witnessed an amplification of published kinship studies that have grown increasingly dependent on diverse lines of evidence and engagement with sociocultural theory. Consideration of kin-based social organization can complement a wide array of research topics about the past. Furthermore, I believe that bioarchaeology has the potential to offer significant contributions to the study of kinship.

I have reviewed bioarchaeological approaches to kinship in light of recent theoretical developments in sociocultural kinship studies to provide both historical foundation and theoretical orientation for a new model of bioarchaeological kinship research. Results of quantitative and qualitative literature reviews suggest bioarchaeologists realize that Western conceptions of biogenetic relatedness are unlikely to capture the diversity of family organization that likely existed in the past (e.g., Deguilloux et al., 2011; Pilloud and Larsen, 2011). Notably, there is growing recognition that conceptions of family common among modern Western societies (i.e., nuclear families based on consanguineal and affinal relations) may not be “suitable to the people of antiquity” (Simón et al., 2011:10; see also Gilbert et al., 2007; Haak et al., 2008; Deguilloux et al., 2011). Scholars are beginning to use broader, more flexible conceptions of relatedness to access that diversity and postulate examples of non-biological forms of kinship (e.g., fictive and practical kin) in archaeological contexts (e.g., Lozada, 2011b; Pilloud and Larsen, 2011; Gregoricka, 2013; Paul et al., 2013). The careful combination of diverse types of data and consideration of both biological and social aspects of relatedness demonstrated by Meyer et al. (2012) provides a model of research design and conceptual clarity on which future efforts should build. Stojanowski’s (2013) examination of the role of kinship in the structuring and/or institutionalization of intergenerational social inequality illustrates the potential of bioarchaeological research to link kinship to broader social issues that have real consequences on the lives of individuals in the present.

These advances are laudable, but conceptual challenges must be addressed if the field is to realize its potential. There continues to be a lack of precision in key terms. Within discussions of kinship and family, it is helpful to identify whether one is referring to genetic relatedness (e.g., Alt et al., 2013), social relatedness (e.g., Pilloud and Larsen, 2011; Gregoricka, 2013), or some combination of these (e.g., Meyer et al., 2012). Even when scholars embrace non-biological forms of relatedness, there persists a reliance on Western modes of relatedness in non-Western contexts (cf. Lozada, 2011b), including approaches that frame kinship as social identity, as I propose here. Efforts to apply our own epistemology to understand other ontologies will always struggle (Viveiros de Castro, 2009), but unless we are able to develop and operationalize theoretical frameworks for investigating kinship in ancient contexts using non-Western ontologies (a challenging goal), a social identity framework seems well adapted to incorporate both biological and cultural data without inherently prioritizing one over the other.

There is room for the incorporation of recent theoretical developments into all phases of bioarchaeological kinship research. Contextually relevant conceptions of relatedness are essential to bioarchaeological family research; they should inform not only the interpretations generated but also the hypotheses formulated, the data collected, and the analyses performed in the course of these studies. Clear expectations of data patterns consistent with non-biological forms of relatedness combined with either rigorous hypothesis testing or evaluation of alternative explanatory models will help scholars avoid the “just so” stories that accompany ad hoc or post hoc applications of social theory to one’s data. At present, nuanced reconstructions of kinship and relatedness in the past may only be possible in contexts with clearly established chronology and availability of diverse data, including ethnohistoric, epigraphic, or ethnographic evidence of kinship organization to aid inferential precision. Notwithstanding, much can be learned about the past through the study of kinship, even in contexts where these criteria are not met. Bioarchaeologists can contribute to an understanding of the fluctuating biological and social realities of kinship experienced throughout the history of our species. Such an understanding might, in turn, inform sociocultural theory, which often assumes that the range of human experiences observed today encompasses all of the forms of human experiences that existed in the past, a biased and likely untenable assumption.

In addition to providing a fruitful course of future research, a bioarchaeology of kinship as multiscalar social identity has the potential to build bridges within the academy and provide a conduit for anthropological scholarship to reach a wider audience. Bioarchaeology is well suited to incorporate both biological and social perspectives into holistic understandings of kinship (Meyer et al., 2012), as well as to provide the time-depth that sociocultural approaches are lacking and that most evolutionary approaches fail to directly access. Bioarchaeological kinship research should provide a common ground that facilitates collaborative research among archaeological, sociocultural, and evolutionary anthropologists specifically and contribute to cross-disciplinary research initiatives in general.

Within academia, a bioarchaeology of kinship as social identity would be ideally positioned to contribute to one of the 25 most important scientific challenges for archaeology presented by Kintigh et al. (2014). One of their 25 challenges (Challenge D2) concerns how people form social identities; specifically, the authors state that a critical aspect of future research will be understanding "how human identities (vs. the modes of affiliation among other species) form with respect to biological and emotional bonds" (Kintigh et al., 2014:14-15). By exploring the ways in which multiscalar family identities are formed, modified, and interact with other forms of social identities, bioarchaeologists can provide important insights into the long-term and large-scale effects of the processes of identity formation and transformation.

Stojanowski and Duncan (2015) note that for the field of bioarchaeology to remain relevant in contemporary public discourse, bioarchaeologists must develop research projects of general interest and disseminate findings among broad audiences. The investigation of families in the ancient and recent past has the potential to attract widespread interest via major media outlets and science news aggregators. Today, as North American media attention centers on the "crisis of the [Western] family," scientific/technological endeavors (e.g., genetic counseling, in vitro fertilization, prenatal medicine) intersect with social endeavors (e.g., same-sex marriage and adoption legislation, foster parenting systems, an increasing number of stay-at-home fathers) in both complementary and conflicting ways (e.g., McKinnon, 1991; Stone, 2001; Carsten, 2004, 2011; McKinnon and Cannell, 2013). Holistic bioarchaeological perspectives on relatedness can inform popular imaginations of kinship and, perhaps, influence the ways in which we advocate, legislate, and approach changes to current social structure.

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CHAPTER 3

PERFORMANCE ANALYSIS OF DECIDUOUS MORPHOLOGY FOR DETECTING BIOLOGICAL SIBLINGS

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Kinship is an essential facet of personhood and an important unit of social, political, economic, and ideological organization (MacCormack and Strathern, 1980; McKinnon, 2000; Faubion, 2001; Franklin and McKinnon, 2001; Carsten, 2004). Kinship also figures prominently in studies of the behavioral and cultural evolution of the human species as an important determinant of group composition, with much recent work based on ethnographic studies of modern hunter-gatherer/forager bands (e.g., Hill and Dunbar, 2003; Sear and Mace, 2008; Hill et al., 2011; Walker et al., 2013; Bailey et al., 2014; Ellsworth et al., 2014; Hill et al., 2014). However, directly studying the dynamics of kinship and group composition in the past must rely on bioarchaeological analyses of human skeletal remains and, in particular, reconstruction of cemetery structure and the identification of groups of biological kin (Stojanowski and Schillaci, 2006). Previous bioarchaeological work on kinship analysis has almost exclusively emphasized relationships between adults using permanent tooth crown phenotypes, which omits the crucial periods of infancy and childhood. This is unfortunate because adult-centered analyses ignore burgeoning broad-based interests in the "anthropology of children" (Baxter, 2005; Lancy, 2008; Montgomery, 2009), which can benefit from the temporal perspectives that only bioarchaeology can offer, as demonstrated in a number of recent publications (e.g., Perry, 2006; Lewis, 2007; Halcrow and Tayles, 2011; Thompson et al., 2014). For the most part, the increased visibility of childhood research in bioarchaeology has lacked a comprehensive biodistance component that might integrate children into more holistic understandings of kinship in the past (but see Pilloud and Larsen, 2011).

The dearth of kinship studies of subadults results from two phenomena. First, historically there has been a tendency to downplay the importance of children in research on past human social dynamics. In archaeology, this reflects perceptions of childhood agency. Prior to the last three decades, children were rarely conceptualized as social actors, but instead as passive beings on a predetermined, developmental course to adulthood (Derevenski 1997, 2000; Wilkie, 2000; Lewis, 2007). However, research on living communities suggests that children *are* essential to understanding kin and social structure in prehistoric contexts. For example, Hill et al. (2011) found that adult kin comprise less than 10 percent of an individual foraging band on average and that the proportional representation of co-residing siblings declines as cohorts age, a pattern generally determined by out-marriage practices. In addition, infancy and early childhood mark a near universal peak in human mortality (Kaplan, 1997; Gurven and Kaplan, 2007; Hill et al., 2007), which indicates that higher proportions of very young, closely related individuals will not only co-reside, but will also experience co-interment. Mortality profiles for archaeological hunter-gather samples corroborate a bimodal pattern with mortality peaking during the earliest years and then again at a later stage in life (Angel, 1969; Owsley and Bass, 1979; Mensforth, 1990; Nagaoka et al., 2012; Flensborg et al., 2013). Second, analysis of biological kinship patterns among very young individuals in archaeological contexts requires using information from deciduous (or mixed) dental phenotypes, which are comparatively underdeveloped as research tools in bioanthropology. For example, there is little development of highly-visible scoring protocols for deciduous teeth as only one deciduous trait is included in the Arizona State University Dental Anthropology System (Turner et al., 1991) and deciduous traits were not included at all in the Standards volume—Buikstra and Ubelaker, 1994 (but see Hanihara 1961, 1963, 1965, 1967; Sciulli, 1998; Lease, 2003). In addition, few studies have generated heritability estimates for deciduous morphological characters or assessed their performance as markers of genetic relationships in samples of known pedigree.

Here, I explore the utility of deciduous dental morphology for identifying biological siblings in a sample of children from the Burlington Growth Study. I review previous work on intracemetery kinship analysis and summarize research focusing on deciduous tooth crown characters, including trait definition, past bioanthropological analyses, and past heritability studies. Acknowledging the limitations of heritability as a parameter of interest (Feldman and Lewontin, 1975; Kempthorne, 1997; Vitzthum, 2003; Stojanowski and Schillaci, 2006) and the large sample size needed to generate meaningful heritability estimates (Hansen et al., 2011), I instead introduce the concept of "performance" as reflecting the ability of phenotypic traits to reconstruct known genealogical relationships at the inter-individual scale. I consider performance of deciduous crown morphology within two analytical frameworks: 1) from a general comparative perspective using multivariate phenetic approaches and bootstrap resampling (i.e., comparing phenotypic distances between relatives to phenotypic distances between non-relatives), and 2) from a simulated bioarchaeological analytical perspective based in pattern-recognition using multidimensional scaling (i.e., identifying potential relatives within a broader sample). Results are discussed with respect to the importance of bioarchaeological studies of children for elucidating broad-scale social phenomena.

Intracemetery Biodistance Analysis

Biodistance analysis reconstructs evolutionary processes in past populations using information from heritable skeletal and dental phenotypes (Buikstra et al., 1990; Konigsberg, 2006). Buikstra et al. (1990) defined three scales of analysis (continental, regional, and intrasite), the smallest of which focuses on patterns of phenotypic variation at the intrasite or intracemetery level (Stojanowski and Schillaci, 2006). These studies include examinations of temporal microchronology (Lande, 1976; Owsley and Jantz, 1978; Konigsberg, 1990), cemetery structure and formation processes (such as the social determinants of grave placement) (Stojanowski, 2003, 2005, 2013; Shimada et al., 2004; Stojanowski et al., 2007), post-marital residence practices (Lane and Sublet, 1972; Spence, 1974; Konigsberg, 1988; Schillaci and Stojanowski, 2002, 2003; Bigoni et al., 2013), and patterns of kinship and biological affinity (Alt and Vach, 1995; Corruccini and Shimada, 2002; Stojanowski and Schillaci, 2006). The last of these is of primary interest here. Kinship analysis assumes that closely related individuals are more likely than non-relatives to share genes that are identical by descent (Thompson, 1986; Konigsberg, 2000; Blouin, 2003). Assuming a proportional relationship between shared genes and phenotypes, closely related individuals should exhibit greater phenotypic similarity than non-relatives; however, the sensitivity of resolution remains unknown (Stojanowski and Schillaci, 2006). This relationship is expected to be particularly strong when biological and social family units correspond, because environmental factors affecting phenotypes are often similar for individuals sharing a uterine and post-uterine ontogenetic setting (e.g., diet, immunization practices, socioeconomic-related factors) (Hughes et al., 2000; Dempsey and Townsend, 2001; Townsend et al., 2009) as is the case with siblings raised in the same household. Thus, shared environments may actually enhance our ability to identify closely related individuals in archaeological contexts.

Despite a multifactorial inheritance, dental data on tooth size and morphology are commonly used in biodistance studies due to their relatively high degree of preservation in the archaeological record, long history of research on trait standardization, and previous heritability studies showing a moderate to strong genetic component to patterns of phenotypic variation (e.g., Goose, 1971; Alvesalo and Tigerstedt, 1974; Berry, 1978; Scott and Potter, 1984; Dempsey et al., 1995; Kabban et al., 2001). In addition, tooth crowns do not remodel after formation and thus are subjected to a brief period of ontogenetic plasticity (Smith, 1991). Previous studies confirm the utility of these approaches by merging multiple lines of evidence (e.g., mtDNA, odontometrics) for two reasons: 1) identifying relatives within ancient contexts, 2) verifying the reliability of certain phenotypic traits in genetic kin detection (Shinoda et al., 1998; Shinoda and Kanai, 1999; Adachi et al., 2003, 2006).

Deciduous Dental Phenotypes in Physical Anthropology

The majority of physical anthropological and bioarchaeological research that involves teeth focuses on the permanent dentition, in part, because deciduous elements have thinner enamel that is more susceptible to wear (Sumikawa et al., 1999; Lease, 2003; Grine, 2005), are shed early in life and incrementally (Sciulli, 1998), and are less consistently represented in the archaeological/fossil record. The most visible research on deciduous crown morphology was presented in a series of papers by Hanihara who described primary tooth variation across European and African Americans and among Japanese children (Hanihara, 1956, 1961, 1963, 1965, 1967). Hanihara's work was essential for advancing the standardization of deciduous morphological trait recording (see Hanihara, 1961, 1963). Sciulli detailed temporal trends in deciduous crown morphology within Ohio Amerindian populations (Sciulli, 1977, 1990, 1998). In so doing, Sciulli (1998) expanded Hanihara's (1961, 1963) system, ultimately compiling a suite of 57 morphological traits including 33 crown and 24 root features (see Sciulli, 1998:192-196). As part of her dissertation work that compared deciduous postcanine morphology between European and African Americans (Lease, 2003; Lease and Scuilli, 2005), Lease expanded these systems further by adding recording standards for mandibular molar cusp number (Lease, 2003:153-159). Appendix A of Lease's dissertation outlines various standards, most originally described in Hanihara (1961, 1963), Sciulli (1998), or augmented from Turner et al.'s (1991) standards for scoring permanent dental morphology (i.e., the Arizona State University Dental Anthropology System or ASUDAS) (Lease, 2003:153-159). Rare morphological traits or anomalies have also been described but are given less attention in the literature (e.g., Brook and Winter, 1970; Butler and Hughes, 1984; Benazzi et al., 2010).

Investigations into primary dental development and/or emergence patterns are common in the clinical literature (e.g., Friedlaender and Bailit, 1969; Baghdady and Ghose, 1981; Holman and Jones, 1991; Liversidge and Molleson, 2004; Mahoney, 2012), while a number of deciduous tooth studies are descriptive, defining phenotypic variability within and across populations. These include examinations of deciduous crown dimensions in living and ancient samples (e.g., Hanihara, 1970; Lukacs et al., 1983; García-Godoy et al., 1985; Sciulli, 1990, 2001; Farmer and Townsend, 1993; Kuswandari and Nishino, 2003) and a limited number of cross-population surveys (e.g., Harris, 2001; Harris and Lease, 2005). Within modern humans, anthropologists have considered the utility of deciduous elements for discerning bioregional affiliation and/or ancestry (e.g., Sciulli, 1977, 1980; Kitagawa et al., 1995; Kitagawa, 2000; Harris, 2001; Lease, 2003; Lease and Sciulli, 2005). The feasibility of using tooth size to estimate the sex of subadults has also been explored (De Vito and Saunders, 1990; Alvrus, 2000; Adler and Donlon, 2010; Cardoso, 2010; Viciano et al., 2013); this topic is of great importance to bioarchaeologists working in prehistoric contexts where subadult (skeletal) sex is often elusive. Recent paleoanthropological literature has examined deciduous crown morphology and shape (e.g., Benazzi et al., 2011, 2012; Bailey et al., 2014) or differential rates of primary and overall dental development (e.g., Bayle et al., 2009, 2010; de Castro et al., 2010; Smith et al., 2010) as features distinguishing between hominin taxa. However, small-scale kinship studies based on deciduous phenotypes are rare (but see Pilloud and Larsen, 2011; Pilloud and Hillson, 2012), which may be attributed to a relative lack of pedigree-based research on deciduous crown morphology.

Previous pedigree-based or twin research has yielded heritability estimates for a number of dental phenotypic traits in human and non-human primates (e.g., Hlusko et al., 2002, 2004; Koh et al., 2010). In humans, heritability estimates show permanent tooth crown dimensions, overall, to be under moderate to strong genetic control (Osbourne et al., 1958; Goose, 1971; Alvesalo and Tigerstedt, 1974; Dempsey et al., 1995; Kabban et al., 2001; Townsend et al., 2009), while permanent dental morphological characters yield similar to moderately lower heritability estimates (Biggerstaff, 1970, 1973; Scott and Potter, 1984; Boraas et al., 1988; Townsend and Martin, 1992; Townsend et al., 1992; Kabban et al., 2001; Hanihara, 2008). A number of studies have generated heritability estimates for deciduous dental characters (*crown dimensions*: Di Salvo et al., 1972; Townsend, 1980; Mizoguchi, 1998; Hughes et al., 2000; *occlusal topography*: Su et al., 2008), and the results are comparable, if not slightly higher, than estimates generated for adult crown features ($\sim h^2=0.58\text{-}0.98$). That the deciduous tooth estimates are slightly higher for some traits likely reflects differences in their developmental environments (natal versus post-natal). Deciduous teeth begin mineralization as early as 12 weeks in-utero, with most teeth crown-complete at birth (Kraus, 1959; Lunt and Law, 1974; Smith, 1991; Liversidge and Molleson, 2004). Deciduous odontogenesis spans two to three years, with most primary teeth emerging during the second year of life. Permanent crown odontogenesis lasts between eight and fourteen years, with all permanent teeth mineralizing post-natally (Schour and Massler, 1940; Anderson et al., 1976; Smith, 1991). Because primary elements form rapidly and mineralize within the first year of life, some scholars suggest deciduous phenotypes may better reflect an individual's underlying genotype than do their permanent successors (Alberch et al., 1979; Alberch, 1980; Saunders and Mayhall, 1982; Smith et al., 1997; cf. Guatelli-Steinberg et al., 2006). As compared to dimensional traits, published heritability estimates for deciduous morphological crown traits are rare, possibly due to the underrepresentation of deciduous morphology research in the literature.

Moving Beyond Heritability Estimates in Assessing "Performance"

The aim of this study is to test the performance of deciduous morphological traits in genealogy reconstruction. When considering a character's utility for biodistance analysis, researchers typically reference trait-specific heritability estimates, as discussed above. Narrow-sense heritability estimates provide predictive ratios of additive genetic to total phenotypic variance within a population, ranging from 0.0-1.0 (Fisher, 1918; Hartl and Clarke, 1997; Townsend et al., 2009). Traits with high heritability are those for which additive genetic variation in the population is high compared to variation in environmental factors that affect final phenotypes (Fisher, 1918; Falconer, 1960; Hartl and Clark, 1997). Neither parameter is fixed or necessarily tied to the genetic architecture of the trait itself. As such, those that draw upon Fisher's (1918) concept often confound the statistical value (Fisher, 1958) with the common term *heritability,* meaning "familial" or "heritable" (Feldman and Lewontin, 1975; Hartl and Clark, 1997; Scott and Turner, 1997; Vitzthum, 2003). In addition, the degree to which trait expression is genetically controlled is completely unrelated to potential environmental "interventions" that can affect the phenotypic outcome (Smith and Bailit, 1977; Townsend et al., 2009). Notwithstanding, heritability estimates are useful when researchers account for their interpretive limits and recognize that these values apply to *populations*, not to individuals or species (Osbourne, 1967; Feldman and Lewontin, 1975; Vitzthum, 2003; Sesardic, 2005). Due to the small-scale of the relationships of interest (i.e., kin relationships), traits with high levels of within-sample variability may be more useful in detecting genetic relatedness than those associated with high narrow-sense heritability (Stojanowski and Schillaci, 2006). Indeed, if a trait is under strong genetic control but is monomorphic across a sample, it is impossible to discern biological relationships based on this trait alone. As such, heritability, in the formal quantitative genetic sense, is an imperfect measure of performance at the inter-individual level. Instead, I evaluate performance as the extent to which deciduous morphological traits can accurately reproduce known genetic relationships, specifically sibships.

MATERIALS AND METHODS

Pedigree information and deciduous dental morphological data were collected from 69 subadult participants of the Burlington Growth Centre's Family Study (housed at the University of Toronto Faculty of Dentistry, Ontario). Initiated in 1952, the Burlington Growth Study marks an ongoing effort to record longitudinal craniofacial developmental data in the form of both family and individual health histories, cephalometric radiographs, orthodontic records, photographs, stone dental casts, and most recently three-dimensional orthodontic models (Thompson and Popovich, 1976). All study participants were residents of Burlington, Ontario at time of recruitment, and most are of European ancestry. Each of the 69 individuals included in the sample had at least one sibling represented in the Family Study, allowing us to collect data across 24 families. Although this sample includes nuclear families, to my knowledge no relationships are shared across families; no cousin, half sibling, or extended genealogical relationships are represented in the sample. Overall, the Burlington Growth Study recruited nearly 90% of Burlington's child residents during the 1950s, when the greater Toronto region (Burlington's location) comprised approximately 40 percent of the Canadian population (University of Toronto, Faculty of Dentistry, 2015). Therefore, I assume that relationships shared among individuals from different families approximate relationships between individuals drawn from a random sample deriving from a larger, fairly diverse population. To ensure the anonymity of participants, I recoded all individuals and associated dental casts using a unique numbering system. The following research protocols were reviewed and granted exemption by Arizona State University's Institutional Review Board and the Burlington Growth Centre (Appendix B).

Data Recording Methods

Deciduous crown morphology was observed and recorded under a supplemental light source using a suite of scoring standards outlined in Dahlberg (1949), Hanihara (1961, 1963), Grine (1986), Sciulli (1998), and Lease (2003) (Table 5 and Appendix D). In addition, standards designed for recording permanent dental morphology (i.e., Arizona State University Dental Anthropology System standards – Turner et al., 1991) were used to record deciduous morphology where corresponding features were observable in the primary dentition (Turner et al., 1991). In total, data were collected for 46 morphological traits (Tables 5 and Appendix D). Character expression was recorded as binary or ordinal scale as dictated by published scoring standards (see Table 5). Because this study is concerned with detecting small-scale genetic relationships (i.e., within-sample kin relationships) ordinal grades were not dichotomized in order to maximize variation in the dataset. Although data were recorded for both left and right antimeres, the sides were collapsed using the highest degree of observable expression. This is standard practice and mitigates genetic redundancy in the dataset given the strong correlation between morphology scores among antimeres (Turner and Scott, 1977; Turner et al., 1991).

Analytical Methods

A series of preliminary adjustments were made to ensure that the morphological dataset most accurately represented underlying genotypic information (see Appendix D). Because the morphological data matrix was incomplete, individuals and variables represented by a relatively high number of missing cells were removed from the analysis. Common causes of missing data included wear, casting imperfections that obscured crown features, and the presence of mixed dentitions in a number of individuals whose participation in the project initiated in later childhood. Individuals represented by less than 10 morphological trait scores, and traits observable in less than 40 individuals were omitted from the study. In addition all monomorphic traits were removed from the dataset (i.e., those that do not vary in expression between any individuals in the sample). To quantify intra-observer error, I rescored ~15% of the original sample to evaluate absolute grade differences between observation sessions, which were separated by approximately seven months. Traits with error ranges exceeding a single ordinal grade were removed from the sample (Hillson, 1996:99); here, the use of error range instead of average error provided a conservative approach to trait removal. Correlation between sex and trait expression was assessed using Kendall's tau-*B* coefficient (Kendall, 1975; Kendall and Stuart, 1979). Those characters found to be significantly sex-dependent ($p \leq 0.05$) were removed from the analysis. Because crown morphology is complete upon tooth eruption, age differences should only reflect wear effects. Fortunately, Burlington Growth Study participants' dentitions were cast at various points throughout their lives, allowing for observation of deciduous morphology on the least-worn cast for elements and/or traits of interest. For this reason, age and wear should not account for any non-random variation in the sample.

Inter-trait correlation was assessed using Kendall's tau-*B* correlation coefficients (Kendall, 1975; Kendall and Stuart, 1979). Because the sample is relatively small, I removed inter-correlated traits while discounting spurious correlation among traits that likely have no biological and/or developmental foundation. Associated traits within the same region of the dentition (i.e., anterior or postcanine) were removed when significantly correlated ($p \leq 0.05$). Correlation between morphological characters occurring on teeth across distinct regions of the dentition was considered significant when tau-*B* coefficients were less than -0.4 or greater than 0.4. In each instance of inter-trait correlation or redundancy between multiple scoring systems, the character or data recorded under the scoring system representing the least variability in the sample were omitted from the dataset. Appendix D lists all morphological traits omitted from the final biodistance analysis and the reason for omission. All statistical analyses were conducted using SPSS v. 21 (IBM Corporation, 2012) or Systat v. 11 (Wilkinson, 2010).

After variable winnowing, Clustan v. 7.05 was used to calculate 2,145 inter-individual Euclidean distances from the reduced morphological dataset of 20 traits and 66 individuals (see results and Tables 5-6) (Wishart, 2004). This program calculates distances with mixed data types and with minimal missing data. Only 192 of 1320 (14.5%) cells were missing, which is within the acceptable range considering that individuals with large amounts of missing data were removed and missing values were fairly evenly distributed across the sample (Brown et al., 2012).

Multivariate phenetic similarity is the primary way in which biological affiliation is assessed in bioarchaeological kinship analyses. The key parameter of performance is the degree to which close relatives are phenotypically similar with respect to the broader sample to which those individuals are not related. I evaluated the performance of deciduous crown morphology from two analytical perspectives: 1) from a general comparative perspective, and 2) from a simulated bioarchaeological perspective. Within the first analytical framework, performance was assessed by comparing the pairwise phenetic distances between relatives (in this case full siblings) and the pairwise phenetic distances between non-relatives. Because closely related individuals are more likely than distant or non-relatives to share genes that are identical by descent (Thompson, 1986; Konigsberg, 2000; Blouin, 2003), I expected that sibling pairs would be significantly more similar in dental morphology than expected by chance and that pairwise distances between relatives would be smaller than pairwise distances between non-relatives (Stojanowski and Schillaci, 2006). Because inferential statistics are not directly applicable to distance statistics I used bootstrap resampling in Excel's Resampling Stat add-in to generate p-values for these tests (Microsoft 1999, 2003). Distances were first averaged across all relatives, across all non-relatives, and across all families for comparison. Because I ultimately winnowed the dataset to include 69 sibling pairs (see results below), I generated a resample of 69 pseudo-distances from the larger sample of unrelated individuals and 69 pseudo-distances from the combined sample of related and unrelated individuals. This process was repeated for 9,999 replicates to generate a robust p-value. Resampling was also conducted by family, varying the number of resampled pseudo-distances according to the number of sibling pairs represented in each family unit.

Table 5. Deciduous morphological variables and scoring standards included in performance analysis.

Morphological Variables[a]	Included Standards	Secondary Standards[b]
WINGING i^1	Turner et al. (1991)	
LABIAL CURVE i^1	Turner et al. (1991)	
DOUBLE SHOVEL i^2	Sciulli (1998)	Turner et al. (1991)
DOUBLE SHOVEL c^1	Sciulli (1998)	Turner et al. (1991)
DISTAL ACCESSORY RIDGE c^1	Turner et al. (1991)	
METACONE m^1	Turner et al. (1991)	
METACONE m^2	Turner et al. (1991)	
HYPOCONE m^2	Turner et al. (1991)	Hanihara (1963)[c]
CUSP 5 m^2	Turner et al. (1991)	Sciulli (1998)
CARABELLI'S CUSP m^2	Turner et al. (1991)	Grine (1986)
PARASTYLE m^2	Turner et al. (1991)	
SHOVEL c_1	Hanihara (1963)	
TUBERCULUM DENTALE c_1	Grine (1986)	Turner et al. (1991)
CUSP 5 m_1	Turner et al. (1991)	
GROOVE PATTERN m_2	Turner et al. (1991)	Sciulli (1998)
CUSP NUMBER m_2	Turner et al. (1991)	Sciulli (1998)
DEFLECTING WRINKLE m_2	Turner et al. (1991)	Sciulli (1998)
PROTOSTYLID m_2	Turner et al. (1991)	Grine (1986)
CUSP 6 m_2	Turner et al. (1991)	
CUSP 7 m_2	Turner et al. (1991)	Sciulli (1998)

[a]Maxillary and mandibular arcades are indicated by superscripts and subscripts, respectively. [b]A number of morphological variables were scored according to multiple published standards. The data scored according to the scoring system that maximized within-sample variation for a given variable were included in the analysis. The scoring standards yielding data that captured the least amount of within-sample variation for a given trait (i.e., that were excluded from the analysis) are listed in the final column of the table. [c]Augmented from Dahlberg (1949) and referred to as "crown pattern of the deciduous upper second molar" in Hanihara (1961) or "cusp number, hypocone of maxillary first deciduous molar" in Hanihara (1963).

Each of these distance sets was generated from 9,999 replicates of related and unrelated inter-individual distances. To generate a two-sided p-value, replicates were seriated and the rank of the actual average value for each test was divided by the total number of samples. For families represented by only a single sibling pair, Euclidean distances were compared across 9,999 replicates of a single resampled pseudo-distance generated from the sample of relative and non-relative distances. This approach provides a test of the hypothesis that related individuals exhibit phenetic distances that are simply a random sample of all possible distances and are not smaller than expected by chance given the degree of deciduous morphological variation within the broader population.

Within the second analytical framework, I assessed performance according to bioarchaeological standards in which multivariate phenetic similarity is used to infer whether any two individuals are closely related. Mimicking a bioarchaeological analytical design, multidimensional scaling (MDS) was used to ordinate the resulting inter-individual distance matrices set at 300 trials and 300 iterations. Kruskal stress was used to determine whether the MDS was acceptable. I then used the output of the two-dimensional multidimensional scaling to quantify the relative dispersion of individual families. In other words, I calculated the relative area of multidimensional space occupied by each family by multiplying the distances between the family's most peripheral coordinates along each dimension on the MDS plot (i.e., Family1 maxX-minX * Family 1 maxY-minY) (see Fig. 2). This produced a plot area of dispersion along both axes that was then divided by the area occupied by the total sample (e.g., Family 1 Area ÷ Total Sample Area) (see Fig. 2). The result indicates the proportion of multidimensional space occupied by the family relative to the total sample in which smaller values reflect overall phenotypic similarity with respect to the population from which those individuals are drawn. The key question is whether close phenetic similarity in multivariate space provides a reliable assessment of whether those individuals are closely related, as is generally assumed in bioarchaeological kinship reconstruction. Conversely, I am also interested in whether large phenotypic distances can reliably be inferred to represent unrelated individuals.

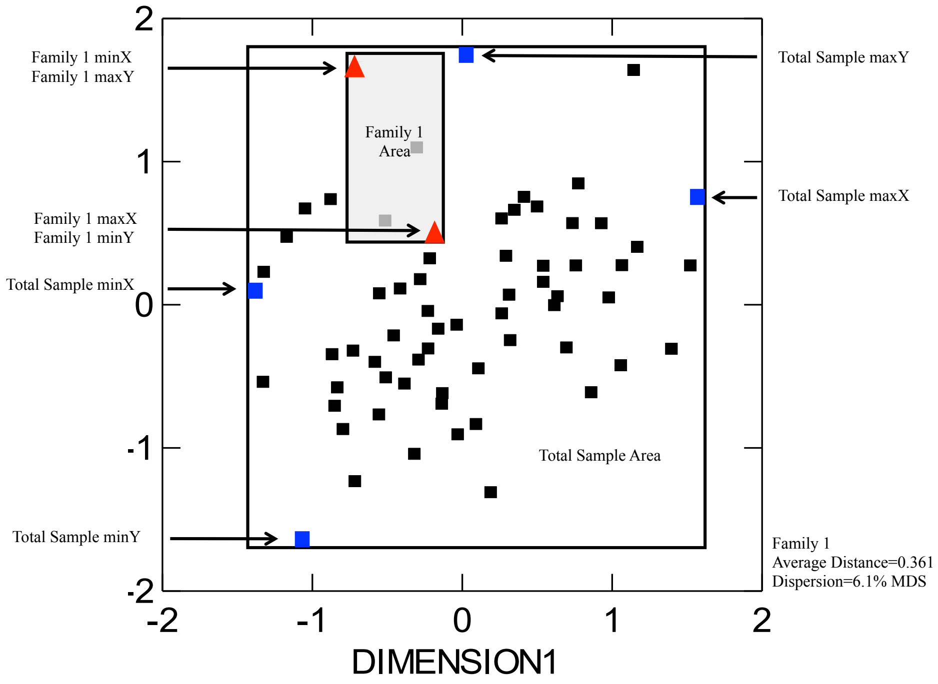

Figure 2. MDS plot highlighting Family 1's (triangles) dispersion or multidimensional space occupied relative to the multidimensional space occupied by the total Burlington Growth Study sample (squares). Points in color represent those peripheral MDS coordinates used to calculate the multidimensional space occupied (area) for both Family 1 and the total sample.

RESULTS

Results of the intra-observer error analysis indicate a high degree of repeatability. Average error ranged from 0-1 ordinal grade for all characters. Maximum error ranged from 0-1 grade with the exception of two traits: tuberculum dentale of the maxillary canine (maximum error=3 grades) and anterior fovea of the mandibular first molar (maximum error=2 grades) (Appendix D). These variables were removed prior to calculating Euclidean distances. Based on tau-*B* correlation coefficients, five traits were removed due to sex dependency and 10 traits were removed due to inter-trait correlation (Appendix D). Six traits were removed because they exhibited no variation across individuals (Appendix D). Three individuals and four traits were removed from the dataset due to large amounts of missing data. After variable winnowing the morphological dataset was reduced to 20 deciduous crown traits and 66 individuals representing 69 sibling pairs (67 full sibling pairs and 2 twin pairs) across 21 families (see Tables 5 and 6). Based on this multivariate morphological dataset, a total of 2,145 pairwise Euclidean distances were generated: 69 inter-sibling distances and 2,076 non-relative distances.

Biological Distance Results

My first analytical aim was to test whether siblings are significantly more similar in deciduous dental morphology than unrelated individuals by comparing the pairwise distances between siblings to the pairwise distances between non-relatives. The average inter-sibling Euclidean distance was 0.252 (range: 0.046 to 0.566). This average distance was significantly smaller than the average pairwise distance for the sample of non-relatives (0.323; $p<0.001$; range: 0.079 to 1.083), the smallest of 69 resampled pseudo-distances generated from 9,999 replicates of non-relative pairs (0.277; $p<0.001$), as well as the smallest of 69 resampled pseudo-distances generated from 9,999 replicates of relative and non-relative pairs (0.270; p<0.001). These results suggest moderate to high correspondence in deciduous morphology between siblings.

I extended this analysis to consider not just similarity among sibling dyads but among entire families. Nine out of the 21 families were characterized by average inter-sibling distances that were significantly smaller than the average of resampled pseudo-distances generated from 9,999 replicates of non-relative pairs (p-value range: <0.001 to 0.036). Nine out of 21 families were characterized by average inter-sibling distances that were significantly smaller than the average of resampled pseudo-distances generated from 9,999 replicates of combined relative and non-relative pairs (p-value range: <0.001 to 0.043) (Table 6). Family 16's average also approached significance when compared to the pseudo-samples generated from both the non-relative (p=0.076) and combined samples (p=0.079) (Table 6). Overall, 14 out of the 21 families exhibited average inter-sibling distances that fell in the lower half of the distribution of resampled pseudo-distances, and in only one family were siblings significantly dissimilar in their dental morphology (Family 5: average distance=0.456, upper-tail p=0.042 based on non-relative resampling) (Table 6). Of note are the distances representing the two twin pairs within the sample (KP18/KP19=0.103; KP45/KP46=0.133): they each fell below the smallest one percent of distances in the total sample (KP18/KP19=0.285% and KP45/KP46=0.996%) and are significantly smaller than pseudo-distances generated from 9,999 replicates of non-relative pairs (p<0.001) and combined relative/non-relative pairs (p<0.001).

Figure 3 depicts the range of 69 sib-pair distances plotted against all 2,076 unrelated inter-individual distances seriated from least to greatest along the x-axis. Although the majority of sibling pairs are concentrated to the far left of the plot, variability in the performance of the morphological dataset is emphasized by the range of space that these pairs occupy along the x-axis. I explored whether the disparities in sib-pair correspondence across the sample were related to differences in sibling pair "type" (i.e., male-male versus female-female versus male-female). Results of non-parametric correlation analyses revealed a non-significant relationship between sib-pair "type" and phenotypic distance (*same sex versus opposite sex*: tau-*B* coefficient=0.013, p=0.899; *male-male versus female-female versus male-female*: tau-*B* coefficient=0.086, p=0.362). Therefore, inter-sex comparisons do not perform worse than intra-sex comparisons. Further, I found a weak negative correlation between family size (i.e., a family's sibling pair count) and family average distance (tau-*B* coefficient=-0.093, p=0.599), suggesting there is no bias caused by differences in family size.

My second analytical goal was to assess the performance of deciduous morphology in identifying relatives within a simulated bioarchaeological research scenario using multidimensional scaling and pattern recognition. As evidenced in the MDS output, biological relatives occupied, on average, 3.83% of the multidimensional space; this fell far below the proportion of space occupied by the total sample (63.10%) and supports the inference that deciduous dental morphology does perform well in spatially clustering closely related individuals (see Figs. 4-6). However, family-specific MDS plots also revealed variability in performance that is masked by consideration of averages across all families or sibling pairs (Fig. 4-9 and Appendix E). For example,

Table 6. Average inter-sibling distance and bootstrap resampling results by family.

Family[a]	Individuals (*Sex*)[b]	No. Dist.[c]	Ave. Euc. Dist.[d]	p-value 1[e]	p-value 2[e]
1	KP1 (*M*), KP26 (*M*)	1	0.361	0.292*	0.292*
2	KP3 (*M*), KP4 (*M*), KP5 (*M*), KP6 (*M*), KP7 (*M*)	10	0.235	0.002	0.002
3	KP8 (*M*), KP9 (*M*), KP23 (*M*)	3	0.271	0.208	0.224
4	KP10 (*M*), KP49 (*M*)	1	0.418	0.154*	0.154*
5	KP12 (*M*), KP13 (*M*), KP29 (*F*)	3	0.456	0.042*	0.035*
6	KP14 (*F*), KP15 (*F*), **KP45 (*F*)**, **KP46 (*F*)**, KP47 (*M*)	10	0.198	<0.001	<0.001
7	KP17 (*F*), **KP18 (*F*)**, **KP19 (*F*)**	3	0.152	<0.001	0.001
8	KP31 (*F*), KP34 (*F*), KP35 (*F*), KP43 (*F*)	6	0.367	0.161*	0.152*
9	KP38 (*F*), KP39 (*F*)	1	0.248	0.253	0.256
12	KP51 (*F*), KP53 (*M*), KP54 (*F*)	3	0.219	0.031	0.036
13	KP57 (*F*), KP58 (*F*), KP59 (*F*)	3	0.211	0.018	0.024
14	KP60 (*F*), KP61 (*M*), KP62 (*F*)	3	0.357	0.270*	0.243*
15	KP63 (*M*), KP64 (*F*), KP65 (*M*), KP66 (*F*)	6	0.159	<0.001	<0.001
16	KP69 (*M*), KP70 (*F*)	1	0.189	0.076	0.079
17	KP73 (*M*), KP74 (*F*), KP75 (*F*)	3	0.190	0.006	0.005
18	KP78 (*F*), KP79 (*F*), KP80 (*M*)	3	0.263	0.169	0.180
19	KP83 (*F*), KP84 (*F*), KP87 (*M*)	3	0.225	0.036	0.043
20	KP88 (*F*), KP91 (*F*)	1	0.110	0.004	0.003
21	KP92 (*M*), KP95 (*M*)	1	0.354	0.325*	0.312*
22	KP96 (*M*), KP99 (*M*)	1	0.248	0.251	0.260
23	KP100 (*M*), KP103 (*F*), KP104 (*F*)	3	0.316	0.490*	0.479*
All Sibships		**69**	**0.252**	**<0.001**	**<0.001**

[a]Families 10 (KP20-*F*), 11 (KP50-M), and 24 (KP30-F) each had one individual removed during the course of pre-analysis data treatments, precluding the calculation of inter-sibling distances. Individual KP41 (F) did not belong to any of the families in the sample. These individuals contributed to the sample of unrelated inter-individual distances. [b]Twin pairs listed in bold. [c]Number of sibships. [d]Average inter-sibling Euclidean distance. [e]P-values indicate whether family-specific averages differ from 9,999 replicates of average pseudo-distances randomly drawn from a sample of non-relatives (p-value 1) and a sample of combined relatives/non-relatives (p-value 2). For distances in the upper 50% of the pseudo-value distribution, upper tail p-value reported (1-lower tail p-value; marked with asterisks). Average distances that are significantly smaller or larger than would be expected by chance based on their position in the resampled pseudo-value distribution are underlined ($p \leq 0.05$).

individual family areas ranged from between 0.20% (Family 20) to 33.49% (Family 14) of the total sample area indicating considerable variation in dispersion or clustering among families (average=10.56%; see Table 7). Though sex explains little performance disparity across the sample, differences in MDS dispersion may relate to the number of sibling pairs represented in each family. I found a relationship between family size

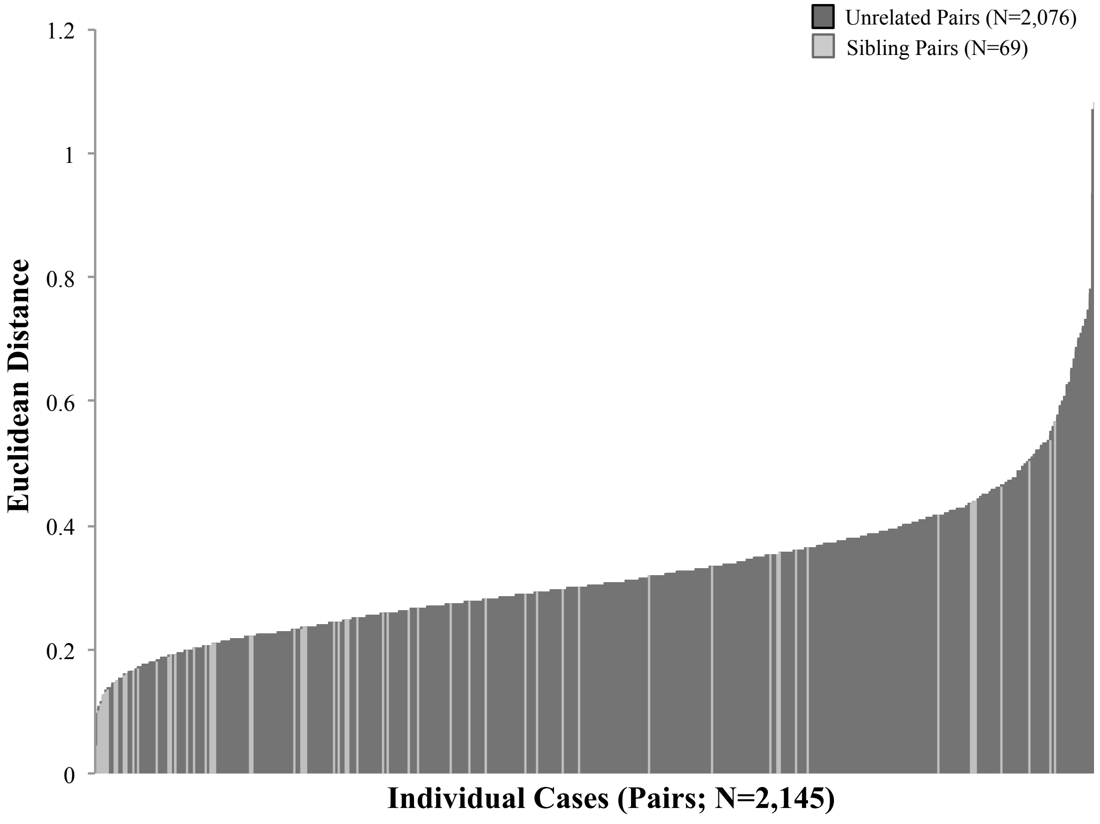

Figure 3. Pairwise Euclidean distances for all siblings (light grey) and non-relatives (dark grey) seriated from smallest to largest along the x-axis.

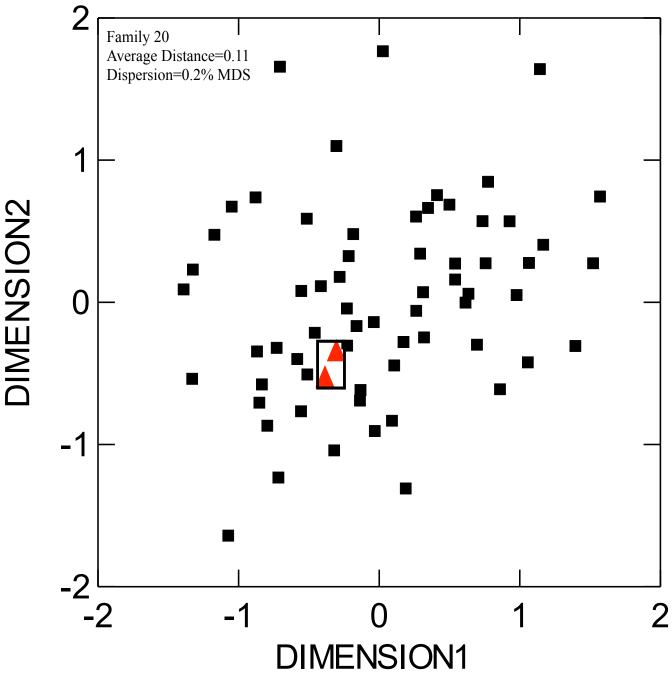

Figure 4. Family 20 MDS plot, with siblings marked by triangles and multidimensional space occupied (Family 20 Area) enclosed in a rectangle.

and plot area that approached significance (tau-*B* coefficient=0.324, p=0.066). Variation in MDS dispersion, in part, reflects an effect of family size on the results not captured by inter-sibling distance averages. Despite a weak negative relationship between family size and average distance, larger families more often include an individual that plots distantly from the remaining siblings in multivariate space.

DISCUSSION

The results of this study indicate that the use of deciduous morphology is moderately successful in the blind reconstruction of sibships within a broader sample of unrelated subadults. Although the strength of morphological correspondence varies between families and, indeed, sibling pairs, the overall patterning of biological distances across differing degrees of relatedness (i.e., non-relatives, siblings, twins) reflects expected patterns of affinity based on models of genetic inheritance and identity by descent (Thompson, 1986; Blouin, 2003). These robust results may be due, in part, to the use of a pre-treated, multivariate morphological dataset that captures the highest possible degree of variability within the sample. Capturing a large amount of variability is essential for elucidating biological patterns on such a small (intra-population and intra-familial) scale, and may be more effective than relying solely on traits associated with high narrow-sense heritability estimates in phenotypic kinship analyses (Rösing, 1986; Hartl and Clark, 1997; Eades and Desideri, 2003; Vitzthum, 2003; Stojanowski and Schillaci, 2006).

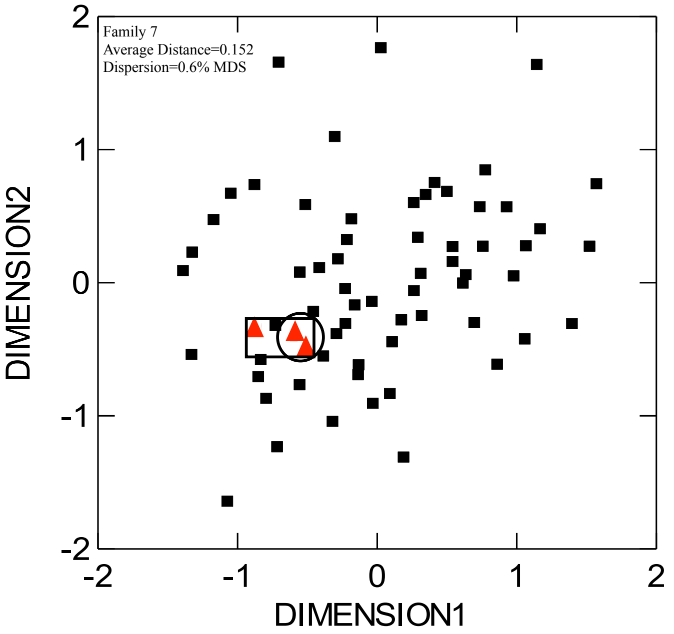

Figure 5. Family 7 MDS plot, with siblings marked by triangles. The multidimensional space occupied by the entire family is enclosed in a rectangle, and the twin pair is enclosed in a circle.

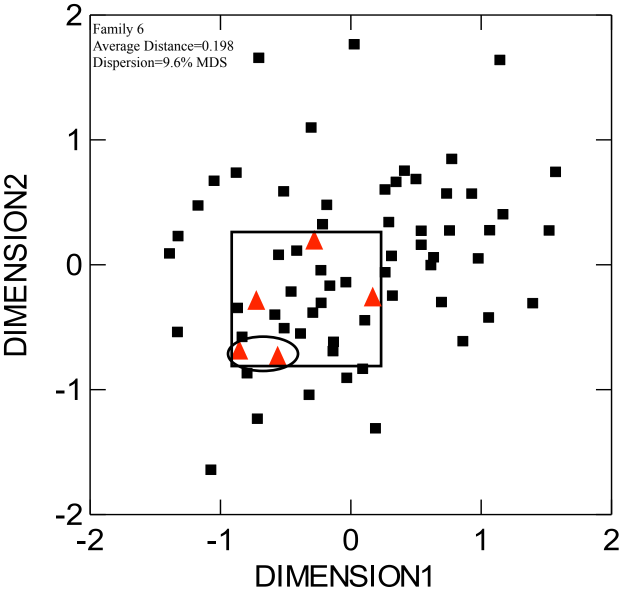

Figure 6. Family 6 MDS plot, with siblings marked by triangles. The multidimensional space occupied by the entire family is enclosed in a rectangle, and the twin pair is enclosed in a circle.

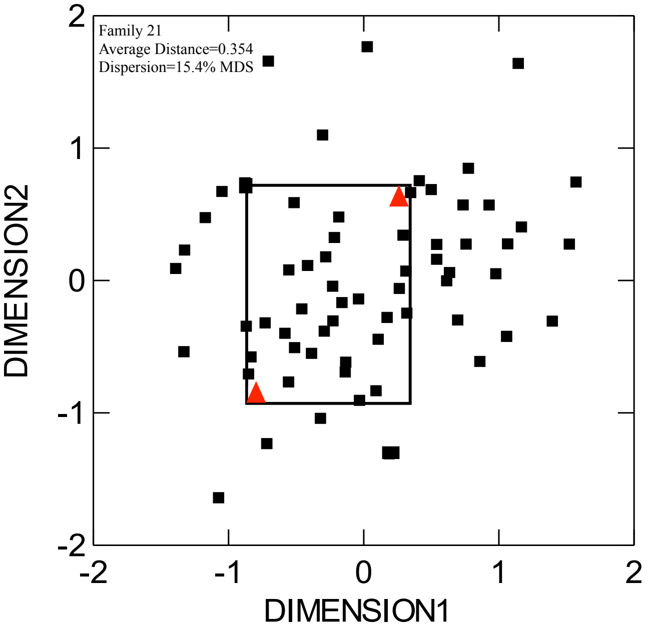

Figure 7. Family 21 MDS plot, with siblings marked by triangles and multidimensional space occupied (Family 21 Area) enclosed in a rectangle.

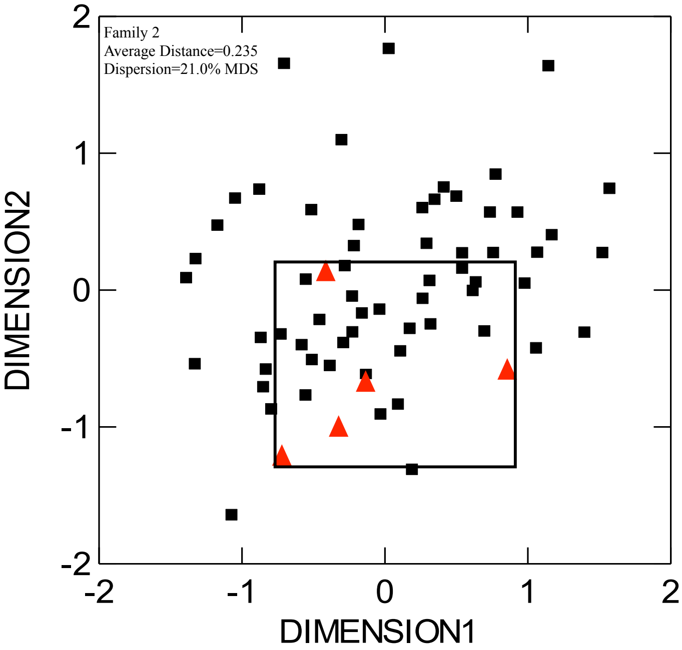

Figure 8. Family 2 MDS plot, with siblings marked by triangles and multidimensional space occupied (Family 2 Area) enclosed in a rectangle.

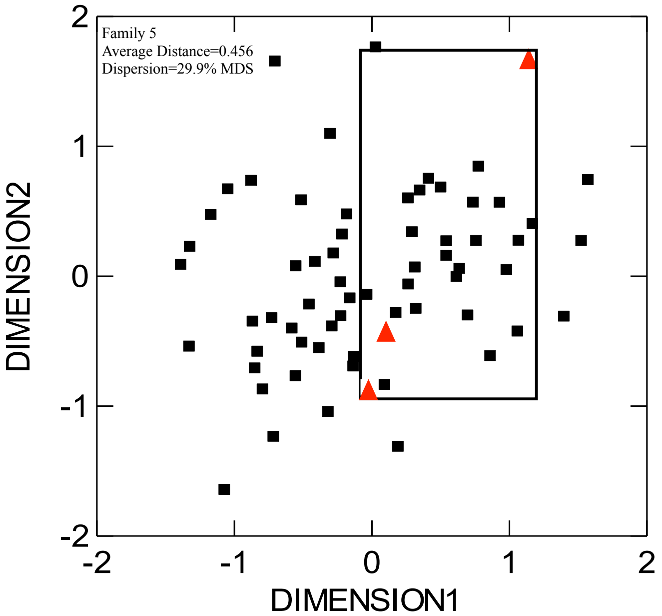

Figure 9. Family 5 MDS plot, with siblings marked by triangles and multidimensional space occupied (Family 5 Area) enclosed in a rectangle.

The results for the two twin pairs in the sample are particularly encouraging (Figs. 5-6). Unfortunately, Burlington Growth Study records do not directly specify twin zygosity. Both KP18/KP19 and KP45/KP46 are female-female twin pairs, and while longitudinal photographic records suggest that both are monozygotic, this information is not directly reported. In reality, accurate zygosity assessment is difficult without comparing highly polymorphic DNA regions between twins (Townsend et al., 2009). Theoretically, monozygotic (MZ) twins share a relatedness coefficient of 1.0 (i.e., all of their genes are expected to be shared by descent), while dizygotic (DZ) twins share a relatedness coefficient of 0.5 (i.e., half of their genes are expected to be shared by descent, on average); the latter coefficient (0.5) is also shared between full siblings. In classic twin-design heritability studies, relatively high phenotypic correspondence between MZ twins is reasoned to be driven by genetic factors (Neale and Cardon, 1992; Townsend et al., 2003; Hughes and Townsend, 2012), while environment is thought to strongly drive trait expression when phenotypic correspondence is greater between DZ twins **(**Dempsey and Townsend, 2001; Townsend et al., 2009). If this sample, indeed, includes MZ twins, my results would corroborate the foundational expectations of biological distance analysis: individuals who are more closely related (genetically identical—MZ twin relatedness coefficient=1.0) are more similar in their deciduous dental morphology than individuals who are more distantly related (not genetically identical—full sibling relatedness coefficient=0.5) or unrelated (relatedness coefficient<0.5). However, if the twin pairs in the sample are, in fact, DZ twins, this might suggest that sharing a uterine ontogenetic environment *contemporaneously* leads to greater phenotypic correspondence between DZ twins than would be expected for full siblings who share a uterine ontogenetic environment but at different times.

Environmental differences between siblings may also be an important factor behind the differential performance of the morphological dataset across families. Although nine of the 21 families in the sample are characterized by significantly smaller average inter-sibling distances than would be expected by chance, one might question why this was not the case for the other families. Generating heritability estimates for these morphological traits would provide a general measure of relative environmental contribution to phenotypic variation for the sample, but would fail to identify specific environmental, developmental, and maternal factors that strongly influence morphological correspondence between siblings. A number of classic studies have explored potential influences, with most published in the clinical literature (Garn et al., 1959, 1979, 1980; Bailit and Sung, 1968; Heikkinen, 1992). Stanley Garn and colleagues have provided essential insights in this area, for example, finding that prenatal factors such as maternal effects or "gestational determinants" strongly contribute to crown size variability (Garn et al., 1979). They found that factors such as maternal diabetes and hyperthyroidism lead to increased deciduous crown size, while maternal hypertension and reduced birth weight/gestation period account for reduction in deciduous dimensions (Garn et al., 1979). Fearne and Brook (1993) also identified low birth weight and poor pre/perinatal growth as driving factors in deciduous crown reduction (Fearne and Brook, 1993; cf. Harila et al., 2003). More recently, Seow and Wan found birth weight to have a "dose-response effect" on primary crown morphometrics; their results showed crown dimensions to range from smallest to intermediate to largest across very low, low, and normal birth weight categories, respectively (Seow and Wan, 2000:67). These studies focus specifically on dental metrics; developing similar models to test environmental variables/maternal effects as predictors of inter-sibling phenotypic distance might prove a productive step in examining *morphological trait performance* for identifying child relatives within a pedigreed sample.

While performance as approximated by MDS dispersion was moderate to strong for the morphological dataset, it is important to stress how difficult interpretation of any bivariate plot will be for bioarchaeological contexts for which little supplemental data on biological relatedness is available. Here I have shown that close phenetic distance is, on average, a feature of siblings but that this pattern becomes muddled once the sample size included in an analysis increases. Unlike DNA, for which genomic comparisons provide very fine resolution, I see no evidence for unique configurations of traits or a clear path to setting a likelihood or probability of relatedness in the absence of other contextual data. There are simply not enough unique configurations of traits (i.e., the variability one observes) to expect completely distinct placements of individuals based on phenetic grounds alone. Small phenetic distances do, on average, suggest close biological relatedness in the sample, but this is not absolute. Large phenetic distances, however, suggest the individuals are *not* closely related. As such there is polarity to the strength of inference deciduous morphological data offer. Linking these results to environmental variables that may explain poor performance is a critical next step. Most relevant would be linking these results to environmental variables that are visible in the archaeological

Table 7. Absolute and relative multidimensional space (2D) occupied by each family.

Family	No. Sibling Pairs	MD Space Occupied[a]	Relative MD Space Occupied[b]
1	1	0.613	0.061
2	10	2.121	0.210
3	3	0.379	0.038
4	1	0.911	0.090
5	3	2.988	0.299
6	10	0.969	0.096
7	3	0.058	0.006
8	6	2.705	0.268
9	1	0.125	0.012
12	3	0.508	0.050
13	3	0.891	0.088
14	3	3.378	0.335
15	6	0.580	0.057
16	1	0.349	0.035
17	3	0.200	0.020
18	3	0.904	0.090
19	3	0.697	0.069
20	1	0.016	0.002
21	1	1.556	0.154
22	1	0.504	0.050
23	3	1.929	0.191

[a] Multidimensional space occupied in the two-dimensional plot as calculated from the ordinated coordinates (units^2).

[b] Dispersion or multidimensional space occupied in the two-dimensional plot as scaled by the multidimensional space occupied by the total sample (10.088 units^2, 0.631 relative MD space occupied). Note that this number is less than the total plot area (16 units^2) because the total sample is not dispersed to the axis margins.

record – indicators of early childhood stress such as linear enamel hypoplasia, accentuated striae of Retzius, or markers of systemic skeletal stress with possible metabolic or dietary etiologies.

Incorporating children into bioarchaeological kinship analyses, though not without its challenges, provides critical data on ancient family and social group composition. Demographic and ethnographic data on modern foraging societies have underscored the importance of children to understanding kinship within ancient contexts. In most societies, childhood marks the phase in the life course during which the highest proportion of kin co-reside (Hill et al., 2011). This, coupled with elevated mortality during early childhood, underscores the importance of identifying potential subadult relatives within cemetery samples if one is investigating family-structured behavior in the past. For example, accessing information on child relatives could implement finer-grained analyses of inter-generational distributions of wealth or status, contributing to broader interests in the rise of social inequality (Flannery and Marcus, 2012; Kintigh et al., 2014). There is also considerable potential to enhance studies of differential health and frailty. Examinations of comparative subadult health (e.g., Storey, 1997; Holland, 2013) have provided new insights into heterogeneous frailty and will likely further contribute to studies of the "Osteological Paradox" in paleopathology (Wood et al., 1992). These analyses gain considerable power if couched within a familial framework and the results presented here provide initial support for the ability of biological distance analyses to contribute to this literature.

CONCLUSION

Deciduous dental morphology performed moderately well in the detection of genealogical relationships (full sibships) within a broader sample of unrelated individuals. Although performance varied across families, the average inter-individual sibling distance (0.252) was significantly smaller than would be expected by chance in a sample of non-relatives or a mixed relative/non-relative sample ($p<0.001$). Important to bioarchaeologists, it should be noted that while MDS plots may show tight clustering among siblings, non-relatives often plot closely to these individuals in multidimensional space, making interpretation difficult without use of additional lines of evidence (e.g., mortuary patterning, ethnohistoric data, material cultural evidence). That said, I found deciduous morphology to perform strongly in identifying *non-relatives* within the sample. Pairs of individuals characterized by large distances can more confidently be categorized as non-relatives, and I present this as an alternative method for exploring cemetery patterns. These results are promising considering that only morphological data were used to generate biological distances. By including deciduous crown dimensions—traits generally characterized by moderate to high heritability estimates—in biological distance generation, performance might improve considerably. Unfortunately, this study sample lacked complex pedigrees that would allow for a performance assessment involving more distant degrees of genetic relatedness (e.g., cousins or half siblings). I cite this as a fruitful next step in ground-truthing the foundational assumptions of biodistance research, along with the exploration of data approximating latent environmental factors that may explain inconsistent performance across families.

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CHAPTER 4

COMPARATIVE PERFORMANCE OF DECIDUOUS AND PERMANENT DENTAL MORPHOLOGY IN DETECTING BIOLOGICAL RELATIVES

Paul KS, Stojanowski CM. 2017. American Journal of Physical Anthropology 164:97-116.

Research that applies deep time perspectives to biological and cultural phenomena often operates under a number of theoretical and analytical assumptions that need to be validated using experimental approaches with modern datasets. Biological distance analysis (henceforth "biodistance") is no exception. Biodistance analysis uses phenotypic data (cranial and dental dimensions, as well as cranial non-metric and dental morphological trait expression) to infer evolutionary processes in past populations (Buikstra et al., 1990; Konigsberg, 2006). The approach has a deep history in anthropology, dating back to early cranial typological studies that were reformulated as part of the New Physical Anthropology of the 1950s and the emergence of bioarchaeology as a distinct field of practice (Washburn, 1951; Buikstra, 1977; Larsen, 2015). While global scale analyses continue to be important for ascertaining the evolutionary history of our species (Relethford, 2002, 2009, 2010; Roseman and Weaver, 2004, 2007; von Cramon-Taubadel, 2008, 2014; von Cramon-Taubadel and Pinhasi, 2011; Scott et al., 2016) biodistance has also been incorporated into regional-scale and site-specific analyses for which the focus is on local patterns of gene flow, population boundaries, and the identification of biological relationships at the inter-individual scale (Lane and Sublett, 1972; Buikstra, 1976, 1980; Konigsberg, 1987; Buikstra et al., 1990;

Alt and Vach, 1991, 1995; Alt, 1997; Stojanowski and Schillaci, 2006). Thus, biodistance is aligned with historical anthropological genetics, to some degree, but with a distinct dataset that *approximates* the behavior of genetic data (Buikstra et al., 1990; Konigsberg and Buikstra, 1995; Konigsberg, 2000; Stojanowski and Schillaci, 2006; Relethford, 2007).

It is this *approximate* nature of biodistance analysis that is the subject of criticism. Considerable effort has been expended on assessing the evolutionary significance and value of phenotypic datasets, incorporating insights from evolutionary developmental biology, genomic and allelic association studies, and matrix-based neutral model comparisons at various scales of analysis. Collectively, I refer to these papers as validation studies because they evaluate the foundational assumption of biodistance that phenotypic data carry a meaningful evolutionary signal. Earlier, now classic, studies from the 1950s through 1970s considered the correlation between phenotypic traits and various serological markers collected from small-scale or non-Western societies at the regional scale of interaction (reviewed in Droessler, 1981; for recent intriguing examples see Hájek et al., 2008; Herrera et al., 2014; Smith and von Cramon-Taubadel, 2015). The analytical approach used in these papers assessed whether phenotypic and genotypic data produced the same patterns of relationships, usually visualized in a multivariate output. More recently, craniometric data have been compared against patterns of relatedness based on neutral genetic variation at the global scale (Harvati and Weaver, 2006; Perez et al., 2007; Smith, 2009; von Cramon-Taubadel, 2009; Strauss and Hubbe, 2010; Reyes-Centeno et al., 2014, 2017). Results of these studies generally support the value of craniometric data (but see Roseman, 2016). Similar results have been obtained using dentition (e.g., Hanihara and Ishida, 2005; Hanihara, 2008, 2013; Scott et al., 2016), which provide broadly similar patterns as neutral genetic variation at the global scale.

Studies on the heritability, transmissibility, and concordance of dental traits between twins or among family members are nearly a century old (see Bachrach and Young, 1927) with continued research on the determinants of dental size and shape (e.g., Apps et al., 2004; Townsend et al., 2006, 2009, 2012; Ribeiro et al., 2013), including among non-human primates (see Hlusko and Mahaney, 2003, 2009; Hlusko et al., 2004, 2007; Rizk et al., 2008; Koh et al., 2010). Model organism research has identified the molecular signaling mechanisms that result in multi-cusped teeth and the patterning of cusp variation across taxa (Jernvall and Jung, 2000; Jernvall and Thesleff, 2000, 2012; Kangas et al., 2004; Kavanagh et al., 2007; Salazar-Ciudad and Jernvall, 2010; Brook et al., 2014). As research on dental phenomics is emerging (Yong et al., 2014), linkage analyses have identified associations between genetic markers and tooth size and shape that suggest considerable pleiotropy in the dentition, while delineating specific alleles associated with phenotypic trait expression (Kimura et al., 2009, 2015; Lee et al., 2012; Park et al., 2012; Haga et al., 2013; Tan et al., 2014). Collectively, this research seeks to understand the causes of variation in dental morphology and to determine the relationship between genetic and phenotypic covariance at different scales. Most of this work considers patterning in aggregate, however, and not at the level of the individual, which is the focus in this paper given the scope of intracemetery bioarchaeology (Stojanowski and Schillaci, 2006; Johnson and Paul, 2016). Likewise, much of the existing literature focuses on development and the general understanding of dentition as organs and not on the specifics of practice and methodology, which is my concern here.

Previous archaeological validation studies at the individual level can be divided into two approaches. The first uses individuals of known ancestry from small grave contexts to evaluate the ability of phenotypic data to reconstruct a known genealogy (e.g., Rösing, 1986; Spence, 1996; Usher et al., 2003; Usher, 2005; Velemínský and Dobisíková, 2005; Usher and Weets, 2014). Results across studies indicate mixed success, which suggests the results are not generalizable because family resemblance manifests idiosyncratically (if at all). The second approach records genotypic and phenotypic data from matched individuals from sites for which genealogies are unknown but assumed to emerge from the genetic component of the analysis (e.g., Shinoda et al., 1998; Shinoda and Kanai, 1999; Corruccini et al., 2002; Adachi et al., 2003, 2006; Shimada et al., 2004; Ricaut et al., 2010). These analyses are more similar in scope to macro-scale concordance studies in that the correlation between reconstructed matrices of relationships is the parameter of interest (Corruccini et al., 2002; Adachi et al., 2003, 2006; Shimada et al., 2004). For example, Ricaut et al. (2010) found that cranial non-metric and dental morphological data were weakly, though significantly, correlated with mtDNA data collected from matched individuals, although the molecular data provided considerably more power in ascertaining degrees of relatedness at the within-site scale.

One limitation of previous work is that each paper presents a case study of a specific cemetery, and it is unknown how generalizable the results may be. Similarly, reliance on heritability (h^2) as the key measure of trait utility in genealogy reconstruction is problematic because of its potential for misinterpretation (Feldman and Lewontin, 1975; Kempthorne, 1997; Vitzthum, 2003; Joseph, 2004; Hansen et al., 2011; Conley et al., 2014; Liu et al., 2015), population specificity, and the difficulty incorporating heritability estimates into actual practice in the archaeological record. Comparison of heritabilities across traits is of limited value because the measure is not reflective of genetic determination and tells us little about the utility of different traits for identifying biological relatives (Konigsberg, 2000; Vitzthum, 2003). Another limitation of the existing literature is that most previous validation studies have focused on comparing the results generated from genetic data with different types of phenotypic data. Missing from this literature, however, is an assessment of the comparative performance of *different* types of phenotypic data in pedigreed samples. In the previous chapter I considered how well deciduous dental morphology identified known biological siblings using a sample of 69 sibling pairs (see Chapter 3; Paul and Stojanowski, 2015). I evaluated whether Euclidean distances based on a set of 20 uncorrelated morphological variables were significantly smaller among siblings than expected by chance and whether sibling dyads and nuclear family sets could be discerned within multidimensional scaling plots against a backdrop of unrelated individuals (see Chapter 3; Paul and Stojanowski, 2015). This tested whether high phenotypic similarity was reliably indicative of close biological relatedness, and vice versa, which is the assumption of most intracemetery biodistance papers in bioarchaeology.

Here, I extend the results of Chapter 3 (Paul and Stojanowski, 2015) and evaluate the utility of permanent dental morphology as a genetic proxy. This paper has two goals. First, I assess whether permanent dental variation can consistently identify known biological relatives in a broader sample using distance-based ordination methods as typically used in bioarchaeology. I expect that relatives are more phenotypically similar than are non-relatives because they share alleles that are identical by descent (see Doi et al., 1986; Thompson, 1986; Scott and Turner, 1997; Konigsberg, 2000; Blouin, 2003; Stojanowski and Schillaci, 2006). As such I expect that sibling pairs exhibit more similar dental morphology scores than expected by chance given the range of permanent dental morphological variation in the overall population. I also expect that pairwise distances between non-relatives would be greater than pairwise distances between siblings, and that these patterns would be reflected through visualization approaches (i.e., multidimensional scaling plots).

Second, I compare these results to those of Paul and Stojanowski (2015) to assess the relative performance of deciduous and permanent crown features for a matched set of individuals of known biological relation. Previous studies have shown that while deciduous and permanent homologues are similar in overall crown form (despite size differences), they can vary greatly in morphological character expression, even within individuals (Hanihara, 1961; Smith et al., 1987; Edgar and Lease, 2007; Paul et al., 2017). This may suggest one or the other is a better reflection of patterns of relatedness. Patterned variation in trait expression is thought to arise from differences in crown formation rates and timing for deciduous and permanent teeth (Saunders and Mayhall, 1982; Edgar and Lease, 2007). In particular, deciduous dentition may better reflect underlying genetic variation because it is subject to less environmental perturbation during crown development (Sofaer, 1973; Alberch et al., 1979; Alberch, 1980; Saunders and Mayhall, 1982; Smith, 1989; Smith and Tillier, 1989; Smith et al., 1997; cf. Guatelli-Steinberg et al., 2006). This paper provides one of the first tests of this hypothesis. I structure the analyses with respect to bioarchaeological practice, which uses multivariate datasets and ordination techniques from ancient populations for which trait heritabilities and genealogical relationships are unknown and likely unknowable.

MATERIALS AND METHODS

Data for 71 dental morphological variables were collected from 69 individual participants of the Burlington Growth Centre’s Family Study. The individuals included in this study were the same as those included in a previous performance analysis of deciduous morphology for the identification of siblings (see Chapter 3; Paul and Stojanowski, 2015). Use of the same individuals was possible due to the longitudinal nature of the Burlington Growth Study, which began recording long-term craniofacial developmental data in the 1950’s and includes orthodontic records, participant health histories, and genealogical data for all participants (Thompson and Popovich, 1976; University of Toronto, Faculty of Dentistry, 2015). Ultimately, this sample includes siblings across 24 nuclear families of European ancestry. No extended pedigree relationships (e.g., cousins, half-siblings) are represented in the sample. Further, based on the comprehensive sampling strategy employed in the Burlington Growth Study (see Paul and Stojanowski, 2015; University of Toronto, Faculty of Dentistry, 2015), I assume that relationships between individuals belonging to different families approximate those shared between individuals randomly sampled from a broader and reasonably diverse population. To ensure subject anonymity, I recoded all individuals in the sample using a numbering system unique to this study. Research protocols were reviewed and granted exemption by Arizona State University’s Institutional Review Board and the Burlington Growth Centre (Appendix B).

Data Recording Methods

Permanent crown morphology was observed and recorded from stone dental casts under a supplemental light source using Arizona State University Dental Anthropology System (ASUDAS) standards (Turner et al., 1991). Data were collected for a total of 71 morphological traits on both left and right antimeres (Table 8). The first author (KSP) recorded all data with the aid of ASUDAS reference plaques. Trait expression was recorded as binary or ordinal scale as dictated by published scoring standards (see Turner et al., 1991). Following Paul and Stojanowski (2015), ordinal data were not dichotomized to maximize intra-individual variation for the purpose of detecting small-scale, inter-individual relationships.

Analytical Methods

Prior to analysis, a series of preliminary "data cleaning" procedures were performed to ensure that the phenotypic dataset most faithfully reflects latent genotypic information. Approximately seven months after data collection, I rescored ~15% of the original sample. Absolute ASUDAS grade differences between scoring sessions were used as measures of intra-observer error (Nichol and Turner, 1986). Variables with error ranges that exceeded a single ordinal grade were omitted. Traits for which differences in scoring between observation sessions altered presence/absence dichotomization were also omitted (Hillson, 1996:99).

For each trait, I then collapsed left and right ASUDAS scores to a single data point, preserving scores from the antimere exhibiting the highest degree of expression. This minimized genetic redundancy and inter-trait correlation among antimeres (Turner and Scott, 1977; Turner et al., 1991). I evaluated sex dependency using Kendall's tau-*B* coefficients (Kendall, 1975; Kendall and Stuart, 1979); traits whose expression was significantly correlated with sex ($p \leq 0.05$) were removed from the analysis. Data were not pre-treated for age and wear dependency because each individual's dentition was casted multiple times throughout their life, allowing observations to be made on the least-worn cast for elements/traits of interest. Finally, I removed inter-correlated variables based on Kendall's tau-*B* coefficients (Kendall, 1975; Kendall and Stuart, 1979). Morphological characters occurring within the same region of the dentition (i.e., anterior or postcanine dentitions) were removed when significantly correlated ($p \leq 0.05$). To prevent the removal of traits due to incidental correlation, characters occurring in different regions were only considered significantly correlated when tau-*B* coefficients were less than -0.4 or greater than 0.4. In each instance of inter-trait correlation, the trait characterized by the least amount of variability in the sample was omitted from subsequent analyses. Monomorphic traits were also omitted from the analysis. All statistical analyses were conducted using XLSTAT (Addinsoft, 2014). After variable winnowing, only 132 of 1452 (~9%) possible data points were missing from the data matrix; these were evenly distributed among individuals/variables and within an acceptable range (see Brown et al., 2012). Following pre-analysis data treatments, Clustan v. 7.05 was used to calculate 2,145 inter-individual Euclidean distances using a reduced morphological dataset of 22 traits for 66 individuals (see Table 8) (Wishart, 2004).

Performance analyses. Performance of the permanent crown morphology was evaluated using two analytical approaches. First, I compared pairwise phenotypic distances between relatives and non-relatives, which evaluates the fundamental assumption of intrasite biodistance that relatives are more phenotypically similar than are non-relatives. To assess this, distances were averaged among non-relatives, among sibling pairs, and among families that contain more than two siblings. I then used bootstrap resampling in Excel's Resampling Stat add-in to generate pseudo-distances against which the observed average distances for the three sample subsets (non-relative, sibling, family) could be compared (Microsoft Corporation, 1999, 2010). Because the dataset included 69 sibling pairs (see results below), I generated a resample of 69 pseudo-distances from the larger sample of pairwise non-relative distances and 69 pseudo-distances from the combined sample of pairwise relative and pairwise non-relative distances. Robust p-values were obtained by resampling for 9,999 replicate averages of inter-individual distances. I also resampled by family, which involved modifying the number of resampled pseudo-distances to match the number of sibling pairs represented in each nuclear family. All distance sets were produced from 9,999 replicate averages of related and unrelated inter-individual distances. To generate a p-value, replicate averages were seriated, and the rank of the average for each subset (all relatives and individual families) was divided by the total number of samples (n=10,000). For families represented by only a single sibling pair, Euclidean distances were compared across 9,999 replicates of a single resampled pseudo-distance generated from the sample of non-relative and combined relative/non-relative distances. In combination, these analyses assess whether the average inter-sibling and intra-family phenotypic distances are smaller than expected by chance given the range of variation in inter-individual distances within the entire sample.

The second analysis evaluated performance using a simulated bioarchaeological

Table 8. Permanent morphological traits collected from the Burlington Growth Centre Family Study sample.

Included Traits[a,b]	Omitted Traits[a,c]	Reason for Omission[c]
Winging I^1	Shovel I^1, C^1, I_2	Inter-trait Corr.
Labial Curve I^1	Double Shovel I^2, C^1, P^2	Inter-trait Corr.
Peg/Reduced I^2	Tuberculum Dentale I^1, I^2	Error (I^1); Inter-trait Corr. (I^2)
Shovel I^2, I_1	Congenital Absence I^2, P^2, M^3, M_3	Inter-trait Corr. (I^2, P^2), <40 Obs. (M^3, M_3), Monomorphic (M^3)
Double Shovel I^1, P^1	Mesial Ridge C^1	Error
Tuberculum Dentale C^1	Distal Accessory Ridge C^1, C_1	Error (C^1), Sex Corr. (C_1)
Metacone M^1, M^2	Uto-Aztecan P^1	Monomorphic
Hypocone M^2	Odontome P^1, P^2, P_1, P_2	Monomorphic
Carabelli's Trait M^1	Metacone M^3	<40 Obs.
Parastyle M^1, M^2	Hypocone M^1, M^3	Inter-trait Corr. (M^1), <40 Obs. (M^3), Monomorphic (M^3)
Congenital Absence I_1, P_2	Cusp 5 M^1, M^2, M^3	Inter-trait Corr. (M^1), <40 Obs. (M^2, M^3), Monomorphic (M^3)
Lingual Cusp P_1	Carabelli's Trait M^2, M^3	Inter-trait Corr. (M^2), <40 Obs. (M^3)
Protostylid M_1, M_2	Parastyle M^3	<40 Obs., Monomorphic
Cusp 5 M_1	Peg/Reduced M^3	<40 Obs., Monomorphic
Cusp 6 M_1	Lingual Cusp P_2	Error, Sex Corr.
Cusp 7 M_1	Anterior Fovea M_1	<40 Obs.
	Deflecting Wrinkle M_1	<40 Obs.
	Groove Pattern M_1, M_2, M_3	<40 Obs.
	Cusp Number M_1, M_2, M_3	Inter-trait Corr. (M_1,M_2), <40 Obs. (M_3), Monomorphic (M_3)
	Distal Trigonid Crest M_1, M_2, M_3	Inter-trait Corr. (M_2), <40 Obs. (M_3), Monomorphic (M_1, M_3)
	Protostylid M_3	<40 Obs., Monomorphic
	Cusp 5 M_2, M_3	Error (M_2), <40 Obs. (M_3)
	Cusp 6 M_2, M_3	Inter-trait Corr. (M_2), <40 Obs. (M_3), Monomorphic (M_3)
	Cusp 7 M_2, M_3	Inter-trait Corr. (M_2), <40 Obs. (M_3), Monomorphic (M_3)

[a] Maxillary and mandibular arcades are indicated by superscripts and subscripts, respectively. [b] Morphological variables included in the distance analysis. [c] Morphological variables omitted from the distance analysis and reason for removal from the ultimate dataset. Corr.=Correlation, Obs.=Observation.

analytical design. Bioarchaeologial kinship analyses (which lack genotypic data and knowledge of genealogical structure) typically rely on quantification or visualization of phenotypic similarity to infer the degree of genetic relatedness among individuals in a skeletal sample. Smaller dispersion values are generally interpreted as reflecting closer genetic relationships, and vice versa. Mimicking this analytical approach, multidimensional scaling (MDS) was used to ordinate the inter-individual distance matrices. Kruskal stress was used as the criterion to determine whether the ordination was representative of the distance matrix (Kruskal, 1964a, 1964b; Kruskal and Wish, 1978). I then measured the relative dispersion of individual families with reference to the resulting two-dimensional MDS plot. To do this, I quantified the relative area of multidimensional space occupied by each family. This involved calculating the product of the distances between each family's most peripheral coordinates along the axes of the MDS plot (i.e., Family1 maxX-minX * Family 1 maxY-minY) (see Appendix F). The plot area of dispersion for each family was then divided by the plot area occupied by the entire study sample (e.g., Family 1 Area ÷ Total Sample Area) (see Appendix F). The resulting values represent the proportion of multidimensional space occupied by the individual families relative to the total sample.

I then compared the results of the performance analyses of the permanent dental morphology to the results of previous performance analyses of the deciduous morphology (see Chapter 3 and Paul and Stojanowski, 2015). Because both the deciduous and permanent morphological data were collected from the same individuals, genealogical relationships were held constant, and a direct comparison could be made between the results of the two studies. With reference to the documented genealogies, I generated a matrix representing the biological relationships between all individuals in the sample based on the *relatedness coefficient*, which is a theoretical measure of genealogical proximity between two individuals. Monozygotic (MZ) twins share a relatedness coefficient of 1.0 (i.e., all of their genes are expected to be shared by descent), while dizygotic (DZ) twins and full siblings share an average relatedness coefficient of 0.5 (i.e., half of their genes are expected to be shared by descent) (Thompson, 1986; Blouin, 2003). Theoretically, the probability that unrelated individuals share genes that are identical by descent approaches 0 (Thompson, 1986; Blouin, 2003). Each cell in this matrix contained the value *1-relatedness coefficient*, in essence converting each measure of proximity into a distance. This allowed for direct comparison with the phenotypic distances based on dental morphology. Using XLSTAT (Addinsoft, 2014), Mantel tests were performed to quantify the correlation between the genetic distance matrix and the two phenotypic distance matrices based on deciduous (from Chapter 3; Paul and Stojanowski, 2015) and permanent morphological data. Because the genetic distance matrix contained only the values 0 (matrix diagonal and MZ twins), 0.5 (full siblings and DZ twins), and 1 (non-relatives), output included a conservative non-parametric correlation coefficient, with probability values estimated from 10,000 permutations. Referencing results from Chapter 3 (Paul and Stojanowski, 2015), family-specific MDS dispersion values obtained from the deciduous dataset were compared to those obtained from the permanent dataset on a family-by-family basis.

Finally, to directly compare deciduous and permanent crown morphology scores in the sample I conducted a series of bivariate correlation analyses on homologous characters (e.g., shoveling lxi^1 versus shoveling LXI^1, cusp 6 rm_2 versus cusp 6 RM_1).

Traits were examined separately for left and right antimeres and at maximum expression (i.e., using the antimere exhibiting the highest trait score). While permanent morphology was only scored according to ASUDAS standards (Turner et al., 1991), deciduous morphology was scored twice—once using ASUDAS and again using a suite of published standards designed specifically for the primary dentition (Hanihara, 1961, 1963; Grine, 1986; Sciulli, 1998; Lease, 2003; see Chapter 3; Paul and Stojanowski, 2015). Where scoring systems differed between homologues, data were converted to a new scale so that individual expression grades were equivalent across elements (following Edgar and Lease, 2007). These scoring conversions are outlined in Appendix G. The newly scaled trait scores were compared between corresponding deciduous and permanent characters; for traits scored using ASUDAS standards in both dentitions, the original scores were also compared. Following Edgar and Lease (2007), Goodman-Kruskal Gamma (γ) tests (Goodman and Kruskal, 1954, 1963, 1972; Göktaş and İşçi, 2011) were performed for all ordinal variables in SPSS v. 24 (IBM Corporation, 2016). For binary traits scored as “present” or absent”, tetrachoric correlation (Pearson, 1900; Brown, 1977; Brown and Bendetti, 1977) coefficients were estimated using the R ‘polycor’ package v. 07-9 (Fox, 2016).

RESULTS

Average intra-observer error ranged from 0-1 ordinal grade for all 142 traits scored (71 traits per antimere). Maximum error ranged from 0-1 ordinal grade for all but two traits. Accordingly, the following characters were removed from further analyses: P_2 lingual cusp variation and M_2 cusp 5 (max. error=2). Three additional traits were removed because presence/absence dichotomization differed between scoring sessions: I^1 tuberculum dentale (breakpoint: grade 3), C^1 mesial ridge (breakpoint: grade 1), C^1 distal accessory ridge (breakpoint: grade 2) (Table 8). Twenty traits were removed from the analysis because data were missing for more than 40 individuals, and 17 traits were removed because they were monomorphic (Table 8). Tau-*B* correlation coefficients indicated two traits were sex dependent and 17 traits were inter-correlated; these traits were removed from the biodistance analysis (Table 8). Three individuals were removed from the analysis due to excessive missing data.

Pre-analysis data treatments resulted in a winnowed dataset comprised of 22 morphological variables and 66 individuals representing 69 sibling pairs (Table 8). These are the same sibling pairs (67 full sibling pairs and 2 twin pairs) across the same 21 families included in the previous study that focused on deciduous crown morphology (see Chapter 3; Paul and Stojanowski, 2015). Using the final pre-treated dataset, a Euclidean distance matrix was generated that contained a total of 2,145 pairwise distances, 69 between siblings and 2,076 between unrelated individuals.

The average inter-sibling distance was 0.321 (range: 0.160 to 0.482), which is significantly smaller than the average pairwise distance between non-relatives (range 0.101-0.754; $\bar{x}$=0.361; p<0.001) and for the combined sample of relatives and non-relatives ($\bar{x}$=0.359; p<0.001) based on resampling (Table 9). Further, the average sibling distance ($\bar{x}$=0.321) was smaller than all 9,999 replicate averages of the 69 pseudo-distances resampled from the relatives and non-relatives. This suggests the degree of phenotypic similarity among siblings is much higher than expected by chance—that is by randomly selecting the same number of individuals from the sample that may or may not be related. A similar result is obtained when the resampling is restricted to non-relatives; only three of the 9,999 replicate averages are smaller than the average inter-sibling distance. This also indicates that the degree of phenotypic similarity among siblings is higher than expected by chance. Turning to individual sibling dyads, the sample included two female twin pairs. The distances for these two twin sets (KP18/KP19=0.196; KP45/KP46=0.218) fell below the smallest six percent of distances in the total sample (KP18/KP19=3.6% and KP45/KP46=5.8%). The twin distances are significantly—or *near* significantly—smaller than would be expected by chance if drawn from a sample of non-relatives (KP18/KP19: p=0.037 and KP45/KP46: p=0.057) or from a sample of combined non-relatives and relatives (KP18/KP19: p=0.032 and KP45/KP46: p=0.051) based on pseudo-distance resampling. Still, this result is unremarkable given the presumed zygosity status for these individuals (see Discussion).

Six of the 21 families included in the study were characterized by average inter-sibling distances that were significantly smaller than the average distance in a sample of unrelated individuals (p-value range: 0.005 to 0.043) and in a combined sample of related and unrelated individuals (p-value range: 0.007 to 0.046) based on pseudo-distance resampling (9,999 replicate averages) (Table 9). Averages for Families 5, 7, and 23 also approached significance when compared to pseudo-samples generated from the non-relative (p-value range: 0.060 to 0.080) and combined relative/non-relative distances (p-value range: 0.055 to 0.077) (see Table 9). However, a third of the 21 families were characterized by average inter-sibling distances that fell in the upper half of the distribution of resampled pseudo-distances, including Family 15. This family included

Table 9. Average inter-sibling distance and bootstrap resampling results by family.

Family *(No. Sibs)*[a]	Individual *(Sex)*[b]	Permanent Ave. Dist.[c]	p1[d]	p2[d]	Deciduous Ave. Dist.[e]	p1[d]	p2[d]
Family 1 *(1)*	KP1 *(M)*, KP26 *(M)*	0.437	0.800	0.807	0.361	0.708	0.708
Family 2 *(10)*	KP3 *(M)*, KP4 *(M)*, KP5 *(M)*, KP6 *(M)*, KP7 *(M)*	**0.308**	**0.039**	**0.046**	**0.235**	**0.002**	**0.002**
Family 3 *(3)*	KP8 *(M)*, KP9 *(M)*, KP23 *(M)*	0.320	0.238	0.249	0.271	0.208	0.224
Family 4 *(1)*	KP10 *(M)*, KP49 *(M)*	0.335	0.409	0.427	0.418	0.846	0.822
Family 5 *(3)*	KP12 *(M)*, KP13 *(M)*, KP29 *(F)*	0.282	0.079	0.077	0.456	0.958*	0.965*
Family 6 *(10)*	KP14 *(F)*, KP15 *(F)*, **KP45 *(F)*, KP46 *(F)*,** KP47 *(M)*	**0.286**	**0.005**	**0.007**	**0.198**	**<0.001**	**<0.001**
Family 7 *(3)*	KP17 *(F)*, **KP18 *(F)*, KP19 *(F)***	0.274	0.060	0.055	**0.152**	**<0.001**	**<0.001**
Family 8 *(6)*	KP31 *(F)*, KP34 *(F)*, KP35 *(F)*, KP43 *(F)*	0.360	0.513	0.517	0.367	0.839	0.848
Family 9 *(1)*	KP38 *(F)*, KP39 *(F)*	0.378	0.589	0.610	0.248	0.253	0.256
Family 12 *(3)*	KP51 *(F)*, KP53 *(M)*, KP54 *(F)*	0.386	0.690	0.708	**0.219**	**0.031**	**0.036**
Family 13 *(3)*	KP57 *(F)*, KP58 *(F)*, KP59 *(F)*	0.420	0.857	0.870	**0.211**	**0.018**	**0.024**
Family 14 *(3)*	KP60 *(F)*, KP61 *(M)*, KP62 *(F)*	**0.264**	**0.043**	**0.038**	0.357	0.730	0.757
Family 15 *(6)*	KP63 *(M)*, KP64 *(F)*, KP65 *(M)*, KP66 *(F)*	0.482	0.998*	0.997*	**0.159**	**<0.001**	**<0.001**
Family 16 *(1)*	KP69 *(M)*, KP70 *(F)*	0.235	0.082	0.089	0.189	0.076	0.079
Family 17 *(3)*	KP73 *(M)*, KP74 *(F)*, KP75 *(F)*	**0.248**	**0.022**	**0.020**	**0.190**	**0.006**	**0.005**
Family 18 *(3)*	KP78 *(F)*, KP79 *(F)*, KP80 *(M)*	**0.243**	**0.017**	**0.016**	0.263	0.169	0.180
Family 19 *(3)*	KP83 *(F)*, KP84 *(F)*, KP87 *(M)*	0.290	0.102	0.103	**0.225**	**0.036**	**0.043**
Family 20 *(1)*	KP88 *(F)*, KP91 *(F)*	0.282	0.209	0.211	**0.110**	**0.004**	**0.003**
Family 21 *(1)*	KP92 *(M)*, KP95 *(M)*	0.439	0.805	0.812	0.354	0.675	0.688
Family 22 *(1)*	KP96 *(M)*, KP99 *(M)*	**0.187**	**0.026**	**0.027**	0.248	0.251	0.260
Family 23 *(3)*	KP100 *(M)*, KP103 *(F)*, KP104 *(F)*	0.282	0.080	0.077	0.316	0.510	0.521
All Sibships *(69)*		**0.321**	**<0.001**	**<0.001**	**0.252**	**<0.001**	**<0.001**

[a] Number of unique sibships. Families 10, 11, and 24 represented by a single individual: KP20 *(F),* KP50 *(M)*, KP30 *(F)*. Additionally, KP41 *(F)* does not belong to any of the families. These individuals contributed to the unrelated distances. [b] Twin pairs bolded. [c] Average inter-sibling Euclidean distances generated from the permanent data. [d] P-values indicate whether family averages differ from 9,999 replicates of average pseudo-distances randomly drawn from a sample of non-relatives (p1) and combined relatives/non-relatives (p2). [e] Average distances that are significantly smaller than resampled replicate averages are bolded, while those that are significantly larger are listed with an asterisk (p≤0.05).

four siblings that, on average, were significantly *dissimilar* in their permanent morphology (average distance = 0.482; upper-tail p=0.002 based on non-relative resampling; upper-tail p=0.003 based on combined resampling) (Table 9).

In short, while *overall* permanent morphology performed moderately well in distinguishing relatives from non-relatives, I observed high levels of variation in performance between sibling dyads and between family units. Results of non-parametric correlations analyses show that disparities in performance between families cannot be attributed to family size. There was a weak positive correlation between family size—as represented by a family's number of sibships—and family average distance (tau-*B* coefficient=0.081, p=0.669). I also found a weak correlation between inter-sibling distance and sibling pair "type" (*same sex versus opposite sex*: tau-*B* coefficient=0.160, p=0.110; *male-male versus female-female versus male-female*: tau-*B* coefficient=0.128, p=0.176), which suggests that performance is not contingent upon siblings' sex.

Multidimensional scaling outputs (see Figs. 10-15; Appendix H) indicate relatives occupy an average of 7.5% (range: 0.1% to 30.8%) of the total available multidimensional space. In other words, related individuals do cluster; however, this degree of clustering is not unique within the sample. Further, when family-specific MDS outputs are considered there is inconsistency across the sample (see Table 10). Individual family MDS dispersion ranged from 0.2% (Family 22) to 59.3% (Family 15) of the multidimensional space occupied *only* by the Burlington study sample (average 14.4%) (Figs. 10-11). Twin pairs clustered relatively tightly, as might be expected (Fig. 12-13), but overall dispersion across families varied greatly (e.g., Figs. 14-15). Disparity in

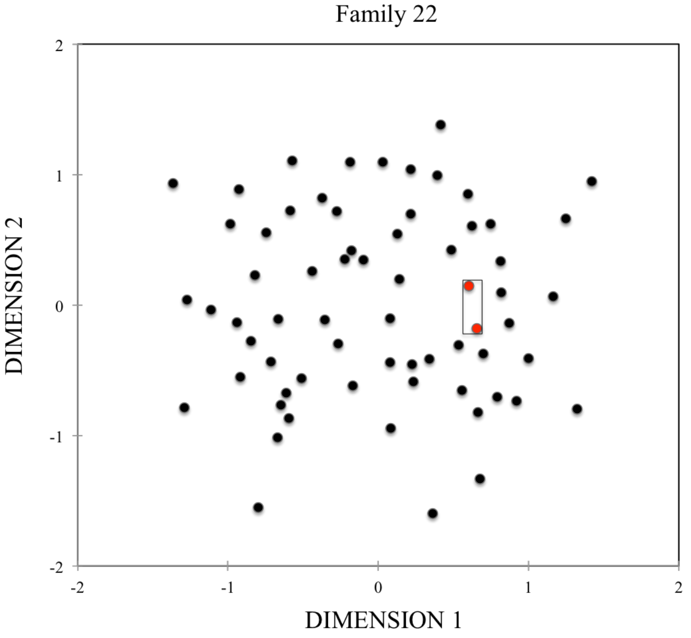

Figure 10. Family 22 MDS plot, with siblings marked in red and multidimensional space occupied (Family 22 Area) enclosed in a rectangle (relative dispersion = 0.2%).

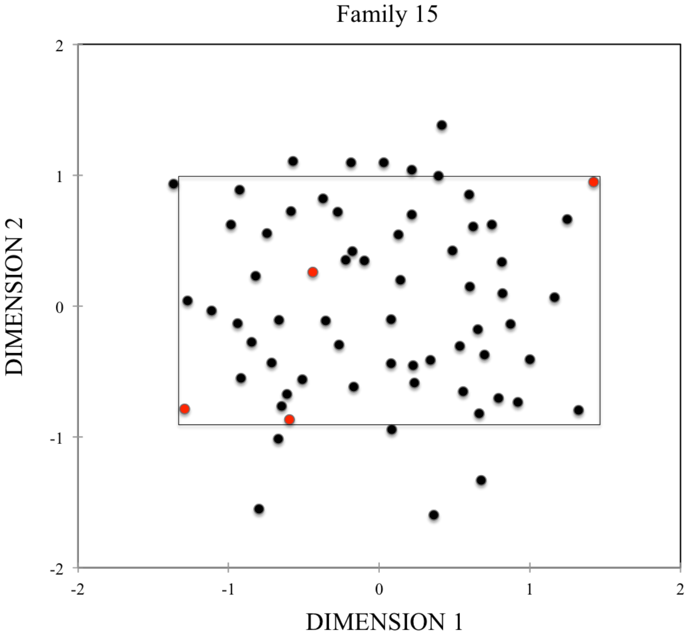

Figure 11. Family 15 MDS plot, with siblings marked in red and multidimensional space occupied (Family 15 Area) enclosed in a rectangle (relative dispersion = 59.3%).

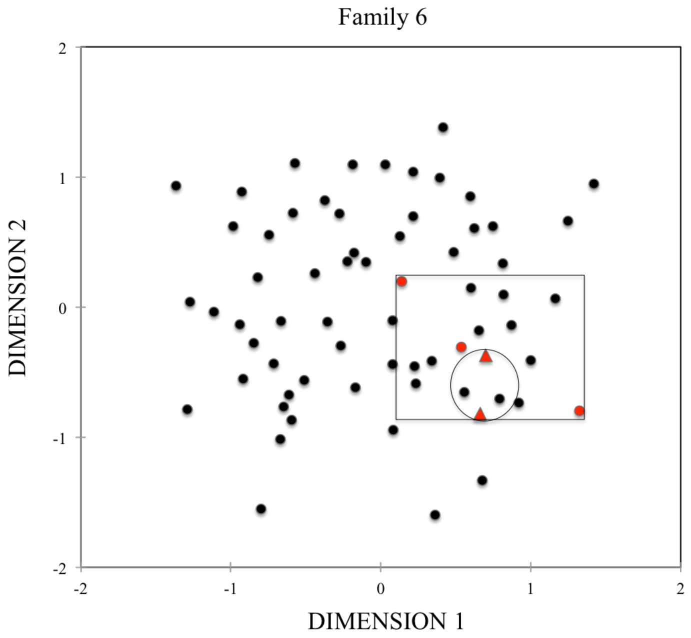

Figure 12. Family 6 MDS plot, with siblings marked in red and multidimensional space occupied (Family 6 Area) enclosed in a rectangle (relative dispersion = 14.5%). Twins are marked by triangles and enclosed in a circle.

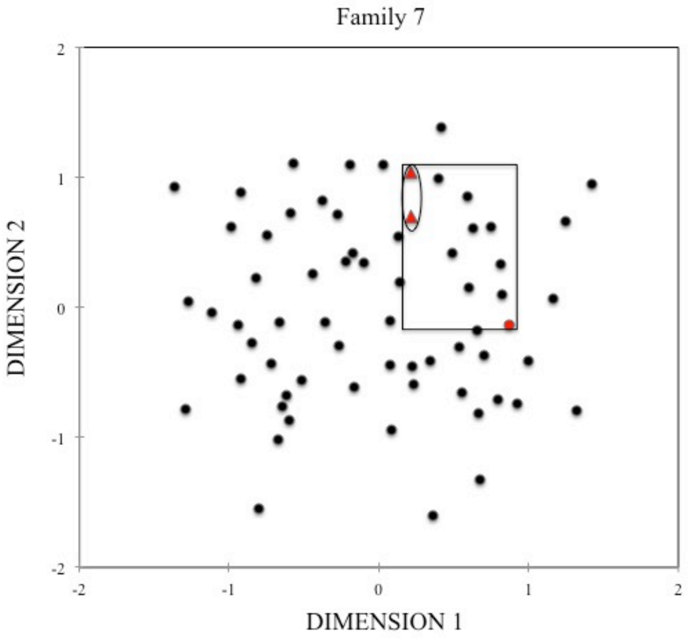

Figure 13. Family 7 MDS plot, with siblings marked in red and multidimensional space occupied (Family 7 Area) enclosed in a rectangle (relative dispersion = 9.3%). Twins are marked by triangles and enclosed in a circle.

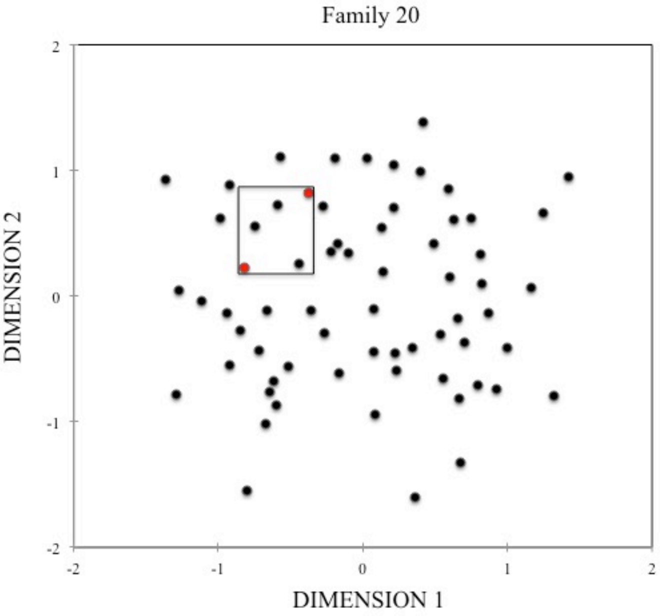

Figure 14. Family 20 MDS plot, with siblings marked in red and multidimensional space occupied (Family 20 Area) enclosed in a rectangle (relative dispersion = 3.2%).

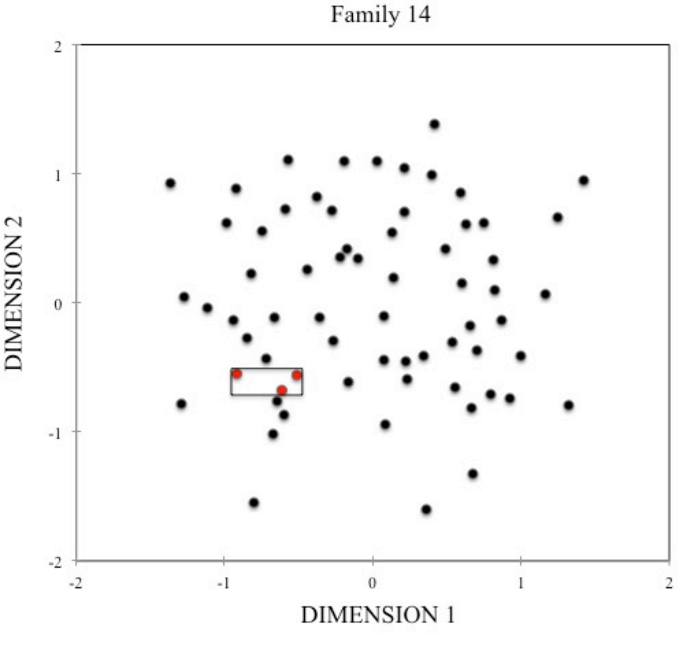

Figure 15. Family 14 MDS plot, with siblings marked in red and multidimensional space occupied (Family 14 Area) enclosed in a rectangle (relative dispersion = 0.6%).

performance across the sample may be related to aspects of family composition, namely family size. The results showed a strong positive relationship between family sibling pair count and dispersion (tau-*B* coefficient=0.424, p=0.016) (Table 10; Figs. 10-15; Appendix H).

To more comprehensively gauge the performance of the deciduous and permanent morphological datasets, I measured the correlation between each phenotypic distance matrix and a genetic distance matrix representing the documented genealogical relationships between individuals in the sample. Mantel test results show both the deciduous phenotypic distance matrix and the permanent phenotypic distance matrix are significantly positively correlated with the genetic distance matrix (deciduous r=0.120, p<0.001; permanent r=0.077, p<0.001). While the correlation coefficient values are small, this is expected given that sibling dyads comprised a relatively limited portion of the total sample (3.2%, 69 inter-sibling distances versus 2,076 non-relative distances) and biological distances between unrelated individuals varied greatly across both samples (see Chapter 3; Paul and Stojanowski, 2015).

Finally, in bivariate comparisons, individual traits vary greatly in correspondence between deciduous and permanent homologues (γ range: -1.000 to 1.000, rTet range: -0.987 to 0.936). Twenty-four of the 63 (~38%) traits scored using ASUDAS standards are characterized by significant γ estimates, along with 10 of the 39 (~26%) scaled traits (Appendix I). All but one of these significant correlations are positive, right i^2/I^2 double shovel being the exception. Over half (~59%) of the 17 tetrachoric correlations estimated were moderate to strong (cutoff |0.36| following standards accepted by Edgar and Lease (2007) and Knoke and Bohrnstedt (1991)), with both positive and negative correlations represented (Appendix I). I observed robust correlations (i.e., significant across antimeres and across scoring scales) for a limited number of traits. Notably, the γ coefficients for Carabelli's trait and cusp 7 are significant for both the original and scaled data and across both antimeres (Appendix I). For both cusp 7 and Carabelli's trait, the deciduous molar more often exhibited some degree of expression than did the permanent molar (scaled max. Carabelli's: m2≅ 98% versus M1≅ 95%; scaled max. C7: m2≅ 37% versus M1≅ 15%). These percentage frequencies are higher than those previously reported from this sample, likely because they represent maximum expression and included even the slightest degree of pitting and/or grooving associated with low-grade expression.

DISCUSSION

This paper evaluated whether permanent dental morphology can be used to reconstruct known genealogical relationships using standard bioarchaeological approaches to intracemetery biodistance. Two measures of performance were implemented: 1) raw distance statistics for which bootstrapping was used to generate p-values to test the hypothesis that relatives share significantly smaller inter-individual distances than expected by chance, and 2) the patterning of familial dispersion within MDS space as represented by the plot area. These results are compared to those of a previously published study that used the same methodology for deciduous dental morphology (see Chapter 3; Paul and Stojanowski, 2015). The goal of this comparison is to evaluate whether permanent or deciduous morphology better reflects biological relatedness.

Results presented in this paper indicate moderate to strong correspondence in permanent dental morphology between siblings when compared against a backdrop of unrelated individuals. In this way, the findings are similar to those of the previous study that assessed the performance of deciduous morphology for detecting biological siblings within the same set of individuals (see Chapter 3; Paul and Stojanowski, 2015). While the distance values themselves are not directly comparable, the average inter-sibling distance based on deciduous morphology ($\bar{x}$=0.252) was also significantly smaller than the average pairwise distance for the sample of non-relatives ($p<0.001$) and for the combined sample of relatives and non-relatives ($p<0.001$) based on resampling (see Table 9). The other points of similarity between the two datasets include the fact that some (but not all) families with multiple siblings show significantly small distances and that there was variation from family to family in terms of performance, which was not related to family size or the sex composition of the sample. Likewise, and similar to the previous study, families generally occupy restricted areas within the multidimensional scaling plots (see Chapter 3; Paul and Stojanowski, 2015).

There were, however, differences between the two studies that support the hypothesis that the deciduous dentition provides a better measure of genetic relatedness. For example, when biological distances were calculated using the deciduous morphological data, the two twin pairs in the sample were represented by distances that fell within the smallest one percent of distances in the sample (KP18/KP19=0.3% and

Table 10. Absolute and relative multidimensional space (2D) occupied by each family.

Family (*No. Sibships*)[a]	Perm. MD Space[b]	Perm. Rel. MD Space[c]	Decid. MD Space[b]	Decid. Rel. MD Space[c]
KP1 (*1*)	0.603	0.073	**0.613**	**0.061**
KP2 (*10*)	2.297	0.277	**2.121**	**0.210**
KP3 (*3*)	0.638	0.077	**0.379**	**0.038**
KP4 (*1*)	1.554	0.187	**0.911**	**0.090**
KP5 (*3*)	**0.566**	**0.068**	2.988	0.299
KP6 (*10*)	1.205	0.145	**0.969**	**0.096**
KP7 (*3*)	0.774	0.093	**0.058**	**0.006**
KP8 (*6*)	2.772	0.334	**2.705**	**0.268**
KP9 (*1*)	0.787	0.095	**0.125**	**0.012**
KP12 (*3*)	2.129	0.257	**0.508**	**0.050**
KP13 (*3*)	2.203	0.265	**0.891**	**0.088**
KP14 (*3*)	**0.051**	**0.006**	3.378	0.335
KP15 (*6*)	4.922	0.593	**0.580**	**0.057**
KP16 (*1*)	**0.060**	**0.007**	0.349	0.035
KP17 (*3*)	0.467	0.056	**0.200**	**0.020**
KP18 (*3*)	1.033	0.125	**0.904**	**0.090**
KP19 (*3*)	0.681	0.082	**0.697**	**0.069**
KP20 (*1*)	0.264	0.032	**0.016**	**0.002**
KP21 (*1*)	1.601	0.193	**1.556**	**0.154**
KP22 (*1*)	**0.017**	**0.002**	0.504	0.050
KP23 (*3*)	**0.475**	**0.057**	1.929	0.191

[a]Number of siblings pairs listed in parentheses. [b]Multidimensional space occupied in the two-dimensional plot as calculated from the ordinated coordinates (units^2). For each family, results for the dataset resulting in least dispersion (permanent versus deciduous) are bolded (see below). [c]Relative MD space occupied refers to the dispersion or multidimensional space occupied in the two-dimensional plot as scaled by the multidimensional space occupied by the total sample (permanent sample=8.297 units^2, 0.519 relative MD space occupied; deciduous sample=10.088 units^2, 0.631 relative MD space occupied). Note that these areas are less than the total plot area (16 units^2), as the total sample is not dispersed to the axis margins. For each family, the results for the dataset resulting in least dispersion (permanent versus deciduous) are bolded.

KP45/KP46=1.0%) (see Chapter 3; Paul and Stojanowski, 2015), as compared to the smallest six percent of distances based on permanent morphology. While zygosity data were not recorded, Burlington Growth Study photographic records suggest the twin pairs are monozygotic. Even if they were dizygotic, I expect the twin pairs to be more similar in their dental morphology than full siblings because they share a maternal environment *contemporaneously* and are, therefore, exposed to identical environmental influences and stressors during the earliest stages of tooth crown formation. To this extent, the deciduous morphology outperformed the permanent morphology in distinguishing the twin pairs—those expected to be most phenotypically similar—from the rest of the sample.

In the deciduous study, nine of the 21 families exhibited average inter-sibling distances that were significantly smaller than expected by chance based on pseudo-distance resampling. In the current paper, only six of 21 families exhibited significantly low distances, although the difference in these proportions is not significant (p=0.339). When you compare the degree of dispersion for the same families but with the different datasets, sixteen of the 21 families exhibited greater dispersion within the MDS plot when represented by permanent morphological data (Table 10). This deviates significantly from random expectation (p=0.013). For the deciduous performance analysis families occupied, on average, 10.6% of the multidimensional sample space with individual family areas ranging between 0.2% and 33.5% (see Chapter 3; Paul and Stojanowski, 2015) (Table 10). In the current study the comparable estimates are 14.5%, on average, with a range from 0.2% to 59.3%. Clearly the deciduous dataset produces tighter clustering of related individuals. Finally, the Mantel tests also suggest that variation in deciduous morphology provides a more direct reflection of biological relatedness. Both dental phenotypic distance matrices were significantly correlated with the genetic distance matrix, however, the correlation coefficient was higher for the deciduous dataset. Note, however, that the magnitude of the difference was small and likely not significant.

These results may help contextualize the univariate correlations between deciduous and permanent anatomical homologues. I found significant correlations for a number of traits, and in fact, this dataset yielded a greater number of moderate to strong correlations than reported in Edgar and Lease's (2007) study of the Bolton-Brush Longitudinal Growth Study sample. One noteworthy result was the observed correlation between dm2 and M1 expression for Carabelli's trait and cusp 7 (see Edgar and Lease, 2007), which together corroborate earlier results reported from a broader subset of the Burlington Growth Study sample (Saunders and Mayhall, 1982). These two early forming traits are more commonly present in the dm2 than in the M1 when considering all potential grades of expression. This result also supports previous suggestions that early-forming traits with a dentin component are more likely to be observed in the earlier-forming deciduous tooth (Kraus and Jordan, 1965; Saunders and Mayhall, 1982; Smith et al., 1987; Edgar and Lease, 2007). Like Edgar and Lease (2007), I highlight methodological complications related to the scaling of trait scores and limitations related to sample size, both of which have the potential to generate spurious results. However, previous simulation work has shown the Goodman-Kruskal γ to be fairly conservative when applied to small samples and cross tabulation matrices of relatively limited dimensions (Göktaş and İşçi, 2011).

The fact that the correlations were mostly positive but low in magnitude indicates why univariate correlations between homologous crown features do not easily translate into predictions about genealogical reconstructions. In fact, one of the more interesting results of this study is that the families for which the deciduous morphology performed "strongly" were not always the same as those for which the permanent morphology performed "strongly", and vice-versa. Only three of the families characterized by significantly small average distances based on deciduous morphology were also characterized by significantly small average distances based on permanent morphology: Families 2, 6, and 17 (Table 9). It is unclear why this is so, but the specific timing of any environmental influences on crown development is a likely explanation.

Together, these findings provide support for the hypothesis that deciduous crown morphology, to some extent, tracks underlying genetic relationships with greater fidelity than that of the permanent dentition. The comparative results may be explained by differential formation times for deciduous and permanent tooth crowns, with deciduous teeth initiating crown formation early in-utero and completing mineralization within the first year of life (see Schour and Massler, 1940; Kraus, 1959; Lunt and Law, 1974; Anderson et al., 1976; Ubelaker, 1978; Mizoguchi, 1980, 1998; Smith, 1991; Liversidge and Molleson, 2004). Individuals are exposed to unique environmental stressors during the more protracted, postnatal mineralization of the permanent dentition, and therefore, siblings—whether MZ twins, DZ twins, or full siblings—would be expected to differ more in morphology of their permanent teeth than of their deciduous teeth, which are developmentally sheltered by a shared intra-uterine "buffer" (Kraus and Jordan, 1965;

Sciulli, 1978; Cook and Buikstra, 1979; Saunders and Mayhall, 1982; Smith et al., 1997; Paul et al., 2017; cf. Guatelli-Steinberg et al., 2006).

CONCLUSION

Bioarchaeological research at the intracemetery scale typically relies on patterns of phenotypic data to assess site formation processes and aspects of social organization as reflected in cemetery layout. The identification of biological kin is an important aspect of these analyses. Until recently (Pilloud and Larsen, 2011; Sciulli and Cook, 2016), researchers have relied almost exclusively on permanent dentition to populate their data matrices. For example, Stojanowski and Schillaci's (2006) analysis of the Windover Pond sample only used permanent dentition despite the fact that nearly half of the 168 individual sample was under the age of 18. The reasons for the lack of attention given to deciduous teeth are straightforward. First, research focusing on subadult remains and children, in general, has been more limited, a trend that has recently reversed due to an emphasis on childhood as a distinct research focus in the life course of ancient societies (Perry, 2006; Lewis, 2007; Halcrow and Tayles, 2011; Thompson, et al., 2014). Second, subadult remains are less commonly recovered from archaeological sites, which could reflect preservation biases or mortuary practices that segregate the very young from normative funerary routines. Third, as a result of these issues, the research infrastructure for the deciduous dentition is less well developed. Data recording methods for permanent teeth are more widely integrated into standardized data collection protocols (e.g., Buikstra and Ubelaker, 1994), especially with respect to dental morphology. Scoring systems for permanent dental morphology are widely known and easier to implement due to the existence of data recording systems (e.g., Turner et al., 1991) that retain institutional support (such as the ASUDAS scoring plaques), unlike the lesser known and limitedly available Dahlberg and Hanihara casts that focus on deciduous morphology(see Dahlberg 1949; Hanihara, 1961, 1963). All of this needs to be reconsidered, however, in light of the results presented here. Although permanent dentition performed reasonably well, by all of the informal metrics I present in this chapter the deciduous dental characters were more reliable indicators of biological relatedness. Bioarchaeologists interested in intracemetery analysis would be well-served to incorporate deciduous crown characters into their data collection protocol.

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CHAPTER 5

QUANTITATIVE GENETIC ANALYSES OF DECIDUOUS AND PERMANENT CROWN TRAITS IN THREE PEDIGREED SAMPLES

Due to their durability, tooth crown data feature prominently in bioarchaeological and paleoanthropological efforts aimed at reconstructing biocultural phenomena, including diet, generalized stress, disease processes, and evolutionary relationships. This final research initiative can take the form of broad-scale macro-evolutionary and phylogenetic research (e.g., Suwa et al., 1994, 1996; Bailey, 2004; Strait and Grine, 2004; Quam et al., 2009; Hershkovitz et al., 2011; Gómez-Robles et al., 2013 Irish et al., 2013; Villmoare et al., 2015), studies of global-scale migration (e.g., Turner, 1990; Irish and Guatelli-Steinberg, 2003; Hanihara and Ishida, 2005; Matsumura and Hudson, 2005; Hanihara, 2008, 2013; Stojanowski et al., 2013; Scott et al., 2016), inter- and intraregional biodistance analyses (e.g., Stojanowski, 2004; Irish and Konigsberg, 2007; Lukacs and Pal, 2013; Willermet et al., 2013; McIlvaine et al., 2014; Sutter and Castillo, 2015; Cucina et al., 2017), or small-scale kinship reconstruction (e.g., Alt and Vach 1991, 1995; Alt 1997; Corruccini and Shimada, 2002; Stojanowski and Schillaci, 2006; Pilloud and Larsen, 2011; Paul et al., 2013; Prevedorou and Stojanowski, 2017). Regardless of the analytical scale or aim, these efforts are based on the assumption that dental phenotypic variation approximates the underlying genetic structure of biological (sub)populations (Buikstra et al., 1990; Konigsberg and Buikstra, 1995; Konigsberg 2000, 2006; Stojanowski and Schillaci, 2006; Relethford, 2007; Hefner et al., 2016). Yet, dental phenotypes are not 1:1 proxies for genetic information; they are complex quantitative traits affected by various genetic and non-genetic factors. For this reason, continued ground-truthing efforts are required to improve emerging “phenomic” models of trait determination (Yong et al., 2014) and to delineate the manifold relationships between environment, genes, development, and the observable dental variation that comprises anthropological datasets.

As reviewed in Chapter 4, numerous studies have attempted to validate the fidelity and complexity of the evolutionary signal conveyed by quantitative dental characters (see Paul and Stojanowski, 2017). This body of literature includes studies that quantify the correlation between broad-scale (i.e., global) dental crown variation and neutral genetic variation (Hanihara and Ishida, 2005; Hanihara 2008, 2013), as well as molecular (Kimura et al., 2009, 2015; Lee et al., 2012; Haga et al., 2013), and developmental genetic research (Jernvall and Jung, 2000; Jernvall and Thesleff, 2000, 2012; Kavanagh et al., 2007; Salazar-Ciudad and Jernvall, 2010). Bioarchaeological validation studies, meanwhile, focus on the correspondence between intrasite/intracemetery dental phenotypic variation and a) genotypic variation (Corruccini et al., 2002; Adachi et al., 2003, 2006; Ricaut et al., 2010), or b) documented genealogical information in historic cemeteries (Rösing, 1986; Spence, 1996; Usher et al., 2003; Usher and Weets, 2014). A more recent wave of validation research has emerged, focusing on small-scale (i.e., non-global) concordance between dental and genetic variation in modern samples for which pedigree or genomic data are available (Chapters 3-4; Paul and Stojanowski, 2015, 2017; Stojanowski and Hubbard, 2017). These studies apply standard bioarchaeological analytical procedures to modern dental data to confirm documented pedigrees; in other words, the genealogical relationships are *known* and blindly reconstructed—successfully or unsuccessfully—in a simulated biodistance analysis, using datasets and methods commonly applied in bioarchaeological contexts (see Chapters 3-4; Paul and Stojanowski, 2015, 2017).

While validation efforts generally affirm the utility of dental phenotypic data for reconstructing biological relationships, their findings are yet to be fully integrated into standard bioarchaeological practice. Quantitative genetic studies are no exception, but, comparatively, their findings have had the greatest impact (by far) on biodistance theory and methodology. For example, when considering a character's utility for reconstructing evolutionary processes and biological relationships, researchers generally reference character-specific heritability estimates (e.g., Dempsey et al., 1999; Hughes et al., 2000; Dempsey and Townsend 2001; Townsend et al., 2009, 2012). Heritability has also been incorporated as a key parameter in regional-scale analytical approaches, such as R matrix analysis (implemented using the software RMET) (Williams-Blangero and Blangero, 1989; Relethford and Blangero, 1990; Relethford, 1991a, 1991b, 1996; Relethford et al., 1997), and has the potential to inform differential trait weighting in multivariate site-scale/inter-individual distance calculation (Stojanowski and Schillaci, 2006).

Quantitative genetic theory states that phenotypic variance can be expressed as the sum of genetic variance and environmental variance ($V_P = V_G + V_E$). The genetic component (V_G) can be partitioned into additive allelic effects (V_A), allelic dominance effects at a given locus (V_D), and epistatic interaction effects between loci (V_I) (Fisher, 1918, Hartl and Clark, 1989; Falconer and Mackay, 1996; Lynch and Walsh, 1998). The environmental component (V_E) can be divided into common or shared environmental effects (V_C) and unique/random environmental effects (V_U) (Fisher, 1918, Falconer, 1960; Hartl and Clark, 1989; Falconer and Mackay, 1996; Lynch and Walsh, 1998). While these components of variance are of interest in heritability estimation, it is important to note that additional factors (measurement error, assortative mating, genotype-environment correlation—R_{GE}, genotype-environment interaction—$G \times E$) can impact character expression (Falconer, 1960; Neale and Cardon, 1992; Hopper, 1993; Dempsey et al., 1999) but are typically omitted in standard biometric models (Falconer and Mackay, 1996).

Heritability estimates are generated by partitioning phenotypic variance and quantifying the relative contributions of its components. *Broad-sense heritability (H^2)* refers to the contribution of both additive (i.e., composite parental genetic input) and non-additive (i.e., multigene interaction and dominance) genetic variance ($H^2 = V_G/V_P$), while *narrow-sense heritability* (h^2) represents the relative contribution of, specifically, additive genetic variance to total phenotypic variance ($h^2 = V_A/V_P$; range: 0.0-1.0) (Fisher, 1918, 1958; Falconer and Mckay, 1996; Hartl and Clarke, 1997; Lynch and Walsh, 1998). Both metrics are dynamic and population-specific, but the latter is of interest in the present chapter. Traits associated with high narrow-sense heritability are relatively "genetic" in nature as opposed to epigenetically or environmentally determined (Fisher, 1918; Falconer, 1960; Falconer and Mckay, 1996; Hartl and Clark, 1997). However, the statistical value is often misconceptualized as a measure of how "heritable" or "familial" a trait is, misattributing a deterministic quality to the metric, itself (Feldman and Lewontin, 1975; Kempthorne, 1997; Hartl and Clark, 1997; Vitzthum, 2003; Joseph, 2004; Hansen et al., 2011). This interpretation also overlooks the impact of environment, which can intervene and "override" trait expression, even when the additive genetic contribution to character variation is large (Smith and Bailit, 1977; Falconer and Mckay, 1996; Vitzthum, 2003; Johnson et al., 2011). Nevertheless, heritability is a fundamental parameter that features prominently in the physical and dental anthropological literature as a means of classifying/quantifying the underpinnings of skeletal and dental variation.

Twin and Family Studies: Application to Dental Research

Pedigreed dental collections (i.e., those that include paired dental models and documented genealogies) have long served as invaluable data sources for quantitative genetic research. Since the mid-20th century clinical/longitudinal growth studies and anthropological collections have experienced intensive research (for early example see Korkhaus, 1930; Braun, 1938; Lündstrom, 1948; Horowitz et al., 1958; Osborne et al., 1958; Kraus et al., 1959; Hanna et al., 1963; Garn et al., 1965; Niswander and Chung, 1965; Goose, 1967, 1968; Lewis and Grainger, 1967; Potter et al., 1968; Bowden and Goose, 1969). Twin studies have provided insight into the proportional contribution of additive genetic and environmental effects to dental phenotype (Lauweryns et al., 1993; Townsend et al. 2006; Townsend et al., 2009), including both odontometric (Osborne et al., 1958; Lündstrom, 1967; Biggerstaff, 1976; Corruccini and Potter, 1980; Sharma et al., 1985; Townsend et al., 1986; Corruccini et al., 1988; Dempsey et al., 1995; Dempsey and Townsend, 2001; Townsend et al., 2003; Heikkinen et al., 2016) and morphological characters (Ludwig, 1957; Lündstrom, 1963; Staley and Green, 1971, 1974; Biggerstaff, 1973; Scott and Potter, 1984; Townsend and Martin, 1992; Laatikainen and Ranta, 1996;

Hughes et al., 2007; Camilleri et al., 2008). The classic twin research design compares pairwise phenotypic correspondence in a large sample of monozygotic (MZ) and dizygotic (DZ) twins as a means of estimating genetic contribution to character expression (Nance, 1984; Neale and Cardon, 1992; Martin et al., 1997; Boomsma et al., 2002; Townsend et al., 2003, 2005, 2006, 2009, 2015). Because MZ twins share a relatedness coefficient of 1.0 (i.e., all of their genes are expected to be identical by descent) and DZ twins share a relatedness coefficient of 0.5 (i.e., on average, half of their genes are expected to be identical by descent), greater phenotypic correspondence between MZ twins is reasoned to be driven by genetic factors (Nance, 1984; Neale and Cardon, 1992; Townsend et al., 2003, 2009; Chen, 2006). When a trait is more highly correlated for DZ twins, environment is thought to play a greater role in trait expression (Nance, 1984; Neale and Cardon, 1992; Townsend et al., 2003, 2009, 2015; Chen, 2006).

The twin design involves several assumptions: 1) the focal population experiences random mating (Townsend et al., 2003; Chen, 2006); 2) MZ and DZ twins raised together share equivalent environmental influences (Kang et al., 1977; Christian, 1979; Kendler, 1983; Nance, 1984; Kendler et al., 1993; Pam et al., 1996); 3) principles of gene dominance are in effect (Kang et al., 1977; Chen, 2006); 4) genetic variance is additive and a given trait is not controlled by any single gene (Garn et al., 1979; Townsend et al., 2009); and 5) trait mean values, within-zygosity variances, and environmental covariances are approximately equal between MZ and DZ samples (Kang et al., 1977; Christian, 1979; Harris, 2005; Townsend et al., 2009). Due to the inappropriateness of these assumptions in certain contexts, the traditional twin design has faced criticism in recent years (Townsend et al., 2003, 2009). In addition to the common problem of incorrect zygosity reporting (Nyholt, 2006; Townsend et al., 2009), traditional twin studies often fail to distinguish between shared genetic factors and shared environmental factors that may, in combination, account for within-pair phenotypic correlation or covariance (Hughes et al., 2000; Townsend et al., 2003, 2009). Recognizing this limitation, more recent structural equation and "animal" modeling efforts explicitly define common (i.e., familial) environmental variance as a key parameter upon the premise that traditional "approaches of estimating heritability have probably represented the upper limits of the true values" (Hughes et al., 2000:997; e.g., Martin and Eaves, 1977; Heath et al., 1989; Townsend and Martin, 1992; Dempsey et al., 1995, 1998; 1999; Townsend et al., 2003, 2009, 2012, 2015; Kruuk, 2004; Kruuk and Hadfield, 2007; Hughes and Townsend, 2013). There are several variations of the classic twin design, including: 1) familial versus separately-reared MZ twins (Garn et al., 1979; Bouchard, 1984; Boraas et al., 1988; Tellegen et al., 1988; Bouchard et al., 1990; Michalowicz et al., 1991); 2) same-sex versus opposite-sex DZ twins (to investigate in-utero hormonal diffusion and sex-determined variability) (Lauweryns et al., 1993; Miller, 1994; Lummaa et al., 2007; Tapp et al., 2011; Ribeiro et al., 2012, 2013; Lam et al., 2016); and 3) twin half-sibling designs (comparing phenotypes in children of MZ fathers to examine the impact of distinct uterine and post-uterine environments) (Kang et al., 1974; Potter, 1990; Harrap, 2000; Townsend et al., 2003, 2009).

Twin studies persist in the literature, representing a rich source of information about the foundation of complex trait variation (Martin et al., 1997; Boomsma et al., 2002; Hughes and Townsend, 2012; Townsend et al., 2015). Extended pedigree research has also yielded heritability estimates for dental characters by exploiting complex genealogical data from multigenerational pedigrees or household-level family groups. Twin and family studies have employed a variety of analytical approaches, the most basic of which include correlation analyses across pairwise relatedness categories (Potter et al., 1968; Bowden and Goose, 1969; Sofaer et al., 1972; Harris and Bailit, 1980). The most widely applied correlation-based heritability equation (based on the twin design) is the Bulmer (1970) and Smith (1974) estimate: $h^2 = 2(r_{MZ} - r_{DZ})$. This equation is limited in that it is sensitive to the violation of numerous assumptions and often yields estimates greater than 1.0 (Dempsey et al., 1999). Other analytical approaches include multiple abstract variance analysis (Townsend and Brown 1978; Dempsey et al., 1999; Brown et al., 2011), informal Mendelian inheritance/offspring correspondence analysis (Kraus, 1951; Goose and Lee, 1971, 1972), full-sibling covariance analysis (Alvesalo and Tigerstedt, 1974; Alvesalo et al., 1975), path analysis (Potter et al., 1983), and complex segregation analysis (Nichol, 1989). Today, biometric approaches that employ covariance structure analysis (e.g., SEM) and maximum likelihood variance components analysis are favored because they are more flexible and subject to fewer limitations (Jinks and Fulker, 1970; Eaves, 1978, 1982; Eaves et al., 1978; Almasy and Blangero, 1998; Dempsey et al., 1999).

Across all twin and family studies, heritability estimates for dental crown characters range considerably. Results of quantitative genetic analyses show permanent crown dimensions to be under relatively strong genetic control, with most heritability estimates exceeding 0.50 (e.g., Lündstrom, 1948; Goose, 1971; Alvesalo and Tigerstedt, 1974; Garn 1977; Townsend and Brown, 1979; Dempsey et al., 1995; Dempsey and Townsend, 2001). Analyses of permanent morphological characters typically yield lower heritability estimates, with the majority of estimates ranging between 0.40 and 0.80 (Scott and Turner, 1997:164; see Sofaer et al., 1972; Biggerstaff, 1973; Alvesalo et al., 1975; Mizoguchi, 1977; Berry, 1978; Scott and Potter, 1984; Boraas et al., 1988; Townsend and Martin, 1992; Laatikainen and Ranta, 1996). Note that most morphological studies focus solely on Carabelli's trait expression; to date, heritability estimates have not been generated for the complete suite of crown morphology characters that comprise the Arizona State University Dental Anthropology System (Turner et al., 1991). Further, comparatively few heritability estimates have been published for deciduous characters. As primary teeth are the focus of the dissertation, I review the results of these studies more thoroughly in the section below.

Deciduous heritability studies. Based on a limited number of studies, deciduous odontometrics are characterized by heritability estimates that match or exceed those published for homologous permanent dimensions (Townsend, 1980; Mizoguchi, 1998; Hughes et al., 2000; Su et al., 2008). DiSalvo et al. (1972) marked a landmark effort in quantifying additive genetic and environmental contributions to deciduous crown size, focusing on mesiodistal dimensions of the anterior teeth (DiSalvo et al., 1972). In a sample of MZ and DZ twins and triplets from New Jersey, the authors found "significant" degrees of genetic variation associated with the deciduous maxillary incisors and right canine, as well as the deciduous mandibular canine (DiSalvo et al., 1972:478). In an Australian Aboriginal sample, Townsend (1980) found additive genetic variance to account for 58 percent of deciduous tooth size variance, while common environmental variance (i.e., maternal effects) accounted for 15 percent (Townsend, 1980:297). The additive genetic contribution was similar for homologous permanent dimensions in adults from the same Aboriginal community (approximately 64%), but the shared environmental factors were found to be more influential in the deciduous sample (deciduous=15% versus permanent=6%) (Townsend and Brown, 1978; Townsend, 1980). Mizoguchi's (1998) study of Japanese male twins yielded similar results; for mesiodistal dimensions of deciduous incisors, maximum heritability estimates ranged from 0.59-0.82. Later, Hughes et al. (2000) examined deciduous crown dimensions in Australian twins of European ancestry and found heritability estimates to range from 0.62-0.93 (Hughes et al., 2000:1001). Su et al. (2008) focused on deciduous mandibular molar dimensions in Brazilian twin pairs, revealing a heritability estimate of 0.98. These findings corroborate previous studies that found deciduous crown size variation to be influenced almost completely by additive genetic variance, with any remaining influence originating from unique environmental variance (Hughes et al., 2000). Only the deciduous mandibular central incisors exhibited strong contribution from *common* environmental factors, a finding consistent with their developmental trajectory; these are the earliest prenatally forming teeth (Kraus and Jordan, 1965; Lunt and Law, 1974; Hughes et al., 2000).

Studies have also yielded summary statistics and heritability estimates for deciduous occlusion/orthodontic traits (e.g., Foster and Hamilton, 1969; El-Nofely et al., 1989; Harris and Johnson, 1991). Harris and Johnson (1991) found occlusion traits (overbite, overjet, etc.) to be strongly influenced by unique environmental factors in Bolton Growth Center siblings. However, they found the primary dentition to yield higher heritability estimates for these characters than the permanent dentition (Harris and Johnson, 1991). Hughes et al. (2001) performed a study in a sample of Australian twins, examining inter-element spacing, arch dimensions, overbite, and overjet. Additive genetic variance ranged from approximately 60 to 80 percent for the first two traits, and accounted for 53 percent of overbite and 28 percent of overjet expression (Hughes et al., 2001:861-862). Chen (2006) examined a number of occlusion characters, including arch length, arch breadth, and molar sagittal relationship in a small Brazilian twin sample (n<40). Resulting heritability estimates were fairly low for molar relationships and overbite (42% and 38%, respectively) while all other traits exceeded 80 percent additive genetic contribution (Chen, 2006). Others have explored the relative genetic determination of pathology (e.g., Bretz et al., 2005; Wasmer et al., 2008), asymmetry (e.g., Heikkinen et al., 2016), and three-dimensional crown topography (e.g., Su et al., 2008) in the deciduous dentition; for brevity I will refrain from discussing these results.

A complementary area of research includes longitudinal studies that examine specific environmental factors affecting deciduous phenotypes. This research probes the “black box” of environmental variance in quantitative genetic models to identify tangible effect variables. Most of these studies are published in the clinical literature (Evans, 1944; Bailit and Sung, 1968; Cohen et al., 1977; Garn et al., 1980; Heikkinen et al., 1992; Harila et al., 2003). For example, Stanley Garn and colleagues found that prenatal effects such as maternal effects or “gestational determinants” strongly contribute to crown size variability (Garn et al., 1979). Results showed maternal diabetes and hyperthyroidism to lead to increased deciduous crown size, while maternal hypertension and reduced birth weight/gestation period account for reduction in deciduous dimensions (Garn et al., 1979). Fearne and Brook (1993) also identified low birth weight and poor pre/perinatal growth as driving factors in deciduous crown reduction (Fearne and Brook, 1993; cf., Harila et al., 2003). More recently, Seow and Wan found birth weight to have a “dose-response effect” on primary crown morphometrics; their results showed dimensions to range from smallest to intermediate to largest across, very low, low, and normal birth weight categories, respectively (Seow and Wan, 2000:67). Floyd (2009) examined deciduous caries risk in Taiwanese children from various socioeconomic backgrounds, concluding that nutritional status strongly influences caries prevalence (Floyd, 2009). Guar and Kumar (2012) also found socioeconomic environment to affect dental development in an Indian sample, concluding “even moderate under-nutrition can delay deciduous tooth emergence” (Guar and Kumar, 2012:54). These results corroborate trends described by Holman and Yamaguchi (2005) in a sample of Japanese children.

Unfortunately, published heritability estimates for deciduous morphological crown traits are rare, possibly due to the underrepresentation of deciduous morphology data in the literature (see Chapters 3-4). This chapter addresses the paucity of these estimates and provides a foundation for incorporating deciduous teeth into comprehensive models of the human diphyodont dental complex. One of the key goals of this paper is to expand the suite of heritability estimates for both deciduous and permanent crown morphology and to provide a broadly generalizable knowledge base for future quantitative genetic and biodistance research.

Beyond Heritability: Modeling the Genetic Architecture of Human Dental Variation

As previously mentioned, developmental genetics and evolutionary biology have played an essential role in illuminating the molecular and protein signaling mechanisms (Jernvall et al., 1994, 1998; Sharpe, 1995; Thesleff and Sharpe, 1997; Kettunen et al., 2000; Zhao et al., 2000) responsible for certain patterns of craniofacial variation (*size*:

Kavanagh et al., 2007; *shape*: Jernvall et al., 2000; Jernvall and Jung, 2000; Jernvall and Thesleff, 2000; Salazar-Ciudad and Jernvall, 2002). The predictive models generated by this work have been applied to various mammalian taxa—including extant and fossil hominins—with mixed success (Renvoisé et al., 2009; Hunter et al., 2010; Bernal et al., 2013; Moormann et al., 2013; Schroer and Wood, 2015; Evans et al., 2016; Ortiz et al., 2016; Paul et al., 2017). Conflicting results may be due, in part, to the distinctive rodent dentition upon which developmental genetic models are founded. The mouse model organism possesses a highly derived dentition relative to humans and Great Apes (Jernvall et al., 2000; Salazar-Ciudad and Jernvall, 2002). For this reason, quantitative genetic analyses of pedigreed samples have been an invaluable source of information on the genetic mechanisms underlying primate dental variation, namely in Cercopithecoids (Hlusko et al., 2004a, 2007; Koh et al., 2010; Grieco et al., 2012). Hlusko and colleagues' research on captive baboons has not only shed light on the relative contribution of additive genetic effects to crown trait expression (h^2), but it has also outlined patterns of genetic correlation (ρ_G) within the primate dentition (Hlusko et al., 2004a, 2004b, 2007, 2016; Hlusko and Mahaney, 2009; Koh et al., 2010; Grieco et al., 2012; Hlusko, 2016). This work has provided a platform for exploring broader evolutionary trends, comparing patterns of integration/modularity across mammalian taxa (Hlusko and Mahaney, 2007; Hlusko et al., 2011).

Notably, few quantitative genetic efforts have focused on dental variation in modern human samples. One exception is a study by Stojanowski and colleagues that explored patterns of genetic correlation among dental metric characters in a pedigreed sample of 20th century Gullah individuals (Stojanowski et al., nd). The results of this study indicate a high degree of genetic integration in crown dimensions relative to that reported for rodents and Cercopithecoids (Hlusko and Mahaney, 2007; Hlusko et al., 2011). This suggests that there is considerable intraspecific variation in patterns of modularity/integration as relates to dimensional dental variation in the primate order and highlights the need for replication studies within taxa before drawing broader conclusions about mammalian dental evolution (Stojanowksi et al., nd). Discontinuous morphological characters, which have received little attention in quantitative genetic studies, were also examined in the Gullah sample. Stojanowski and colleagues noted intriguing patterns of genetic correlation between homologous anterior tooth traits of the maxillary and mandibular arcades, between homologous traits across elements, and between traits expressed on different aspects (i.e., labial versus lingual) of the same tooth (Stojanowski et al., nd). These results have implications for biodistance research, which often assumes morphological trait independence or eliminates "genetically redundant" characters upon the basis of pair-wise phenotypic correlation, alone (Stojanowski et al., nd).

Analyses that quantify genetic correlation (pleiotropy) between deciduous dental characters are notably absent from the literature. This is particularly problematic, as deciduous teeth have yet to be incorporated into developmental genetic models of dental variation (mice lack deciduous teeth) (Ungar, 2010). Because humans are diphyodont, a complete understanding of the architecture underlying the dentition of *Homo sapiens* requires exploration of potential morphological integration between deciduous and permanent characters within individuals (Paul et al., nd). These insights are important to the fields of evolutionary and developmental biology but also have the practical impact of ground-truthing biodistance assumptions, as well as the potential to refine analytical “best practices”.

Research Aims and Hypotheses

The overarching aim of this chapter is fourfold. This study’s primary goal is to generate a complete suite of novel univariate heritability estimates for deciduous and permanent morphological crown traits. These estimates will be calculated from three (bio)regionally distinct samples that represent a broad spectrum of modern human dental variation. These samples include nuclear family relationships (including one sample of MZ and DZ twins and their household-level relatives) and extended, multigenerational pedigrees. This means that quantitative genetic analyses will employ data with a complex genealogical structure, capturing varying degrees of relatedness. Heritability estimates will be calculated using methods that provide robust parameter estimates and that minimize biases/standard errors (see Materials and Methods section). The quantitative genetic analyses test the null hypothesis that nongenetic factors alone contribute to phenotypic correspondence among biological relatives (Hlusko and Mahaney, 2009). Significant heritability estimates indicate that observed patterns of variation are explained by genetic relatedness (i.e., additive genetic effects) and the sharing of genes that are identical through common ancestry (Thompson, 1986; Blouin, 2003).

Second, this study will compare heritability estimates between homologous deciduous and permanent dental characters. Because the samples included in this study are longitudinal, it is possible to directly compare heritability estimates for deciduous and permanent phenotypes in matched sets of individuals with (generally) the same underlying genealogical structure. Here, I test the null hypothesis that the relative contribution of additive genetic variance to phenotypic variance is equal for deciduous and permanent homologues (i.e., dh^2=Ph^2).

Third, this study aims to examine the myriad ways in which standard biodistance practices impact the degree to which phenotypic data reflect underlying genotypic information. *1) Scoring Standards.* I will compare heritability estimates for deciduous characters scored using two distinct morphological scoring systems: deciduous-specific standards (see Materials and Methods section) and the Arizona State University Dental Anthropology System (ASUDAS) (Turner et al., 1991). *2) Data Collapsing/Averaging*. Collapsing antimeric data to a maximum expression value is common practice in biodistance research, often applied as a data cleaning procedure aimed at minimizing genetic redundancy and correlation between paired (left and right) traits (Turner and Scott, 1977; Turner et al., 1991). I will compare heritability estimates for traits' left side expression, right side expression, and maximum expression to better inform biodistance practices and provide insight into the underlying biology of crown expression. *3) Dichotomization.* Another common practice in dental anthropology and biodistance research involves reducing ordinal scale trait variation to binary "presence/absence" at designated expression grades or "breakpoints" (e.g., Turner, 1990; Powell, 1995; Scott and Turner, 1997; Lease, 2003). These breakpoints vary between researchers, samples, and scoring standards, and it is unclear if/how the choice to dichotomize (and at what breakpoint) influences the representation of underlying biological variation—and heritability estimates—for these quasi-continuous traits. I will compare heritability estimates within ordinal traits (i.e., between multiple binary traits generated by dichotomizing at each expression grade) (see Materials and Methods section). *4) Frequency Data.* This study will also evaluate how sample frequency impacts heritability estimates. I will compare heritability estimates across corresponding binary traits dichotomized at typically prescribed ordinal "breakpoints" (see Materials and Methods). In each of the above analyses, the null hypothesis to be tested is that additive genetic effects contribute equally to phenotypic expression (i.e., $T1h^2$=$T2h^2$= $T3h^2$).

Finally, this study explores the genetic architecture of the diphyodont dental complex. Genetic correlations will be calculated between deciduous and permanent dental homologues, as well as between characters of the deciduous dentition and permanent dentition, separately. These analyses will test the null hypotheses that all deciduous characters are independent in their sets of genetic effects (i.e., d1-d2 $\rho_G=0$, d1-d2 $\rho_G\neq1$; no pleiotropy), all permanent characters are independent in their sets of genetic effects (i.e., P1-P2 $\rho_G=0$, P1-P2 $\rho_G\neq1$; no pleiotropy), and all deciduous and permanent homologues are independent in their sets of genetic effects (i.e., d1-P1 $\rho_G=0$; d1-P1 $\rho_G\neq1$; no pleiotropy).

MATERIALS AND METHODS

Data for a maximum of 47 deciduous morphological crown characters were collected from casted tooth crowns of 87 participants of the Burlington Growth Study, 290 participants of the University of Adelaide Twin Study, and 115 participants of the University of Adelaide Yuendumu Aboriginal Growth Study (Table 11). Data for 74 permanent morphological traits were collected from dental casts of 128 participants of the Burlington Growth Study, 339 participants of the University of Adelaide Twin Study, and

149 participants of the University of Adelaide Yuendumu Aboriginal Growth Study (Table 11). While, overall, the permanent sample includes data collected from a greater number of individuals, the majority of individuals included in the heritability study are represented by both deciduous *and* permanent datasets. This is due to the longitudinal nature of the three samples, all of which include comprehensive pedigree records and stone dental models cast at multiple points throughout participants' lives.

The first two samples are similar in that they include nuclear families of predominately European ancestry. The Burlington Growth Study (BGS) sample represents family participants of a long-term (starting in 1952) initiative aimed at documenting craniofacial development among residents of Burlington, Ontario (Thompson and Popovich, 1977; University of Toronto, Faculty of Dentistry, 2015). The sample includes 30 families of European ancestry from the BGS. In these families only parent-offspring, full-sibling, and (few) twin relationships are represented. The University of Adelaide Twin Study (UAT) sample represents participants of an active craniofacial genetics study, with data collection and research spanning over three decades and several geographic sites across Australia (Townsend et al., 2006, 2015; Hughes et al., 2013, 2014). Data were collected specifically from members of UAT Cohort 2, which is comprised of monozygotic (MZ) and dizygotic (DZ) twins initially recruited between the ages of three and six years, as well as their immediate family members (Townsend et al., 2006, 2015; Hughes et al., 2013, 2014). Ultimately, the sample includes 107 families of primarily European ancestry recruited from the greater Adelaide, South Australia and Melbourne, Victoria regions (Townsend et al., 2015). To my knowledge only parent-offspring, full sibling, half sibling, and twin relationships are represented in the included

Table 11. Morphological crown variables and associated scoring standards.

Morphological Variables[a]	Deciduous[b]	Permanent[b]
Winging i^1, I^1	Dahlberg (1963)	Turner et al. (1991)
Labial Convexity i^1, I^1		Turner et al. (1991)
Shovel i^1, i^2, c^1, I^1, I^2, C^1	Hanihara (1963)	Turner et al. (1991)
Double Shovel i^1, i^2, c^1, I^1, I^2, C^1, P^1, P^2	Sciulli (1998)	Turner et al. (1991)
Tuberculum Dentale i^1, i^2, c^1, I^1, I^2, C^1	Grine (1986)	Turner et al. (1991)
Mesial Ridge c^1, C^1	Irish and Morris (1996)	Turner et al. (1991)
Distal Accessory Ridge c^1, C^1		Turner et al. (1991)
Uto-Aztecan P^1		Turner et al. (1991)
Odontome P^1, P^2		Turner et al. (1991)
Metacone m^1, m^2, M^1, M^2, M^3		Turner et al. (1991)
Hypocone m^1, m^2, M^1, M^2, M^3	Hanihara (1963)[c]	Turner et al. (1991)
Cusp 5 m^2, M^1, M^2, M^3	Sciulli (1998)	Turner et al. (1991)
Carabelli's Trait m^2, M^1, M^2, M^3	Grine (1986)	Turner et al. (1991)
Parastyle m^1, m^2, M^1, M^2, M^3		Turner et al. (1991)
Peg/Reduced i^2, I^2, M^3		Turner et al. (1991)
Congenital Absence I^2, P^2, M^3		Turner et al. (1991)
Shovel i_1, i_2, c_1[d], I_1, I_2	Hanihara (1963)	Turner et al. (1991)
Double Teeth i_1, i_2, c_1	Sciulli (1998)	
Tuberculum Dentale c_1	Grine (1986)	Turner et al. (1991)
Distal Accessory Ridge c_1, C_1		Turner et al. (1991)
Lingual Cusp P_1, P_2		Turner et al. (1991)
Odontome P_1, P_2		Turner et al. (1991)
Delta form m_1	Dahlberg (1949)	
Cusp Number m_1, m_2, M_1, M_2, M_3		Turner et al. (1991)
Cusp 5 m_1, m_2, M_1, M_2, M_3	Sciulli (1998)[e]	Turner et al. (1991)
Cusp 6 m_1, m_2, M_1, M_2, M_3		Turner et al. (1991)
Cusp 7 m_1, m_2, M_1, M_2, M_3	Sciulli (1998)	Turner et al. (1991)
Cusp Number m_1, m_2, M_1, M_2, M_3		Turner et al. (1991)
Anterior Fovea m_1, m_2, M^1		Turner et al. (1991)[f]
Deflecting Wrinkle m_2, M_1	Sciulli (1998)	Turner et al. (1991)
Groove Pattern m_2, M_1, M_2, M_3		Turner et al. (1991)
Protostyid m_1, m_2, M_1, M_2, M_3	Grine (1986)	Turner et al. (1991)
Distal Trigonid Crest m_2, M_1, M_2, M_3		Turner et al. (1991)
Congenital Absence I_1, P_2, M_3		Turner et al. (1991)

[a] Maxillary and mandibular arcades indicated by superscripts and subscripts, respectively.
[b] "Deciduous" standards are those specifically designed for observation/data recording on deciduous teeth. Standards listed as "permanent" are those designed for permanent morphology observation/data recording, but in instances they were augmented for application to deciduous characters. [c] Augmented from Dahlberg (1949) and referred to as "crown pattern of the deciduous upper second molar" (Hanihara,1961) or "cusp number, hypocone of maxillary first deciduous molar" (Hanihara,1963). [d] Shoveling for c_1 only scored using Hanihara (1963). [e] Dichotomized and referred to as "hypoconulid of the mandibular second deciduous molar" in Scuilli (1998).
[f] Standards augmented for observation on first molar, but removed due to lack of precision.

UAT sample. Based on pedigree records and sampling strategies employed in both studies (Townsend et al., 2006, 2015; University of Toronto, Faculty of Dentistry, 2015), unless otherwise noted, relationships between individuals belonging to different families across the Burlington and Twin samples are assumed to approximate those shared between randomly sampled members of a reasonably diverse population (see Chapters 3 and 4; Paul and Stojanowski, 2015, 2017).

The University of Adelaide Yuendumu Aboriginal Growth Study (UAY) sample includes data collected from pedigree records and dental casts generated as part of a 20-year (1951-1971) anthropological research initiative (Brown and Barrett, 1973a; Barrett, 1976; Townsend and Brown, 1978; Brown et al., 1987; Brown, 1992; Brown et al., 2011). The aim of the UAY study was to document the overall growth and development of Warlpiri Aboriginal children from the isolated community of Yuendumu, Northern Territory during a period of intensifying contact with Western culture, foods, and practices (Barrett et al., 1965; Barrett and Brown, 1971; Barrett, 1976; Brown et al., 2011). This study sample includes 21 extended Aboriginal families from the UAY collections. Due to the complexity of Warlpiri kin networks, the genealogical relationships represented in this sample are diverse and include parent-offspring, aunt/uncle-niece/nephew, full sibling, half sibling, and cousin dyads (Barrett, 1976; Brown et al., 2011).

Throughout the course of data collection, all individuals and families were recoded using a numbering system specific to this study; this preserved subject anonymity in compliance with ethics approvals. Research protocols were reviewed and granted exemption by Arizona State University's Institutional Review Board, the Burlington Growth Centre, and the University of Adelaide School of Dentistry and Craniofacial Biology and Dental Education Research Group (Appendix B).

Data Recording Methods

Deciduous and permanent crown morphology was observed and recorded from stone casts using Arizona State University Dental Anthropology System (ASUDAS) standards (Turner et al., 1991) and, where applicable, a suite of standards designed specifically for deciduous teeth (Dahlberg, 1949; Hanihara, 1961, 1963; Grine, 1986; Sciulli, 1998; Lease, 2003) (Table 11). Data were collected for a total of 47 deciduous and 74 permanent crown characters on both left and right antimeres (Table 11). All data were recorded by using a supplemental light source (where necessary) and with reference to both ASUDAS and Hanihara (deciduous) reference plaques (Hanihara, 1961, 1963; Turner et al., 1991). Trait expression was quantified on an ordinal scale or dichotomized as "present" versus "absent", as prescribed by published standards (see Turner et al., 1991; Sciulli, 1998; Lease, 2003).

Analytical Methods

At least eight weeks after initial data collection, a minimum of 15% of the original samples were rescored (BGS: ~15%; UAT: ~20%; UAY: ~25%). To quantify intra-observer error, absolute grade differences between scoring sessions were calculated (Nichol and Turner, 1986), and summary statistics were generated by variable. I conservatively flagged all variables with error ranges exceeding a single ordinal grade, as well as all associated heritability estimates (Hillson, 1996:99). These traits were omitted from the heritability analysis. For the genetic correlation analyses I relaxed these standards, omitting only variables with mean intra-observer error greater than 0.30 grades.

Prior to heritability estimation, the morphological data were converted into several novel variables. For each trait, three separate variables (sets of expression) were considered: 1) left antimere expression, 2) right antimere expression, and 3) maximum expression. To quantify the third variable, separate antimeric trait scores were reduced to a single data point representing an individual's "maximum expression". Additionally, each ordinal variable in the sample was decomposed to generate multiple binary variables, one at each possible breakpoint. For example, Carabelli's trait is a single ordinal trait with eight grades of expression (0 to 7) following ASUDAS standards (Turner et al., 1991). I dichotomized this trait at each possible expression grade to create seven new binary variables (i.e., 0= absent versus 1+=present; 0-1=absent versus 2+=present; 0-2=absent versus 3+=present, etc.). All ordinal and dichotomized traits were included in the heritability analysis, except in cases where traits were monomorphic.

Quantitative genetic analyses. Sample-specific narrow-sense heritability estimates for all morphological variables were calculated using maximum likelihood variance components analysis. These analyses incorporate documented genealogical information and distinguish fixed effects from random effects in modeling phenotypic variance/covariance (Amos, 1994). Maximum likelihood estimation converges upon optimized parameter estimates via iterative log-likelihood testing that assesses model fit to observed data (Shaw, 1987; Lynch and Walsh, 1998; Konigsberg, 2000; Carson, 2006a, 2006b). Variance components models are appropriate for this task, because they accommodate unbalanced and extended genealogies (Carson, 2006a, 2006b). Accordingly, each sample's pedigree data was structured with careful attention to documented genealogical relationships, especially the UAT sample's for which twin pairs were assigned unique identifiers. Heritability estimates were generated using the computer program SOLAR v. 8.1.1 (Blangero et al., 1995-2016; Almasy and Blangero, 1998). SOLAR employs the phenotypic covariance expression: $\Omega = 2\Phi\,\sigma^2{}_G + I\sigma^2{}_E$, where Ω denotes a covariance matrix, Φ denotes a kinship coefficient matrix , $\sigma^2{}_G$ represents additive genetic variance, I denotes an identity matrix, and $\sigma^2{}_E$ represents random (environmental) variance (Almasy and Blangero, 1998). However, because a separate univariate model was generated for each morphological trait, the covariance term here represents individual-level (not trait-level) covariance (Carson, 2006a, 2006b). SOLAR uses the additive relationship between phenotypic variance and its components ($\sigma^2{}_P = \sigma^2{}_G + \sigma^2{}_E$) to estimate the proportion of quantifiable trait variance attributable to additive genetic variance; this is the reported heritability estimate ($h^2 = \sigma^2{}_G/\sigma^2{}_P$) (Hlusko, 2004). These estimates were informally compared across dentitions (deciduous versus permanent), traits, isomeres (maxilla versus mandible), antimeres (left versus right versus maximum expression), dichotomization breakpoints, and samples.

Genetic correlation analyses were conducted for only the University of Adelaide Twin Study sample (ASUDAS traits only) using a multivariate derivation of the phenotypic covariance expression listed above (Hopper and Mathews, 1982; Boehnke et al., 1983; Lange et al., 1983). Bivariate models were generated in SOLAR using the expression $\Omega = G \,\Upsilon\, 2\Phi \; + E \,\Upsilon\, I$; here, Ω represents a phenotypic covariance matrix, G denotes a genetic variance/covariance matrix, Υ represents a Kronecker product operator, Φ represents a matrix of kinship coefficients, E denotes an environmental variance/covariance matrix, and I denotes an identity matrix (following Mahaney et al., 1995; Hlusko et al., 2004, 2007; see also Blangero et al., 1991; Williams-Blangero and Blangero, 1992; Williams-Blangero et al., 1993; Almasy et al., 1997). The models provided additive genetic and environmental correlation estimates (ρ_G and ρ_E, respectively), as well as phenotypic correlation estimates derived from the following equation: $\rho_P = \sqrt{h_1^2}\,\sqrt{\mathrm{h}_2^2}\,\rho_G + \sqrt{(1 - h_1^2)}\,\sqrt{(1 - h_2^2)}\,\rho_E$. Parameter significance was evaluated via likelihood ratio tests comparing a restricted model (in which the parameter of interest was held constant) and an unrestricted model (in which all parameter values were estimated) (Almasy and Blangero, 1998; Hlusko et al., 2004, 2007; Stojanowski et al., nd). Genetic correlation significance was evaluated in a similar fashion, but for this parameter the unrestricted model was compared to two restricted models; restricted model 1 fixed genetic correlation at 0.0, and restricted model 2 fixed genetic correlation at 1.0. Significant difference between likelihoods for the unrestricted model and restricted model 1 *only* is interpreted here as complete pleiotropy (i.e., the same gene/set of genes contribute to the trait pairs additive genetic variance). Significant difference in likelihood between all three models is interpreted as incomplete pleiotropy (i.e., some portion of the trait pair's additive genetic variance is attributed to effects of the same gene/set of genes) (following Hlusko et al., 2004, 2007; Stojanowski et al., nd.)

Because SOLAR accommodates only continuous and binary discontinuous variables, all ordinal morphological variables were treated as continuous, appealing to the general assumption that these traits are characterized by underlying continuous normal distributions (Corruccini, 1976; Cheverud et al., 1979; Konigsberg et al., 1993; Roff, 1996; Carson, 2006a, 2006b). Data were also transformed using SOLAR's *inorm* function in an attempt ameliorate potential error arising from high kurtosis. Sex, age, and sex*age interaction terms were incorporated as covariates in each variance components model. While coding for sex was straightforward, coding for age was more complex. Birth dates were not recorded for the entire sample, which means that secular effects are not captured by any of the covariates. This would likely impact only the UAY sample, which contains multigenerational pedigrees. However stone dental models were typically labeled with the age at which the individual's teeth were cast. Because each individual's dentition was cast at multiple points throughout their life, observations were made on the least-worn cast for elements and/or traits of interest. I designated a single "deciduous age" value and a single "permanent age" value for each individual in the sample; these values were then used as the age covariate term in all deciduous trait models and permanent trait models, respectively, in an attempt to capture any effects of error related to wear. Each individual's "deciduous age"/"permanent age" was represented by the age corresponding to the cast on which the majority of the deciduous/permanent traits were scored for that individual. Covariates were fixed in bivariate genetic correlation analyses when their mean effects were deemed significant, using the more conservative standard of $p \leq 0.10$ (Stojanowski et al., nd). Note that all traits were included in the genetic correlation analyses, regardless of whether their heritability estimates were significant.

RESULTS

Mean intra-observer error ranged from approximately 0-1 grade for all traits across all samples (BGS and UAT range: 0 to 1; UAY range: 0 to 1.1). Maximum intra-observer error ranged from 0-1 grade for the majority of traits. Traits characterized by maximum intra-observer error greater than one grade were removed from the analysis. For the BGS sample this included c^1 tuberculum dentale (maximum error=3 grades), as well as m_1 anterior fovea, P_2 lingual cusp variation, and M_2 cusp 5 (for all, maximum error=2 grades). For the UAT sample i^1/I^1 labial convexity, i^1/i^2 double shovel, m^1/M^1 metacone, m^1/M^1 parastyle, M_1 anterior fovea, and m_1/M_2 cusp 7 (for all, maximum error=2 grades); m_2/M_2 protostylid (maximum error=3 grades); and P_1/P_2 lingual cusp variation (for all, maximum error =7 grades) were removed from the analysis. Within the UAY dataset the traits I^1 labial convexity, xc/P^2double shovel, m^1 metacone, m^1 parastyle, $M_1/M_2/M_3$ protostylid, and M_2 C6 (for all, maximum error=2 grades); i^2 tuberculum dentale and M^2 hypocone (for all, maximum error=3 grades); P_2 lingual cusp variation (maximum error=6 grades); and P_1 lingual cusp variation (maximum error=7 grades) were removed due to high levels of intra-observer error. Additionally, select deciduous traits were removed from all samples due to high levels of imprecision throughout data collection (i^1 tuberculum dentale), because the traits were monomorphic across all samples (c^1 mesial ridge, i^2 peg-shaped, m^1 cusp 5), or because the traits were not homologous with the permanent characters upon which scoring standards were based (m^1 Carabelli's trait, m_1 anterior fovea, m_1 protostylid, m_1 cusp 7).

Heritability Estimates

Including all ordinal traits and decomposed binary characters, heritability estimates were generated for a total 2,041 deciduous traits (787 mixed standards and 1,254 ASUDAS) and 2,460 permanent traits across the three samples. Heritability estimates vary considerably across traits and across samples, ranging from 0.0-1.0. All estimates are listed in Appendices J-L. A number of models failed to yield estimates due to convergence issues, while several yielded problematic or unstable estimates due to inadequate sample size (and resulting standard error inflation) or model assumption violations related to kurtosis. Considering only the non-problematic estimates for ordinal traits with sample sizes exceeding 80, deciduous (mixed standards) results were as follows: BGC mean h^2=0.512, range=0.394-0.723, n=3 traits (66.6% of estimates significantly different from zero); UAT mean h^2=0.504, range=0.000-0.972, n=52 traits (82.7% of estimates significantly different from zero); UAY mean h^2=0.476, range=0.000-1.000, n=22 traits (54.5% of estimates significantly different from zero). Deciduous (ASUDAS) results were similar: BGC mean h^2=0.493, range=0.130-0.965, n=8 traits (75.0% of estimates significantly different from zero); UAT mean h^2=0.600, range=0.000-0.907, n=56 (94.6% of estimates significantly different from 0.0); UAY mean h^2=0.370, range=0.000-1.000, n=35 traits (51.5% of estimates significantly different from zero). Finally, permanent morphology results were as follows: BGC mean h^2=0.295, range=0.000-1.000, n=89 traits (38.2% of estimates significantly different from zero); UAT mean h^2=0.611, range=0.000-1.000, n=99 (79.8% of estimates significantly different from zero); UAY mean h^2=0.341, range=0.000-1.000, n=99 traits (64.6% of estimates significantly different from zero). Formally comparing estimates via significance testing (F-test) was deemed inappropriate given their wide-ranging confidence intervals. However, by partitioning these estimates into distinct regions of the dentition, patterns do emerge.

Considering only ordinal ASUDAS characters, BGC results yield limited information about the relative influence of additive genetic factors across the dentition. This is because sample size issues invalidated a number of estimates. The deciduous maxillary and mandibular averages (0.446 and 0.965, respectively, based on maximum expression) are each based on a single value, while the permanent results (maxillary mean h^2=0.327, range=0.000-0.762; mandibular mean h^2=0.292, range=0.000-1.000, based on maximum expression) may also be suspect due to their small sample size relative to the UAT and UAY datasets. That said, UAT results indicate, on average, a fairly consistent influence of additive genetic factors on morphological variation across the diphyodont dental complex. Deciduous results show maxillary traits to range from 0.000-0.857 (mean h^2=0.614, based on maximum expression) and mandibular traits to range from 0.400-0.876 (mean h^2=0.649, based on maximum expression); all of the maximum expression estimates significantly differ from zero. The UAT permanent results show maxillary heritability estimates to range from 0.000-0.932 (mean h^2=0.664, based on maximum expression), while mandibular estimates range from 0.000-1.000 (mean h^2=0.514, based on maximum expression); a number of estimates did not significantly differ from zero, but nearly all of these traits are characterized by low sample frequencies and estimates of 0.0 or 1.0 (e.g., distal trigonid crest, congenital absence, odontome). The UAY averages appear similarly consistent across the dentition, but heritability estimates are markedly lower than those obtained for the UAT sample.

The deciduous maxillary estimates ranged from 0.000-0.626 (mean h^2=0.366, based on maximum expression) and deciduous mandibular estimates ranged from 0-0.868 (mean h^2=0.399, based on maximum expression). UAY permanent estimates ranged from 0.000-0.686 in the maxilla (mean h^2=0.356, based on maximum expression) and from 0.000-0.667 in the mandible (mean h^2=0.313, based on maximum expression). It should be noted that interpreting these comparative results is challenging, as summary statistics are not based on the exact same suite of traits across samples. It is for this reason that more detailed comparisons between individual estimates (within and between samples) were necessary.

Deciduous and permanent comparisons. Heritability estimates for homologous deciduous and permanent (ASUDAS) characters are presented side-by-side in Tables 12 and 13. The majority of these estimates are based on individuals' maximum expression values because they provided greater sample sizes for model estimation than left or right side values (for exceptions see Tables 12-13). A number of these models failed to converge or yielded unstable heritability estimates due to small sample size or issues related to kurtosis. Because of small deciduous sample sizes in the BGC and UAY sample, the most valid comparisons (i.e., two estimates generated from sample sizes n>80) can be made between deciduous and permanent homologues in the UAT sample. Looking only at homologue comparisons in the UAT sample (i.e., i1 to I1 traits, i2 to I2 traits, c to C traits, dm2 to M1 traits) one third (4 of 12) of heritability estimates are higher for the morphology of the deciduous dentition (Tables 12-13). Interestingly, this pattern is split for shoveling; heritability estimates are higher for the permanent incisors than for the deciduous incisors (maxillary and mandibular) and lower for the permanent canine than for the deciduous canine (Table 12). The estimate for canine double shoveling is also higher for the deciduous element (a comparison could not be made for expression on the incisors). Comparisons for tuberculum dentale and distal accessory ridge expression reveal higher heritability estimates for the permanent homologues, while additive genetic variance accounted for a greater portion of maxillary postcanine variance (hypocone and Carabelli's trait) for the dm^2 than for the M^1 (Table 13). Note, however, that estimates are almost equivalent between these elements for hypocone expression. For deflecting wrinkle expression, M_1 estimates exceed dm_2 estimates (Table 13). In all cases where homologues could be compared, both estimates are significantly different from zero ($p<0.05$), with the exception of i^1 shoveling expression.

Homologue comparisons were appropriate for certain traits of the UAY sample, as well (deciduous and permanent $n>80$). Maxillary canine shoveling and double shoveling estimates are higher for the permanent homologue (the opposite pattern of that observed in the UAT sample), as well as maxillary canine tuberculum dentale estimates (the same pattern as that observed in the UAT sample) (Table 12). For most maxillary postcanine traits (metacone, metaconule, and Carabelli's trait expression), the deciduous homologue is characterized by a higher estimate of heritability. The exceptions are parastyle and hypocone, whose expression is higher for the M^1; note, however, metacone and hypocone estimates are roughly equal between the deciduous and permanent elements (Table 13). Patterns are less clear when examining the mandibular postcanine traits. Deciduous estimates are higher for molar cusp number and deflecting wrinkle, while permanent estimates are higher for anterior fovea, cusp 5, cusp 6, and distal trigonid crest (Table 13). Unlike the UAT sample, estimates fail to significantly differ from zero for a number of traits, with homologues conflicting in significance for many of the postcanine characters (Tables 12-13). This may be due, in part, to the UAY's smaller sample size.

Sample sizes were problematic for most deciduous characters in the BGC sample. Comparisons were made for select traits of the postcanine dentition (deciduous and permanent n>80). Deciduous heritability estimates are higher for metacone, hypocone, and cusp 7 expression. Most of these estimates equaled approximately zero, with the exception of m^2 metacone expression (Table 13). These low estimates are almost certainly a product of the small BGC sample sizes. The permanent heritability estimate is higher for Carabelli's trait expression, but as in the UAT and UAY sample, both the deciduous and permanent estimates significantly differ from zero (Table 13).

Deciduous scoring standard comparisons. Deciduous heritability estimates were compared within traits across two distinct morphological scoring standards: mixed deciduous standards and ASUDAS standards. Heritability estimates are presented side-by-side in Table 14. For simplicity, the majority of these estimates are based on individuals' maximum expression values because they provided greater sample sizes. Due to small sample sizes for the BGC and UAY data, most comparisons were made for the UAT sample. Comparisons were made for select traits in the UAY sample (n>80), as well. A clear pattern is noted for all anterior tooth characters: the ASUDAS scoring is characterized by higher heritability estimates (Table 14). The one exception is tuberculum dentale of c^1 in both the UAT and UAY sample; however the two UAT estimates are separated by a difference of approximately 0.07 (Table 14). In each (valid) comparison, expression captured under both scoring systems is characterized by a significant additive genetic variance contribution (Table 14).

The pattern is subtler for the postcanine morphology. Of the (valid) comparisons in the UAT sample, the majority of traits (hypocone/cusp number, deflecting wrinkle, cusp 7) are characterized by higher heritability estimates when quantified under the mixed deciduous standards (Table 14). The exception is Carabelli's trait. Interestingly, though, the majority of paired trait estimates are roughly equal for this sample (see Table 14). Across the valid UAY comparisons, the pattern differs slightly. While the majority of traits are still characterized by higher heritability estimates when expression is quantified under the mixed deciduous standards (metaconule, Carabelli's trait, deflecting wrinkle, cusp 7), hypocone/cusp number estimates are higher when dm^2 expression is scored under the ASUDAS (Table 14). Pair-wise estimates are more disparate for this sample, as well. The only BGC traits with an appropriate sample size for comparison were Carabelli's trait and cusp 7. While estimates are roughly equal across scoring systems for Carabelli's trait, the ASUDAS data yield the higher estimate (Table 14). As in the UAT and UAY samples, the mixed deciduous data yield the higher heritability estimate for cusp 7. Notably, in the valid comparisons, all estimates significantly differ from 0.0, with the exception of cusp 7 (see Table 14).

Antimeric comparisons. Antimeric comparisons were made for all traits in samples for which valid heritability estimates were obtained based on left side, right side, and maximum expression data. Results are presented in Table 15, as well as in Appendix M. Due to disparate sample sizes, the most valid comparisons are made within the UAT

Table 12. Deciduous and permanent *h^2* comparisons across samples (ASUDAS maximum expression) for traits of the anterior dentition.

Trait	Element^{a}	BGC h^2 (N)^{b}	UAT h^2 (N)^{b}	UAY h^2 (N)^{b}
Labial Convexity	xi1	0.491 (50)^{r}	------ (e)	0.855 (34)
	XI1	0.193 (122)	------ (e)	------ (e)
Shoveling	xi1	0.369 (44)	0.470 (87)^{r}	------ (34)*
	XI1	**0.718 (119)^{R}**	**0.811 (303)**	**0.345 (142)**
	xi2	------ (54)	**0.513 (126)**^{r}	**1.000 (45)**
	XI2	**0.341 (112)**	**0.816 (254)**	**0.533 (140)**
	xc	0.000 (66)	**0.792 (235)**	**0.423 (82)**
	XC	0.088 (106)	**0.700 (165)**	**0.601 (128)**
	ni1	------ (42)	------ (92)	1.000 (16)
	NI1	**0.313 (125)**	**0.599 (308)**	**0.677 (136)**
	ni2	------ (55)	**0.509 (149)**	0.210 (36)
	NI2	------ (125)	**0.725 (298)**	**0.542 (141)**
Double Shoveling	xi1	------ (52)*	------ (129)*	------ (35)
	XI1	0.215 (122)	**0.541 (311)**	0.145 (140)
	xi2	------ (57)	------ (e)	------ (47)*
	XI2	0.035 (119)	**0.595 (284)**	**0.529 (141)**
	xc	**0.590 (69)**	**0.751 (239)**	0.000 (86)
	XC	**0.627 (112)**	**0.579 (210)**	0.172 (130)
Tuberculum Dentale	xi2	0.000 (42)^{r}	**0.698 (149)**	0.705 (46)
	XI2	**0.743 (91)**	**0.907 (151)**	**0.482 (129)**
	xc	------ (e)	**0.606 (245)**	**0.562 (87)**
	XC	**0.445 (97)**	**0.932 (154)**	**0.686 (129)**
Distal Accessory Ridge	xc	0.500 (49)^{l}	**0.516 (165)**	0.116 (39)
	XC	0.331 (110)	**0.874 (200)**	**0.419 (130)**
	nc	0.168 (52)	**0.468 (166)**	0.601 (34)^{l}
	NC	0.190 (118)	**0.622 (226)**	**0.386 (131)**

^{a}x/X=maxillary; n/N=mandibular; i/I=incisor; c/C=canine; P=premolar; m/M=molar; lowercase=deciduous; uppercase=permanent. $^{b}h^2$=maximum likelihood heritability estimate; N=sample size. Significant heritability estimates (p-value<0.05) and associated probability estimates bolded. Dashes=incalculable parameter estimates. Traits marked with dashes for all parameters represent models that failed to converge. Traits marked with asterisks are associated with less stable heritability estimates because of incalculable parameters, small sample size, or high kurtosis after normalization. Traits marked with an (e) are associated with high levels of intra-observer error (results repressed). $^{l/L,\ r/R}$Where estimates based on maximum expression are unavailable due to model convergence issues or high kurtosis, estimates based on left/right antimere expression are presented because they have the next largest sample size.

Table 13. Deciduous and permanent h^2 comparisons across samples (ASUDAS maximum expression) for traits of the posterior dentition.

Trait	Element[b]	BGC h^2 (N)[a]	UAT h^2 (N)[a]	UAY h^2 (N)[a]
Metacone	xm2	**0.446 (82)**	**0.664 (278)**	0.233 (109)
	XM1	0.000 (119)	------ (e)	0.211 (146)
	XM2	0.249 (105)	**0.464 (170)**	**0.363 (130)**
Hypocone	xm2	0.088 (84)	**0.722 (279)**	**0.626 (107)**
	XM1	0.080 (116)	**0.721 (319)**	**0.628 (146)**
	XM2	0.214 (77)	**0.926 (112)**	------- (e)
Cusp 5	xm2	------ (79)	------ (272)*	**0.459 (88)**
	XM1	**0.224 (106)**	**0.745 (309)**	**0.326 (143)**
	XM2	**0.709 (76)**	**0.915 (90)[L]**	**0.440 (124)**
Carabelli's Trait	xm2	**0.747 (81)[r]**	**0.857 (276)**	**0.523 (98)**
	XM1	**0.762 (116)**	**0.650 (302)**	**0.433 (137)**
	XM2	**0.323 (102)**	**0.834 (153)**	**0.496 (109)**
Parastyle	xm2	------ (84)	0.000 (278)	0.100 (102)
	XM1	0.224 (117)	------ (e)	**0.233 (142)**
	XM2	**0.234 (105)**	------ (154)*	------ (123)*
Anterior Fovea	nm2	**0.672 (65)**	**0.400 (268)**	0.000 (94)
	NM1	------ (57)	------ (e)	**0.362 (136)**
Cusp Number	nm2	------ (78)	------ (282)	**0.868 (102)**
	NM1	0.000 (100)	------ (293)*	**0.374 (137)[R]**
	NM2	0.205 (84)	**0.697 (140)**	0.134 (117)
Deflecting Wrinkle	nm2	0.237 (67)	**0.775 (261)**	**0.512 (97)**
	NM1	0.000 (62)	**0.923 (301)**	0.151 (139)
Protostylid	nm2	**0.965 (79)**	------ (e)	0.000 (69)
	NM1	0.186 (105)	**0.502 (293)**	------ (e)
	NM2	0.094 (100)	------ (e)	------ (e)
Cusp 5	nm2	0.334 (77)	------ (281)*	0.164 (106)
	NM1	0.227 (100)	**0.846 (292)**	**0.563 (143)**
	NM2	------- (e)	**0.699 (145)**	0.039 (118)
Cusp 6	nm2	0.000 (75)	------ (282)	0.420 (100)
	NM1	0.117 (100)	------ (294)*	**0.637 (138)**
	NM2	------ (83)*	------ (144)*	------ (e)
Cusp 7	nm2	0.065 (80)	**0.776 (283)**	0.323 (108)
	NM1	0.000 (111)	------ (330)*	------ (147)*
	NM2	------ (105)	------ (e)	------ (132)*
Distal Trigonid Crest	nm2	0.306 (73)	**0.876 (256)**	0.270 (84)
	NM1	**1.000 (72)**	1.000 (301)	**0.583 (142)**
	NM2	**1.000 (93)**	0.000 (182)	0.000 (132)

[a] h^2=maximum likelihood heritability estimate; N=sample size. Significant heritability estimates (p-value<0.05) and associated probability estimates bolded. Dashes=incalculable parameter estimates. Traits marked with dashes for all parameters represent models that failed to converge. Traits marked with asterisks are associated with less stable heritability estimates because of incalculable parameters, small sample size, or high kurtosis after normalization. Traits marked with an (e) are associated with high levels of intra-observer error (results repressed). [b] x/X=maxillary; n/N=mandibular; i/I=incisor; c/C=canine; P=premolar; m/M=molar; lowercase=deciduous; uppercase=permanent. [l/L, r/R] Where estimates based on maximum expression are unavailable due to model convergence issues or high kurtosis, estimates based on left/right antimere expression are presented because they have the next largest sample size.

Table 14. Deciduous scoring system h2 comparisons across samples (ASUDAS maximum expression versus deciduous system maximum expression).

Trait[a]	Scoring System[b]	BGC h2 (N)[c]	UAT h2 (N)[c]	UAY h2 (N)[c]
Shoveling	xi1 ASUDAS	0.369 (44)	0.470 (87)[r]	------ (34)*
	xi1 Deciduous	------ (44)	------ (101)*	0.000 (33)
	xi2 ASUDAS	------ (54)	**0.513 (126)**[r]	**1.000 (45)**
	xi2 Deciduous	0.325 (56)	**0.400 (145)**	0.000 (48)
	xc ASUDAS	0.000 (66)	**0.792 (235)**	**0.423 (82)**
	xc Deciduous	0.000 (66)	**0.599 (211)**[r]	**0.380 (81)**
	ni1 ASUDAS	------ (42)	------ (92)	1.000 (16)
	ni1 Deciduous	------ (42)	**0.561 (93)**	------ (16)*
	ni2 ASUDAS	------ (55)	**0.509 (149)**	0.210 (36)
	ni2 Deciduous	0.000 (58)[r]	**0.443 (152)**	**1.000 (36)**
Double Shoveling	xi1 ASUDAS	------ (52)*	------ (129)*	------ (35)
	xi1 Deciduous	------ (44)*	------ (e)	------ (36)*
	xi2 ASUDAS	------ (57)	------ (e)	------ (47)*
	xi2 Deciduous	------ (58)*	------ (157)*	------ (47)*
	xc ASUDAS	**0.590 (69)**	**0.751 (239)**	0.000 (86)
	xc Deciduous	**0.778 (72)**	**0.558 (244)**	------ (e)
Tuberculum Dentale	xi2 ASUDAS	0.000 (42)[r]	**0.698 (149)**	0.705 (46)
	xi2 Deciduous	0.000 (49)	**0.402 (151)**	------ (e)
	xc ASUDAS	------ (e)	**0.606 (245)**	**0.562 (87)**
	xc Deciduous	**0.789 (57)**[r]	**0.675 (251)**	**0.832 (92)**
Hypocone/Cusp Number	xm1 ASUDAS	0.339 (74)	**0.534 (251)**	------ (80)*
	xm1 Deciduous	**0.557 (66)**[l]	**0.596 (248)**	**0.879 (80)**
	xm2 ASUDAS	0.088 (84)	**0.722 (279)**	**0.626 (107)**
	xm2 Deciduous	------ (82)*	**0.775 (278)**	**0.355 (107)**
Cusp 5	xm2 ASUDAS	------ (79)	------ (272)*	**0.459 (88)**
	xm2 Deciduous	0.759 (78)	**0.657 (272)**	**0.860 (89)**
Carabelli's Trait	xm2 ASUDAS	**0.747 (81)**[r]	**0.857 (276)**	**0.523 (98)**
	xm2 Deciduous	**0.723 (81)**[r]	**0.818 (276)**	**0.554 (98)**
Deflecting Wrinkle	nm2 ASUDAS	0.237 (67)	**0.775 (261)**	**0.512 (97)**
	nm2 Deciduous	0.505 (72)	**0.972 (262)**	**0.956 (100)**
Protostylid	nm2 ASUDAS	**0.965 (79)**	------ (e)	0.000 (69)
	nm2 Deciduous	**0.418 (79)**[r]	**0.722 (271)**	------ (77)
Cusp 7	nm2 ASUDAS	0.065 (80)	**0.776 (283)**	0.323 (108)
	nm2 Deciduous	0.394 (80)[r]	**0.815 (283)**	**0.575 (106)**

[a]x=maxillary; n=mandibular; i=incisor; c=canine; m=molar. [b]Traits scored using Arizona State University Dental Anthropology System standards abbreviated with "ASUDAS". Traits scored using a suite of standards designed specific for deciduous crown variation indicated with "Deciduous". [l/r]Where estimates based on maximum expression were unavailable due to model convergence issues or unacceptable levels of kurtosis, estimates based on left/right antimere expression are presented because they have the next largest sample size. [c]h2= maximum likelihood heritability estimate; N=sample size for heritability estimation. Significant heritability estimates (p-value<0.05) and associated probability value estimates bolded. Dashes are associated with incalculable parameter estimates. Traits marked with dashes for all parameters represent models that failed to converge. Traits marked with asterisks are associated with less stable heritability estimates because other model parameters could not be estimated, because sample size was too small, or because kurtosis values were too high after normalization. Traits marked with an (e) are associated with high levels of intra-observer error, and results are repressed from the table.

and UAY samples, especially for the deciduous characters. Across all comparisons in the deciduous dentition, traits most often obtain their highest heritability estimate when collapsed to their maximum expression across antimeres (66.7% of comparisons) (Table 15). In 29.2% of the trait/sample-specific deciduous comparisons, left side expression is characterized by the highest estimate (as compared to 4.2% for right side expression) (Table 15). Only five of the 24 comparisons revealed significant differences in estimates between antimeres—three of these occurred within the UAT sample (m^2 Carabelli's trait, m_1 cusp number, m_1 c5), and two occurred in the UAY sample (c^1 tuberculum dentale, m_2 c5). In all but one of these comparisons (UAY c^1 tuberculum dentale), the maximum expression estimates significantly exceeds one or both of the individual antimere estimates (Table 15; Appendix M).

For the permanent dentition, the greatest number of trait/sample-specific comparisons resulted in left side estimates exceeding the right side and maximum expression estimates (39.4%) (Table 15). However, in an almost equal portion of comparisons, right side (31.8%) and maximum expression (28.8%) heritability estimates were the highest of the three (Table 15). Twelve of the 66 comparisons revealed significant differences in estimates between antimeres—ten of these occurred within the UAT sample (I^2 shovel, C^1 double shovel, C^1 distal accessory ridge, M^2 metacone, M^1 hypocone, M^2 Carabelli's trait, I_2 shovel, M_1 deflecting wrinkle, M_1 protostylid, M_1 cusp 5), and two occurred in the UAY sample (M^1 cusp 5, M_2 cusp number) (Table 15). These significant differences are distributed almost evenly across categories (i.e., left side=highest estimate, right side=highest estimate, maximum expression=highest estimate) (Table 15; Appendix M).

Breakpoint dichotomization and frequency comparisons. Heritability estimates were compared within-traits (i.e., across dichotomized traits at each possible breakpoint) in the UAT ASUDAS morphology sample—the largest sample with the greatest number of reliable estimates across traits. The results are presented in Appendix N, which delineate biodistance utility thresholds for traits in this sample. For example in Appendix N, Figure 6, trends in heritability estimates indicate that establishing a presence/absence threshold at grade 2 of ordinal c^1 double shoveling expression might diminish the additive genetic signal of these phenotypic data, as compared to establishing a threshold at grade 1 or grade 3. These trends are highly variable between traits, between elements, and even between antimeres (Appendix N). Sample frequency (presence) was explored as a potential factor influencing these trends. Because heritability and frequency data are quantified as ratios with ranges restricted to 0.0-1.0, their correlation was quantified using a non-parametric Kendall's tau-*B* coefficient (Kendall, 1975; Kendall and Stuart, 1979); correlation analyses were only performed for traits with an appropriately large sample size ($n>80$). For the suite of deciduous characters, no statistically significant relationship exists between heritability and sample frequency (tau-B=-0.062, $p=0.146$). For the suite of permanent characters, results suggest heritability estimates and sample frequency are significantly positively correlated (tau-B=0.123, $p<0.001$).

While these results are informative, the relationship between heritability and sample frequency are further clarified when represented visually. As illustrated in Figure 16, heritability estimates for binary deciduous morphological traits only approach the extremes of their range when they approach a sample frequency of 0.0 or 1.0. Between frequency values of 0.150 and 0.688, heritability estimates fall between 0.447 and 0.940

(with the exception of one estimate). At the extremes of the x-axis, Figure 16 shows a number of data points clustered at both h^2=0.0 and h^2=1.0, which explains the lack of overall correlation. In Figure 17, heritability estimates for the permanent traits follow a similar trend with one exception—even in the middle of the frequency range, heritability estimates equal or approach 1.0. However, no heritability estimate of 0.0 is obtained for traits with a frequency greater than 0.100 and less than 0.908. Fewer 0.0 heritability estimates are observed at the high end of the frequency range; these low estimates seem to cluster to the far left of the plot (Fig. 17). This pattern likely accounts for the statistically significant positive correlation despite the small tau-*B* coefficient value.

Genetic Correlations

Genetic correlation analyses were conducted only for the UAT sample. Results for paired antimeres are presented in Appendix O, Tables 1 (deciduous) and 2 (permanent). Correlation estimates are high for all traits, with many equaling or approaching 1.0. The only antimerically paired deciduous traits that are not completely pleiotropic are i_1 shoveling and m_2 anterior fovea, which yielded incomplete pleiotropic results. It should be noted that the i_1 shoveling result might reflect the model's relatively small sample size (n=94). The only antimerically paired permanent characters that do not share a completely pleiotropic relationship are I^1 shoveling, I^1 and I^2 double shoveling, and M^2 Carabelli's trait; results for these traits indicate incomplete pleiotropy. Overall, these results corroborate the assumption of strong genetic integration among antimeres and validate the standard biodistance procedure of collapsing complete dental datasets to

Table 15. Antimeric comparisons based on ASUDAS left, right, maximum expression.

	DECIDUOUS[a]	
Left =29.17%	Right=4.17%	Maximum=66.66%
c^1 td (**UAY**/UAT)[b]	m^1 hypo (UAT)[c]	c^1 shov (UAT)
m^2 meta (BGC)		c^1 dshov (UAT)
m^1 hypo (UAT)[c]		i^2 td (UAT)
m^2 hypo (BGC)		m^2 meta (UAT)
m^2 Ctrait (UAY)		m^2 hypo (UAT/UAY)
i_2 shov (UAT)		**m^2 Ctrait** (**UAT**)[d]
m_2 c6 (UAY)		nc dar (UAT)
		m_1 cno (**UAT**)[b]
		m_2 cno (UAY)
		m_2 dw (UAT/UAY)
		m_1 c5 (**UAT**)[e]
		m_2 c5 (**UAY**)[d]
		m_2 c7 (UAT/UAY)
	PERMANENT[a]	
Left =39.39%	Right=31.82%	Maximum=28.79%
C^1 Shov (BGC)	I^1 LCvx (BGC)	I^1 Shov (UAY)
I^1 DShov (BGC)	I^2 Shov (BGC)	**I^2 Shov** (**UAT**/UAY)[b]
I^2 DShov (UAT)	I^1 DShov (UAY)	C^1 Shov (UAT/UAY)
C^1 DShov (**UAT**/UAY)[f]	I^2 DShov (BGC)	I^1 DShov (UAT)
P^1 DShov (UAT/UAY)	P^1 DShov (BGC)	I^2 DShov (UAY)
P^2 DShov (BGC/UAT)	C^1 TD (BGC/UAT)	I^1 TD (UAT)
I^1 TD (BGC/UAY)	**M^2 Meta** (BGC/**UAT**)[e]	I^2 TD (BGC/UAT)
I^2 TD (UAY)	M^1 Hypo (BGC/UAY)	C^1 TD (BGC/UAT)
C^1 Dar (BGC)	M^2 Hypo (UAT)	**C^1 Dar** (**UAT**/UAY)[d]
M^1 Hypo (**UAT**)[b]	**M^1 C5** (**UAY**)[e]	M^2 Meta (UAY)
M^2 CTrait (**UAT**)[b]	M^2 C5 (UAY)	I_1 Shov (UAT)
I_2 Shov (UAY)[c]	M^1 C Trait (UAT/UAY)	**I_2 Shov** (**UAT**)[b]
C_1 Dar (UAT/UAY)	M^2 C Trait (BGC/UAY)	C_1 Dar (BGC)
M_1 AFov (UAY)	I_1 Shov (UAY)	**M_1 DW** (**UAT**)[d]
M_2 CNo (**UAY**)[b]	M_1 DW (UAY)	
M_1 PStylid (BGC/**UAT**)[d]	M_2 C5 (UAY)	
M_2 PStylid (BGC)		
M_1 C5 (**UAT**/UAY)[d]		
M_1 C6 (UAY)		
	BOTH[a]	
Left =36.67%	Right=24.44%	Maximum=38.89%

[a] Based on valid estimates (n>80; no kurtosis violations). Traits listed under side for which they are attributed the highest h^2 estimate. Next to each heading is the percentage of (sample-specific) comparisons for which that antimeric expression is characterized by the highest h^2 estimate. lcvx=labial convexity; shov=shovel; dshov=double shovel; td=tuberculum dentale; dar=distal accessory ridge; meta=metacone; hypocone=hypo; Ctrait=Carabelli's trait; afov=anterior fovea; cno=cusp number; dw=deflecting wrinkle; pstylid=protostylid; c5=cusp 5; c6=cusp 6; c7=cusp 7. Maxillary and mandibular teeth indicated by superscripts and subscripts, respectively. [b] Bolded trait's h^2 estimate is significantly greater than the right side estimate for the associated bolded sample. [c] Two sides are equal in h^2 estimates for the same trait within the same sample. Trait listed under both antimeres. [d] Bolded trait's h^2 estimate is significantly greater than the right and left side estimates for the associated bolded sample. [e] Bolded trait's h^2 estimate is significantly greater than the left side estimate for the associated bolded sample. [f] Bolded trait's h^2 estimate is significantly greater than the right side and maximum estimates for the associated bolded sample.

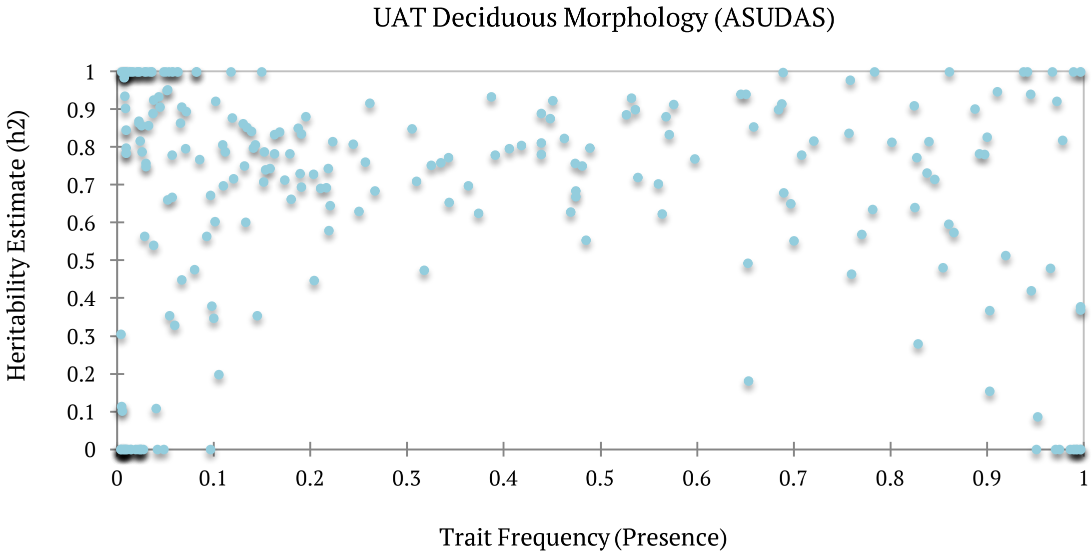


Figure 16. Scatter plot of deciduous morphological traits by frequency and heritability estimate.

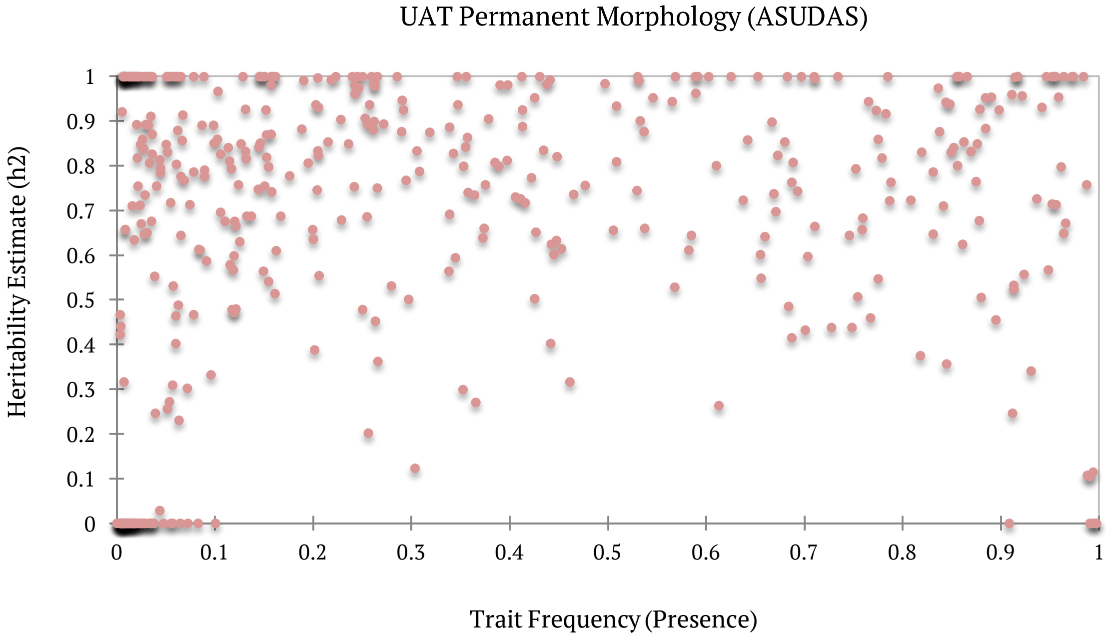


Figure 17. Scatter plot of permanent morphological traits by frequency and heritability estimate.

information collected from a single antimere. Due to the strength of these antimeric correlations, I utilized only maximum expression scores for the following analyses, in part to present results from the largest possible sample (i.e., to increase sample size).

Genetic correlation analyses were conducted only within tooth classes (anterior dentition and postcanine dentition). Deciduous results are presented in Appendix O, Table 3. Results indicate a minimal degree of morphological integration across the deciduous anterior dentition (see also Figs. 18-22), with the exception of the canines. Only one trait pair yielded p-values indicating complete pleiotropy: the canine distal accessory ridge isomeres (c^1 distal accessory ridge-c_1 distal accessory ridge). Incomplete pleiotropy is indicated for five anterior trait pairs; of these character pairs (i^1 labial convexity-c^1 distal accessory ridge, i^2 shoveling-i_2 shoveling, c^1 shoveling-c^1 double shoveling, c^1 double shoveling and c^1 distal accessory ridge, c^1 tuberculum dentale, and c^1 distal accessory ridge) only one does not involve a canine trait: the lateral incisor shoveling isomeres (see Figs. 18-22).

Similarly, results for the postcanine dentition indicate a high degree of developmental modularity underlying deciduous morphological variation (see Appendix O, Table 3; Figs. 19-21). Only one trait pair is completely pleiotropic: m_1 cusp number-m_1 cusp 5. One might intuitively assume strong genetic correlation between these traits, because quantification of one trait directly impacts quantification of the other. Incomplete pleiotropic relationships are indicated for 20 trait pairs, the majority of which are metameric homologues or traits occurring on the same molar (m^1 metacone-m^1 hypocone, m^2 metacone-m^2 cusp 5, m^1 hypocone-m^2 hypocone, m^1 hypocone-m^2 Carabelli's trait, m^2 hypocone-m^2 cusp 5, m^2 hypocone-m^2 Carabelli's trait, m^2 hypocone-m^2 paracone, m^2 cusp 5-m^2 Carabelli's trait, m^2 Carabelli's trait-m^2 paracone, m_2 anterior fovea-m_2 distal trigonid crest, m_2 deflecting wrinkle-m_2 cusp 7, m_2 cusp

5-m_2 distal trigonid crest). All remaining incompletely pleiotropic trait pairs involve the hypocone (m^1 hypocone-m_1 cusp number, m^1 hypocone-m_2 deflecting wrinkle, m^1 hypocone-m_1 cusp 5, m^1 hypocone-m_2 distal trigonid crest, m^2 hypocone-m_2 anterior fovea, m^2 hypocone-m_1 cusp 5, m^2 hypocone-m_2 cusp 5, m^2 paracone-m_2 deflecting wrinkle), which suggests a greater degree of integration for this maxillary molar trait relative to other deciduous characters (see Figs. 18-22). While genetic correlations are both positive and negative across the deciduous trait pairs, of the models that yielded significant p-values (incomplete/complete pleiotropy) correlations were positive with the exception of i^1 labial convexity-c^1 distal accessory ridge, c^1 shoveling-c^1 distal accessory ridge, m^2 metacone-m^2 cusp 5, m^2 hypocone-m_2 anterior fovea, and m_2 cusp 5-m_2 distal trigonid crest (see Figs. 18-20).

Genetic correlations results for the permanent dentition are presented in Appendix O, Table 4. Here, because premolar double shoveling is homologous to a trait that occurs only in the anterior dentition, it is considered an anterior trait. Like the deciduous dentition, the majority of model results suggest a lack of pleiotropy between trait pairs (see Figs. 23-27). In the anterior dentition, complete pleiotropy is indicated for only a single trait pair: C^1 Double Shoveling-P^1 Double Shoveling. These traits are metameric homologues, as are several of the trait pairs for which incomplete pleiotropy is indicated (Appendix O). Nearly all metameric and isomeric homologues are incompletely pleiotropic (*Shoveling*: I^1-I^2, I^1-C^1, I^1-I_2, I^2-C^1, I^2-I_1, I^2-I_2, C^1-I_2, I_1-I_2; *Double Shoveling*: I^1-I^2, I^2-C^1, C^1-P^2, P^1-P^2; *Tuberculum Dentale*: I^1-I^2, I^1-C^1, I^2-C^1; *Distal Accessory Ridge*: C^1-C_1). A number of incomplete pleiotropic relationships occur between traits within the same element (*I^1*: Shoveling-Tuberculum Dentale; *I^2*: Shoveling-Double Shoveling; *C^1*: Shoveling-Double Shoveling, Shoveling-Tuberculum Dentale, Double Shoveling-Distal Accessory Ridge). For the remaining trait pairs characterized as incompletely pleiotropic,

ANTERIOR

	i1 lcv	i1 shov	i2 shov	c shov	i1 dshov	i2 dshov	c dshov	i2 td	c td	c dar
i1 lcv		0.27	-0.08	0.03	-0.25	0.15	0.10	0.10	0.26	-0.41
i1 shov	n		0.17	-0.39	-0.44	0.44	-0.23	0.17	0.26	0.11
i2 shov	n	n		0.09	-0.19	0.17	0.09	0.24	0.10	-0.09
c shov	n	n	n		0.10	-0.21	0.38	-0.13	0.19	-0.39
i1 dshov	n	\	n	n		-0.17	-0.07	-0.01	-0.11	0.01
i2 dshov	n	\	n	\	\		0.23	0.05	-0.11	0.45
c dshov	n	n	n	i	n	n		0.10	-0.18	0.41
i2 td	n	n	n	n	n	n	n		-0.17	0.22
c td	n	n	n	n	n	n	n	n		0.34
c dar	i	n	n	i	n	\	i	n	i	

Figure 18. Genetic correlations for UAT deciduous morphology (ASUDSAS) of the anterior maxillary dentition. Values (above diagonal) are correlation estimates; abbreviations (below diagonal) signify whether significance tests indicate complete (c), incomplete (i), (n) no pleiotropy, or (\) no result. Intensity of green indicates strength of correlation (dark green=>0.60 or <-0.60; intermediate green=0.30 to 0.60 or -0.30 to -0.60; light green=<0.30 and >-0.30) or degree of pleiotropy (dark green=complete; intermediate green=incomplete; light green=none).

POSTCANINE

	m1 meta	m2 meta	m1 hypo	m2 hypo	m2 c5	m2 Ctrait	m2 para
m1 meta		0.08	0.38	0.04	-0.03	0.06	-0.04
m2 meta	n		0.14	0.13	-0.29	0.06	-0.05
m1 hypo	i	n		0.49	0.02	0.35	-0.06
m2 hypo	n	n	i		0.38	0.31	0.28
m2 c5	n	i	n	i		0.25	0.12
m2 Ctrait	n	n	i	i	i		0.38
m2 para	n	n	n	i	n	i	

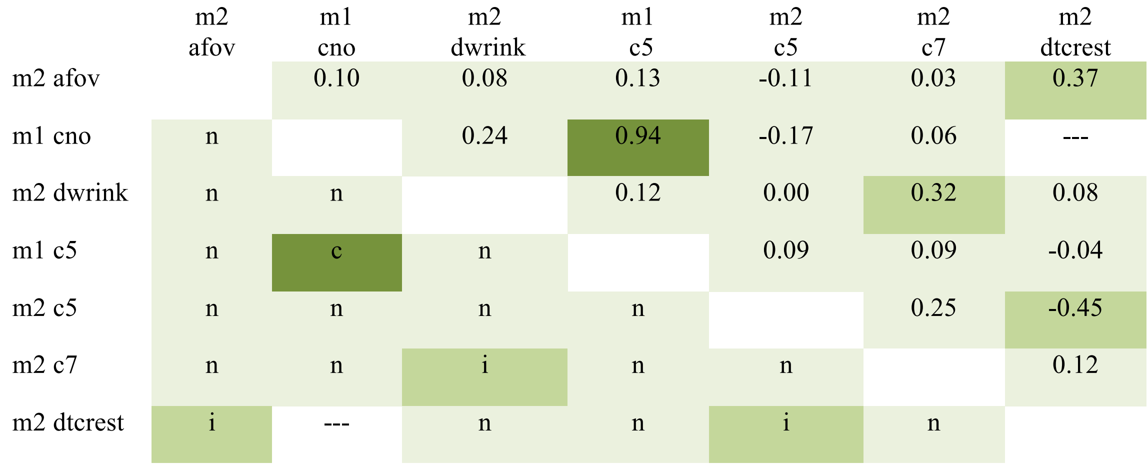
Figure 19. Genetic correlations for UAT deciduous morphology (ASUDSAS) of the postcanine maxillary dentition. Values Values (above diagonal) are correlation estimates; abbreviations (below diagonal) signify whether significance tests indicate complete (c), incomplete (i), or no (n) pleiotropy. Intensity of green indicates strength of correlation (dark green=>0.60 or <-0.60; intermediate green=0.30 to 0.60 or -0.30 to -0.60; light green=<0.30 and >-0.30) or degree of pleiotropy (dark green=complete; intermediate green=incomplete; light green=none).

ANTERIOR

	i1 shov	i2 shov	c dar
i1 shov		0.50	-0.26
i2 shov	\		0.06
c dar	\	n	

Figure 20. Genetic correlations for UAT deciduous morphology (ASUDSAS) of the anterior mandibular dentition. Values (above diagonal) are correlation estimates; abbreviations (below diagonal) signify whether significance tests indicate complete (c), incomplete (i), (n) no pleiotropy, or (\) no result. Intensity of green indicates strength of correlation (dark green=>0.60 or <-0.60; intermediate green=0.30 to 0.60 or -0.30 to -0.60; light green=<0.30 and >-0.30) or degree of pleiotropy (dark green=complete; intermediate green=incomplete; light green=none).

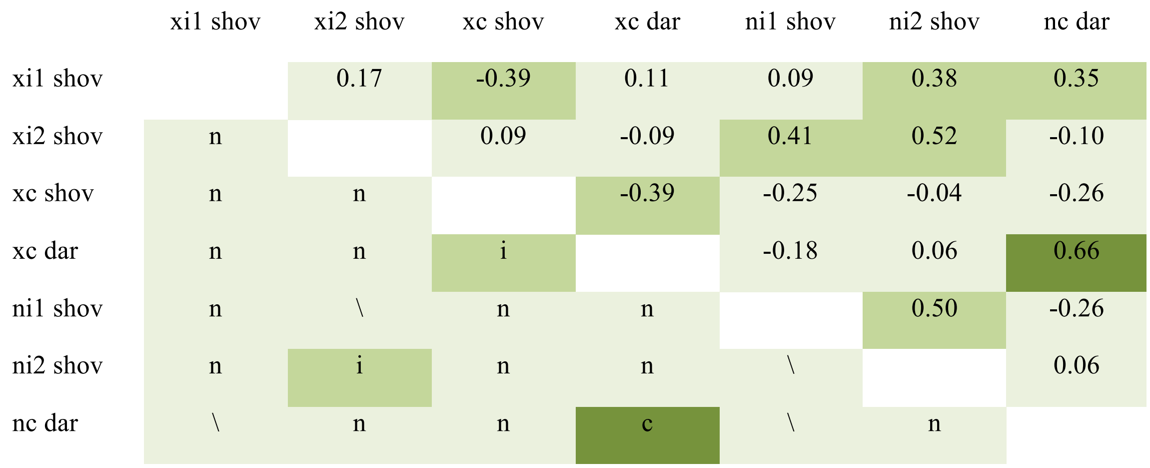
POSTCANINE



	m2 afov	m1 cno	m2 dwrink	m1 c5	m2 c5	m2 c7	m2 dtcrest
m2 afov		0.10	0.08	0.13	-0.11	0.03	0.37
m1 cno	n		0.24	0.94	-0.17	0.06	---
m2 dwrink	n	n		0.12	0.00	0.32	0.08
m1 c5	n	c	n		0.09	0.09	-0.04
m2 c5	n	n	n	n		0.25	-0.45
m2 c7	n	n	i	n	n		0.12
m2 dtcrest	i	---	n	n	i	n	

Figure 21. Genetic correlations for UAT deciduous morphology (ASUDSAS) of the postcanine mandibular dentition. Values (above diagonal) are correlation estimates; abbreviations (below diagonal) signify whether significance tests indicate complete (c), incomplete (i), or no (n) pleiotropy. Intensity of green indicates strength of correlation (dark green=>0.60 or <-0.60; intermediate green=0.30 to 0.60 or -0.30 to -0.60; light green=<0.30 and >-0.30) or degree of pleiotropy (dark green=complete; intermediate green=incomplete; light green=none).

ANTERIOR ISOMERES



	xi1 shov	xi2 shov	xc shov	xc dar	ni1 shov	ni2 shov	nc dar
xi1 shov		0.17	-0.39	0.11	0.09	0.38	0.35
xi2 shov	n		0.09	-0.09	0.41	0.52	-0.10
xc shov	n	n		-0.39	-0.25	-0.04	-0.26
xc dar	n	n	i		-0.18	0.06	0.66
ni1 shov	n	\	n	n		0.50	-0.26
ni2 shov	n	i	n	n	\		0.06
nc dar	\	n	n	c	\	n	

Figure 22. Genetic correlations for UAT deciduous morphological isomeres (ASUDSAS) of the anterior dentition. Values (above diagonal) are correlation estimates; abbreviations (below diagonal) signify whether significance tests indicate complete (c), incomplete (i), (n) no pleiotropy, or (\) no result. Intensity of green indicates strength of correlation (dark green=>0.60 or <-0.60; intermediate green=0.30 to 0.60 or -0.30 to -0.60; light green=<0.30 and >-0.30) or degree of pleiotropy (dark green=complete; intermediate green=incomplete; light green=none).

patterns are more difficult to interpret; however, 11 of these 17 (64.7%) pairs involve the maxillary or mandibular canine (I^1 Labial Convexity-C^1 Shoveling, I^1 Labial Convexity-C^1 Distal Accessory Ridge, I^2 Shoveling-C^1 Tuberculum Dentale, C^1 Shoveling-I^2 Double Shoveling, C^1 Shoveling-P^1 Double Shoveling, C^1 Shoveling-P^2 Double Shoveling, C^1 Shoveling-I^1 Tuberculum Dentale, C^1 Shoveling-I^2 Tuberculum Dentale, I^2 Double Shoveling-C$_1$ Distal Accessory Ridge, P^1 Double Shoveling-C^1 Distal Accessory Ridge, I^2 Tuberculum Dentale-C^1 Distal Accessory Ridge). This is a similar pattern to the one observed in the deciduous dentition, and it suggests a relatively high degree of canine morphological integration (see Figs. 23-27).

Moving onto the permanent postcanine dentition, genetic correlation results suggest a similar degree of developmental modularity, with only three trait pairs sharing a completely pleiotropic relationship (see Figs. 24-26). Each of these pairs involves M_2 Cusp 7: M^1 Paracone-M_2 Cusp 7, M_1 Protostylid-M_2 Cusp 7, and M_1 C7-M_2 C7. While the majority of traits are minimally correlated (no pleiotropy) results indicate incomplete pleiotropy for several trait pairs. Some of these trait pairs represent metameres (*Hypocone*: M^1-M^2, *Carabelli's Trait*: M^1-M^2, *Cusp 5*: M_1-M_2), as well as distinct traits occurring within the same element (*M^1*: Metacone-Hypocone, Metacone-Cusp 5, Hypocone-Cusp 5, Hypocone-Carabelli's Trait, Cusp 5-Carabelli's Trait; *M^2*: Hypocone-Carabelli's Trait; *M_1*: Cusp Number-Cusp 6, Anterior Fovea-Deflecting Wrinkle, Cusp 5-Cusp 6; *M_2*: Cusp Number-Cusp 5) and across isomeres (M^1 Metacone-M_1 Deflecting Wrinkle, M^1 Hypocone-M_1 Cusp Number, M^1 Hypocone-M_1 Cusp 5, M^2 Hypocone-M_2 Cusp 5, M^1 Cusp 5-M_1 Cusp Number, M^1 Cusp 5-M_1 Deflecting Wrinkle, M^1 Cusp 5-M_1 Protostylid, M^1 Paracone-M_1 Cusp Number, M^1 Paracone-M_1 Protostylid). Interestingly, no pleiotropy is indicated for any trait pairs of the second molar isomeres (Appendix O, Table 4). Patterns are difficult to interpret for the remaining trait pairs characterized by incomplete pleiotropy (see Figs. 24-26). Across the permanent dentition, characters are both negatively and positive correlated. However, the majority of models yielding significant p-values (complete or incomplete pleiotropy) indicate positive correlation between traits; the exceptions include those models that involve I^1 Labial Convexity, as well as P^1 Double Shoveling-I_1 Shoveling and M_1 Cusp 5-M_1 Cusp 6 (see Appendix O).

In general, deciduous and permanent homologues are moderately genetically correlated. Results of the genetic correlation analyses are present in Appendix O, Table 5.

Only two of the 29 models that yielded valid results indicate complete pleiotropy (i_1-I_1 shoveling and c_1-C_1 distal accessory ridge), while over half (55.2%) indicate incomplete pleiotropy between homologues. While all shoveling traits (maxillary and mandibular) are incompletely or completely pleiotropic, correlation results for the double shoveling and tuberculum dentale traits only indicate pleiotropy for canine homologues. Despite this outcome, as well as a high degree of canine integration in both the deciduous and permanent dentition, canine distal accessory ridge models only yielded significant p-values for the mandibular homologues. In the postcanine dentition, results were mixed (Appendix O). None of the m2-M2 models suggest pleiotropy for shared characters, with the exception of hypocone and Carabelli's trait. However, metacone and (mandibular) cusp 5 were the only traits for which no pleiotropy was indicated in both the m2-M1 model and m2-M2 model. The majority of homologues are positively correlated, the exceptions being i^1-I^1 and i^2-I^2 double shoveling, as well as m^2-M^2 and m_2-M_2 cusp 5; none of these four models yielded significant p-values (Appendix O).

DISCUSSION

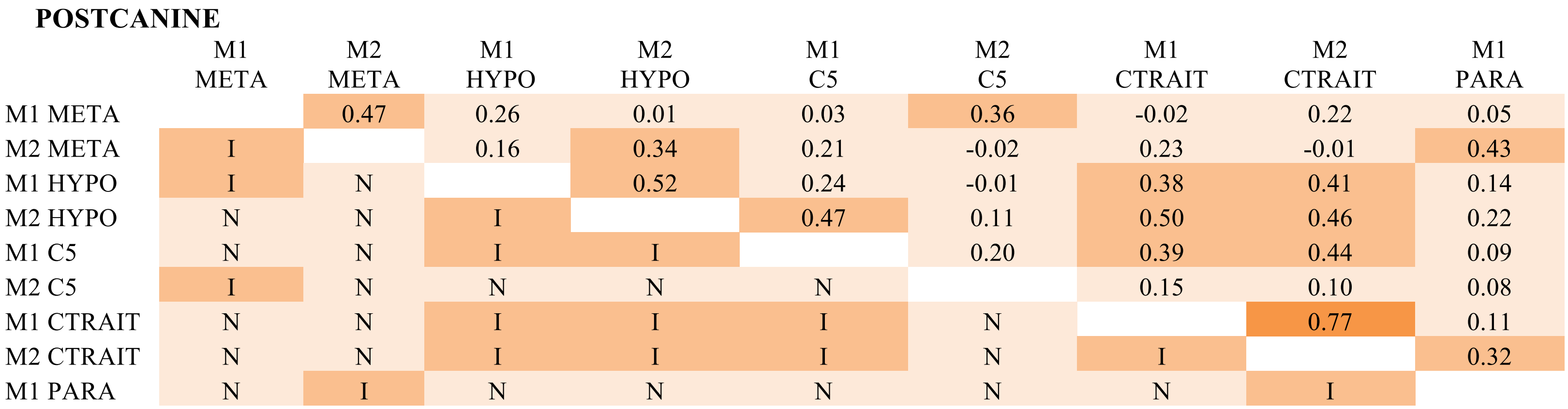
This chapter presents the first comprehensive suite of narrow-sense heritability estimates and genetic correlations for dental morphological characters of the deciduous and permanent human dentition. Results indicate wide-ranging—but, on average, moderate—heritability estimates for these quantitative traits across three bioregionally distinct samples. The high percentage of valid estimates that significantly differ from zero (over 65% of all valid ordinal estimates) led to the rejection of the null hypothesis that nongenetic factors alone contribute to dental morphological correspondence among biological relatives. Further, heritability estimates fall within an expected range. Across the three samples, approximately 70 percent of all valid deciduous estimates (ordinal mixed standards and ASUDAS) fall within the 0.40-0.80 range generally reported for morphology in other samples (Scott and Turner, 1997:164), along with 48 percent of permanent estimates. Not including the BGC models, which have the smallest sample sizes and yielded the greatest number of problematic estimates, approximately 58 percent of permanent estimates fall within the 0.40-0.80 range. For the remainder of this chapter, I will refrain from discussing the BGC estimates, which should be interpreted with caution given their sample size limitations.

Within the UAT and UAY samples, estimate means were approximately equal (range≤0.10) across dentitions and arcades, although permanent mandibular data yielded the lowest average heritability estimate for both samples. This suggests that additive genetic variance accounts for, on average, a relatively consistent amount of morphological variance across the human diphyodont dentition. For all summary statistics presented in the results, UAT averages exceeded UAY averages. Maximum ASUDAS expression data yielded isomeric averages ranging between ~0.51-0.66 for UAT morphology and between ~0.31-0.40 for UAY morphology (deciduous and permanent). The upper ends of the UAT estimate ranges are also higher, with the exception of the deciduous mandibular traits; valid UAT estimates for permanent characters (maximum expression) fail to exceed ~0.69. The lower UAY averages may reflect sample insufficiencies. While the UAY sample is larger than the BGC sample and yielded a greater number of valid estimates, both samples are markedly smaller in size than the UAT sample. Further, the disproportionate number of monozygotic twin pairs

ANTERIOR

	I1 LCV	I1 SHV	I2 SHV	C SHV	I1 DSHV	I2 DSHV	C DSHV	P1 DSHV	P2 DSHV	I1 TD	I2 TD	C TD	C DAR
I1 LCV		0.14	-0.12	-0.57	-0.07	0.03	-0.13	-0.37	-0.10	-0.17	-0.10	-0.10	-0.33
I1 SHV	N		0.63	0.32	-0.04	0.09	0.07	0.03	0.03	0.42	0.21	0.22	0.09
I2 SHV	N	I		0.52	0.13	0.27	0.20	0.02	0.14	0.58	0.07	0.30	0.08
C SHV	I	I	I		0.11	0.39	0.63	0.62	0.47	0.63	0.35	0.43	0.17
I1 DSHV	N	N	N	N		0.31	0.28	0.32	0.32	-0.11	-0.02	0.07	0.08
I2 DSHV	N	N	I	I	I		0.47	0.12	0.23	0.05	0.11	0.15	0.20
C DSHV	N	N	N	I	N	I		0.76	0.65	0.34	0.20	-0.02	0.36
P1 DSHV	I	N	N	I	N	N	C		0.71	-0.15	-0.02	-0.04	0.37
P2 DSHV	N	N	N	I	N	N	I	I		-0.07	0.08	0.14	0.17
I1 TD	N	I	I	I	N	N	N	N	N		0.33	0.46	0.10
I2 TD	N	N	N	I	N	N	N	N	N	I		0.28	0.23
C TD	N	N	I	I	N	N	N	N	N	I	I		0.00
C DAR	I	N	N	N	N	N	I	I	N	N	I	N	

Figure 23. Genetic correlations for UAT permanent morphology (ASUDSAS) of the anterior maxillary dentition. Values (above diagonal) are correlation estimates; abbreviations (below diagonal) signify whether significance tests indicate complete (c), incomplete (i), or no (n) pleiotropy. Intensity of orange indicates strength of correlation (dark orange=>0.60 or <-0.60; intermediate orange=0.30 to 0.60 or -0.30 to -0.60; light orange=<0.30 and >-0.30) or degree of pleiotropy (dark orange=complete; intermediate orange=incomplete; light orange=none).



POSTCANINE

	M1 META	M2 META	M1 HYPO	M2 HYPO	M1 C5	M2 C5	M1 CTRAIT	M2 CTRAIT	M1 PARA
M1 META		0.47	0.26	0.01	0.03	0.36	-0.02	0.22	0.05
M2 META	I		0.16	0.34	0.21	-0.02	0.23	-0.01	0.43
M1 HYPO	I	N		0.52	0.24	-0.01	0.38	0.41	0.14
M2 HYPO	N	N	I		0.47	0.11	0.50	0.46	0.22
M1 C5	N	N	I	I		0.20	0.39	0.44	0.09
M2 C5	I	N	N	N	N		0.15	0.10	0.08
M1 CTRAIT	N	N	I	I	I	N		0.77	0.11
M2 CTRAIT	N	N	I	I	I	N	I		0.32
M1 PARA	N	I	N	N	N	N	N	I	

Figure 24. Genetic correlations for UAT permanent morphology (ASUDSAS) of the postcanine maxillary dentition. Values (above diagonal) are correlation estimates; abbreviations (below diagonal) signify whether significance tests indicate complete (c), incomplete (i), or no (n) pleiotropy. Intensity of orange indicates strength of correlation (dark orange=>0.60 or <-0.60; intermediate orange=0.30 to 0.60 or -0.30 to -0.60; light orange=<0.30 and >-0.30) or degree of pleiotropy (dark orange=complete; intermediate orange=incomplete; light orange=none).

ANTERIOR

	I1 SHOV	I2 SHOV	C DAR
I1 SHOV		0.81	0.08
I2 SHOV	I		0.08
C DAR	N	N	

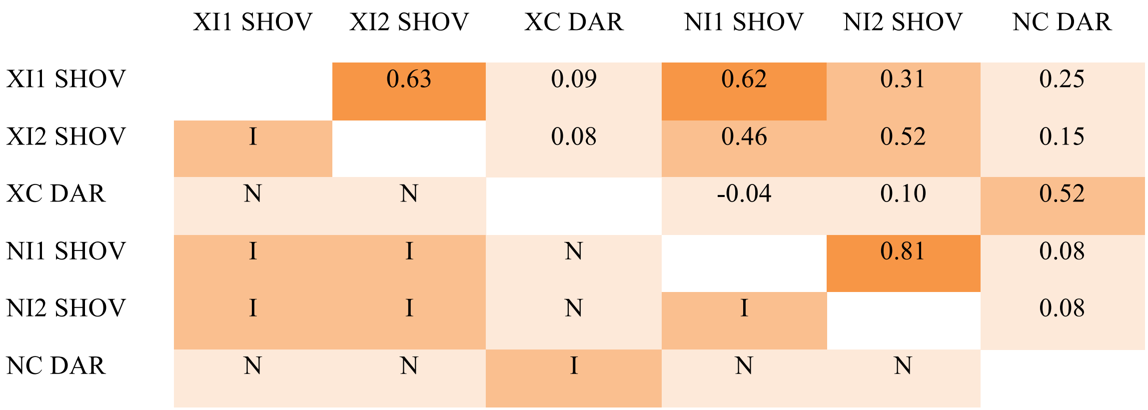
Figure 25. Genetic correlations for UAT permanent morphology (ASUDSAS) of the anterior mandibular dentition. Values (above diagonal) are correlation estimates; abbreviations (below diagonal) signify whether significance tests indicate complete (c), incomplete (i), or no (n) pleiotropy. Intensity of orange indicates strength of correlation (dark orange=>0.60 or <-0.60; intermediate orange=0.30 to 0.60 or -0.30 to -0.60; light orange=<0.30 and >-0.30) or degree of pleiotropy (dark orange=complete; intermediate orange=incomplete; light orange=none).

POSTCANINE

	M1 CNO	M2 CNO	M1 AFOV	M1 DWRINK	M1 PSTY	M1 C5	M2 C5	M1 C6	M1 C7	M2 C7
M1 CNO		0.12	0.05	0.21	0.26	0.17	0.04	0.82	0.09	0.61
M2 CNO	N		0.23	0.38	0.24	0.30	0.96	-0.05	0.12	-0.29
M1 AFOV	N	N		0.26	0.05	0.09	0.16	0.09	-0.02	0.36
M1 DWRINK	N	I	I			-0.12	0.24	0.35	-0.12	0.15
M1 PSTY	N	N	N	N		0.19	0.40	0.09	0.35	0.85
M1 C5	N	I	N	N	N		0.43	-0.27	-0.01	-0.04
M2 C5	N	I	N	N	I	I		-0.14	0.12	-0.02
M1 C6	I	N	N	N	N	I	N		0.07	0.73
M1 C7	N	N	N	N	N	N	N	N		0.86
M2 C7	\	\	\	\	C	\	N	\	C	

Figure 26. Genetic correlations for UAT permanent morphology (ASUDSAS) of the postcanine mandibular dentition. Values (above diagonal) are correlation estimates; abbreviations (below diagonal) signify whether significance tests indicate complete (c), incomplete (i), (n) no pleiotropy, or (\) no result. Intensity of orange indicates strength of correlation (dark orange=>0.60 or <-0.60; intermediate orange=0.30 to 0.60 or -0.30 to -0.60; light orange=<0.30 and >-0.30) or degree of pleiotropy (dark orange=complete; intermediate orange=incomplete; light orange=none).

ANTERIOR ISOMERES



	XI1 SHOV	XI2 SHOV	XC DAR	NI1 SHOV	NI2 SHOV	NC DAR
XI1 SHOV		0.63	0.09	0.62	0.31	0.25
XI2 SHOV	I		0.08	0.46	0.52	0.15
XC DAR	N	N		-0.04	0.10	0.52
NI1 SHOV	I	I	N		0.81	0.08
NI2 SHOV	I	I	N	I		0.08
NC DAR	N	N	I	N	N	

Figure 27. Genetic correlations for UAT permanent morphological isomeres (ASUDSAS) of the anterior dentition. Values (above diagonal) are correlation estimates; abbreviations (below diagonal) signify whether significance tests indicate complete (c), incomplete (i), or no (n) pleiotropy. Intensity of orange indicates strength of correlation (dark orange=>0.60 or <-0.60; intermediate orange=0.30 to 0.60 or -0.30 to -0.60; light orange=<0.30 and >-0.30) or degree of pleiotropy (dark orange=complete; intermediate orange=incomplete; light orange=none).

present in the UAT sample may have led to the artificial inflation of certain estimates. While SOLAR accounts for the presence of monozygotic twin pairs in pedigreed samples, the program often flags values exceeding 0.90, indicating that their presence may lead to overestimation. Researches have long suspected that twin-based estimates likely represent the high end of a typical heritability range (e.g., Hughes et al., 2000; Stojanowski et al., nd); the results presented in this chapter may provide support for this hypothesis.

Another possibility is that the lower UAY estimates are not methodological artifacts, but products of endogamy and/or relatively high environmental variance. Low narrow-sense heritability can result from two factors: 1) low population-level additive genetic variance, and/or 2) high population-level environmental variance (Stojanowski et al., nd). It is possible that both factors are at work in the UAY sample. The Yuendumu Warlpiri Aboriginal population was isolated and lived a traditional nomadic lifestyle prior to moving onto a government settlement during the years preceding the initiation of the University of Adelaide's longitudinal study (Brown et al., 2011). The population was relatively small and endogamous, free of non-Aboriginal admixture, and characterized by complex, matrilineally-structured genealogies (Brown et al., 2011). Warlpiri individuals belonged to one of eight male or female moieties or "skin" name kin groups (Meggitt, 1962; Brown et al., 2011). Indeed, the multi-generational pedigrees included in this study involve a number of half-sibling relationships and more distant biological relationships. Further, the Yuendumu longitudinal study captured a transitional period in Warlpiri lifestyle and culture. A dramatic shift in living conditions occurred throughout the 1950s and 1960s that involved intensified sedentism, increased wages, more reliable access to water, and increased consumption of low-protein/carbohydrate-based foods such as flour, sugar, and processed bread (Brown and Barrett, 1973b; Brown et al., 2011). While these lifestyle changes likely ensured more consistent access to resources, the transition to settlement life was almost certainly accompanied by an increase in (at a minimum) intergenerational environmental variance. Because maternal factors (health, gestational determinants, etc.) affect offspring phenotype (Garn et al., 1979, 1980; Heikkinen et al., 1992; Apps et al., 2004), increased environmental variance in the adult generation, alone, may account for the relatively low heritability estimates obtained for both deciduous and permanent characters in the Yuendumu sample.

In the same vein, the morphology heritability estimates presented in this chapter are lower than those generated for odontometric characters in previous studies of the UAT and UAY samples. An earlier quantitative genetic study of UAT deciduous crown size yielded heritability estimates ranging from 0.62-0.93 (Hughes et al., 2000). Dempsey and Townsend (2001) also found UAT permanent crown size to be strongly influenced by additive genetic effects (h^2 range=0.56-0.92). Many of these estimates exceeded 0.80 (Dempsey and Townsend, 2001; Hughes et al., 2000), which is markedly higher than the mean estimate for UAT crown morphology presented in this chapter. This pattern of higher heritability estimates for crown size applies to the UAY sample, as well. On average, additive genetic variance was shown by Townsend (1980) to account for 58 percent of deciduous crown size variance (md=50%, bl=66%) and 64 percent of permanent crown size variance (MD=63%, BL=66%), as compared to approximately 30 to 40 percent of crown morphology variance across the deciduous and permanent dentitions (see Results). While it has long been assumed that additive genetic effects exert greater influence on crown size than morphological variation, this has never before been confirmed using a broad suite of traits in bioregionally distinct samples. The results presented in this chapter offer support for this assumption, however, it should be noted that individual character estimates varied greatly. Further, I have only discussed the summary statistics for ordinal character expression; indeed, several binary characters (dichotomized ordinal expression) yielded estimates exceeding those obtained for the original ordinal characters. I also highlight the interpretive limitations inherent to heritability meta-analyses. For example, the current study and previous UAT/UAY quantitative genetic studies employed distinct analytical approaches, further complicating the direct comparison of metric and morphological estimates within samples.

As previously discussed in Chapters 3 and 4, researchers have long posited that deciduous phenotypes may offer a better representation of latent genetic information due to their developmental environment (mainly in-utero) (Saunders and Mayhall, 1982; Smith and Tillier, 1989; Smith et al., 1997; Paul and Stojanowski, 2015, 2017; Paul et al., 2017; cf., Guatelli-Steinberg et al., 2006). Deciduous teeth mineralize in-utero, with most crowns fully formed at the time of birth (Kraus, 1959; Kraus and Jordan, 1965; Lunt and Law, 1974; Smith, 1991; Liversidge and Molleson, 2004). They also form quickly (within two to three years), which leaves less time for environmental factors to act upon phenotypic character expression; permanent odontogenesis spans approximately six-seven years, with all teeth mineralizing postnatally (Ubelaker, 1978; Smith, 1991; Liversidge and Molleson, 1999). While heritability estimates are completely unbounded to environmental intervention, the relative dearth of external (i.e., non-maternal or non-gestational) environmental effects at play during deciduous crown formation may result in the diminished contribution of environmental variance and, in turn, increased contribution of additive variance to primary character expression.

The results presented in this chapter do not fully negate this hypothesis, nor do they fully negate the null hypothesis tested in this chapter—that the relative contribution of additive genetic variance to phenotypic variance is equal for deciduous and permanent homologues. In actuality, it is impossible to reject the null hypothesis, as the broad standard error ranges ensure that homologue estimates failed to differ in any statistically significant manner. However, the results should be considered on a trait-by-trait basis. Only one third of deciduous characters yielded higher heritability estimates than their permanent homologues in the UAT sample; these included c^1 shoveling and double shoveling, as well as m^2 hypocone and Carabelli's trait. This is an interesting result given the degree of morphological integration observed for the deciduous canine and molars—specifically, hypocone expression (see discussion of genetic correlation results below). It is also intriguing considering that UAY c^1 shoveling/double shoveling and m^2 hypocone follow an opposite pattern. Across both samples, a general trend is apparent—in the maxilla, deciduous postcanine homologues yield higher heritability estimates, and in the mandible permanent postcanine homologues yield higher heritability estimates. A biological explanation for this trend is not immediately apparent, but as many of the postcanine characters represent accessory features/cusps, further exploration of these trends within the framework of the patterning cascade model might shed light on the role of morphogenesis and cusp configuration (enamel knot placement) in directing patterns of intra- and inter-individual morphological variation (e.g., Paul et al., 2017).

Based on the results presented in this chapter researchers can confidently integrate deciduous morphology into biodistance datasets. A significant portion of (most) deciduous character variance is attributable to additive genetic variance, and heritability estimates for a number of deciduous traits equal or exceed those for their permanent homologues. That said, researchers must carefully decide how to quantify primary trait expression; dental anthropology's premier morphological scoring system (the ASUDAS) was designed only for observation on permanent tooth crowns (Turner et al., 1991; Buikstra and Ubelaker, 1994). The results presented in this chapter indicate that researchers can apply ASUDAS standards to deciduous characters of the anterior dentition, with the exception of c^1 tuberculum dentale, which yielded higher heritability estimates when quantified under the mixed deciduous scoring standards. The consistency of these results across the UAT and UAY samples bolsters this finding. Conversely, mixed deciduous standards yield higher heritability estimates for deciduous postcanine traits in the UAT and UAY samples, with few exceptions (UAY m^2 hypocone/cusp number and UAT m^2 Carabelli's trait). These findings suggest that the most productive data collection protocol for biodistance research would integrate deciduous morphology using ASUDAS scoring for anterior tooth traits (except c^1 tuberculum dentale) and mixed deciduous standards for postcanine tooth traits. This methodology would ensure that the resulting phenotypic dataset captures that greatest portion of crown variance attributable to additive genetic variance, adhering to the foundational assumptions of biodistance analysis. It should be noted that, as with most comparisons in this study, it was impossible to formally reject the null hypothesis—that additive genetic effects contribute equally to phenotypic expression quantified under the mixed standards and ASUDAS—given the standard error ranges associated with the heritability estimates.

The results presented in this chapter also inform preanalytical "best practices" in biodistance research, specifically with respect to reducing the dimensionality of phenotypic datasets. Overall, antimeric patterns of heritability suggest researchers are justified in reducing left and right side scores to a single maximum expression value for deciduous morphology data. For the deciduous dentition, approximately 70 percent of valid comparisons showed the maximum expression score to yield the highest heritability estimate. For four of these traits, the maximum expression estimates significantly exceeded the left and/or right side estimates, leading to a rejection of the null hypothesis (that additive genetic effects contribute equally to phenotypic expression across antimeres) in each instance. A more complex pattern was observed for the permanent morphology. The highest heritability estimates were almost equally distributed across left side, right side, and maximum expression scores for permanent characters. Again the null hypothesis was rejected only in select cases (<20%), with no easily interpretable biological patterns across the UAT or UAY datasets. These permanent heritability results do not immediately indicate a "most appropriate" best practice for data winnowing. Based on these results, biodistance analysts might be best served by randomly selecting antimeric expression for each character (although left side expression yielded the high estimate in the greatest number of comparisons). This approach would be justified given the results presented in this chapter and would curtail potential biases. Notwithstanding, given that using the antimeric maximum also serves to increase trait sample size, researchers should weigh the benefits of these differing approaches.

The results of this study also have implications for biodistance methodology (i.e., data collection, preanalysis data treatment) related to dichotomization. Trends in heritability across dichotomization breakpoints within ordinal variables suggest a high degree of variation across traits, elements, and antimeres. In certain cases, dichotomization at an optimal breakpoint resulted in the new binary character's heritability estimate exceeding the original ordinal estimate. For dental anthropologists interested in optimizing the genetic representation of their morphology dataset, Appendix N might offer specific trait-by-trait guidance on a breakpoint selection. However, one must consider the provenience of the dataset from which these results were obtained;

breakpoint heritability estimates were only compared within the UAT sample, which is comprised of European-Australians. It is possible that these trends would differ in samples of distinct ancestry or biological admixture, as populations vary considerably in their morphological trait frequencies.

Further probing of UAT breakpoint trends focused on the relationships between heritability estimates (for the dichotomized characters) and population frequency. While a significant positive relationship between heritability and frequency was established for only the suite of permanent morphological traits analyzed, a clear pattern was observed for the deciduous dentition: heritability estimates only approach extreme values (~0.0 or ~1.0) when sample frequency values approach 0.0 or 1.0. (In the permanent dentition, this pattern is less clear, because select traits with moderate frequency values yielded heritability estimates of 1.0.) This finding is unsurprising given that heritability is directly quantified as a ratio of variances. If a trait's sample frequency approaches 0.0 or 1.0, this indicates low levels of phenotypic variance, which can inflate heritability estimates or lead to incalculable/problematic model parameter estimates. The range of heritability estimates is relatively restricted for traits in the middle (~0.3-0.7) of the frequency range, with most exceeding 0.4. This suggests that dental anthropologists should dichotomize ordinal traits at breakpoints where sample frequencies are within this middle range where the additive genetic contribution to character variance is more stable and relatively elevated. However, these results should be validated in additional samples of distinct ancestry and/or bioregional affiliation before drawing more generalized conclusions about biodistance methodology.

Morphological Integration in the Human Dentition

Genetic correlation results for the UAT sample suggest a high degree of morphological integration across antimeres, with most estimates equaling or approaching 1.0. Derived phenotypic correlations for antimerically paired characters are also high. These results validate the standard biodistance practice of using only a single antimeric data point to represent trait expression within an individual. Combined with insights generated from side-specific heritability estimates, the findings indicate that by using the maximum expression score (deciduous) or including left/right side expression at random (permanent), researchers might minimize genetic redundancy while maximizing the representation of the dataset's latent genetic structure.

Within tooth classes, deciduous and permanent morphology are minimally integrated. In the deciduous anterior dentition, canine morphology is the one exception. Canine morphology is involved in all but one of the observed instances of anterior pleiotropy, and canine distal accessory ridge isomeres are the only completely pleiotropic traits. The deciduous postcanine dentition exhibits a similar degree of developmental modularity, with only a single completely pleiotropic trait pair (m_1 cusp number-m_1 cusp 5). The majority of traits that share an incomplete pleiotropic relationship are metameres, occur on the same tooth crown, or involve the hypocone. These results have a number of implications for biodistance research. First, c^1 distal accessory ridge and c_1 distal accessory ridge should not be included in the same phenotypic dataset, regardless of the strength of their phenotypic correlation; the same goes for m_1 cusp number and m_1 cusp 5. These characters are influenced by the same genes or set of genes, and therefore add redundant genetic information to a biodistance analysis. Second, while standard phenotypic correlations may indicate no relationship between metameres or between traits occurring on a single crown, the genetic correlations capture a degree of integration for these traits that might undermine the assumption of genetic independence for a traditional multivariate dental dataset. This affirms a common practice in dental anthropology and biodistance analysis; it justifies the use of data from only a single metamere for traits that occur on multiple crowns along the tooth row. Third, hypocone expression and canine morphology data should be integrated into multivariate datasets with caution, given the relatively high degree of morphological integration observed for these characters.

High levels of developmental modularity are also suggested for permanent morphology. For the anterior dentition, only C^1 Double Shoveling and P^1 Double Shoveling are influenced by identical genes. In the postcanine dentition, all completely pleiotropic trait pairs involve M_2 C7. Ultimately, these trait pairs should not be included in the same multivariate biodistance dataset due to their overlapping representation of underlying genotypic information. Incomplete pleiotropy is primarily restricted to metameric and isomeric homologues or to traits occurring on the same tooth crown. As in the deciduous dentition, most remaining incidences of permanent morphological pleiotropy involve the canine. This suggests a pattern of relatively high morphological integration for the canine that spans the primary and secondary dentition. Researchers should exercise caution in selecting canine traits and metameric/isomeric homologues for biodistance analysis, as at least some of their variance is influenced by the same genes.

As compared to previous genetic correlation analyses of crown size, the results presented in this chapter indicate low levels of integration for crown morphology. For the deciduous dentition, average maxillary correlations (anterior=0.04, postcanine=0.14) and mandibular correlations (anterior=0.10, postcanine=0.10) are lower than previously reported averages for metric correlations in Cercopithecoids and humans (humans: maxillary=0.63, mandibular=0.69; baboons: maxillary=0.30, mandibular=0.20) (see Hlusko et al., 2001; Stojanowski et al., nd). Permanent morphological correlations are typically within the range of Cercopithecoid crown size correlations, although on average they fall well below human metric correlations in both the maxilla (anterior=0.18, postcanine=0.24) and mandible (anterior=0.32, postcanine=0.21). Further, several morphological correlations are negative. Negative genetic correlations were only obtained for certain mandibular trait pairs in previous studies of baboon crown size (Hlukso et al., 2011) and for none of the trait pairs in previous studies of human crown size (Stojanowski et al., nd). These results are not unsurprising given the number of ordinal trait combinations analyzed, as well as the complexity of morphological characters, which manifest as grooves, cuspules, divots, and ridges and occur on all sides of the tooth crown.

Finally, this dissertation is the first to present a suite of genetic correlations for deciduous and permanent morphological homologues, thus probing the complex architecture of the human diphyodont dentition. Deciduous and permanent morphology is moderately integrated with over half of the homologue pairs exhibiting some degree of pleiotropy and two traits exhibiting complete pleiotropy. This suggests that the same genes/set of genes act on paired deciduous and permanent elements to the degree that there is moderate morphological correspondence for a majority of discrete traits. The lack of pleiotropy for m2-M2 trait pairs (with few exceptions) is unsurprising, given that M2 is not the permanent replacement tooth for m2. On average, the deciduous/permanent homologue correlations (maxillary=0.27, mandibular=0.32) are higher than the deciduous within-class correlations and permanent within-class correlations. This pattern is only strengthened by removing correlation estimates for m2-M2 pairs; when these values are omitted, the mean homologue correlations increase to 0.31 (maxillary) and 0.55 (mandibular). Further, none of the models with significant values yielded negative genetic correlations between homologues. The results imply, on average, a stronger genetic mechanism for morphological conservation across the diphyodont dentition than within individual tooth rows.

Before broad species- and order-wide patterns can be elucidated, further validation work is required in additional samples. The genetic correlations presented in this chapter were generated using a European-Australian sample, which is characterized by unique morphological trait frequencies and variances. This sample also includes a disproportionately large number of monozygotic twins, which may artificially inflate model parameter estimates. The morphological and metric correlation comparisons are also tenuous, as previous crown size correlation studies employed data collected from an African American Gullah sample and from a captive baboon colony. Additionally, the morphological correlations were calculated solely from maximum antimeric expression data for ordinal variables. An important next step is calculating genetic correlations for binary variables (i.e., ordinal variables dichotomized at optimal breakpoints), as some biodistance analysts employ only binary variables in their applied research.

CONCLUSION

In this chapter, I presented novel estimates of narrow-sense heritability and genetic correlation for a suite of deciduous and permanent morphological characters. Results suggest wide-ranging but moderate heritability for human crown characters, as well as low to moderate integration for morphological characters within (deciduous-deciduous, permanent-permanent) and across (deciduous-permanent) dentitions. Heritability estimates fall within the expected range based on previous studies, however genetic correlation results are difficult to contextualize given the paucity of quantitative genetic research focused on non-continuous morphological characters. That said, human dental morphology is generally characterized by a higher degree of developmental modularity than crown size (see Stojanowski et al., nd). This chapter interprets these results within the framework of biodistance research, prescribing potential “best practices” based on comparative heritability estimates across antimeres, across dentitions, across scoring standards, and across dichotomization breakpoints. Overall, results validate the use of dental morphology as a proxy for underlying genetic information, including deciduous morphology, which has been underutilized in biodistance research.

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CHAPTER 6

CONCLUSION

Kinship, an essential component of collective social identity, is complexly related to childhood. This crucial period of development is often characterized by physical, social, and emotional dependence on close relatives, and, as such, is complexly related to the multiscalar dimensions of family identity (Carsten, 2000; Jenkins, 2008; Johnson and Paul, 2016). The ability to identity potential biological relatives in archaeological contexts is essential to ancient kinships research; for this task, dental data are often recruited. Where DNA fails to preserve, heritable crown traits are used as proxies for latent genetic information. However, deciduous dental data are typically omitted from these analyses, which means that children are less visible in reconstructions of the biological and social structure of ancient communities, as well as perspectives on the conceptualization and experience of family, relatedness, and lineage in deep time.

This dissertation addresses the standard omission of subadults—and specifically deciduous dental datasets—from biodistance studies by using pedigreed samples to explore the foundations of deciduous crown variation. Here, I review the project's overarching goal and each chapter's specific research objectives. I then summarize the major findings and their application to dental anthropology and bioarchaeology. The dissertation closes with an overview of how these findings lay the groundwork for fruitful avenues for future research.

The dissertation's overarching goal is to generate a knowledge-based infrastructure for incorporating deciduous dental data into biodistance research. This involved three distinct research objectives:

1) Evaluate the performance of deciduous crown morphology data in the reconstruction of documented genealogical relationships. Performance is assessed from a comparative perspective (referencing phenotypic distances) and from a simulated bioarchaeological perspective (referencing relative affinity via visualization approaches).
2) Compare the performance of deciduous and permanent morphology in reconstructing genealogical relationships in a matched set of individuals. Performance is assessed using the same informal comparative (pair-wise distance) and simulated bioarchaeological (distance ordination and multidimensional scaling) approaches. Deciduous and permanent morphological distances are also directly compared to genetic distances calculated from relatedness coefficients.
3) Outline a comprehensive "blueprint" for the genetic architecture underlying the human diphyodont dental complex. This involves calculating trait-specific, narrow-sense heritability estimates for deciduous and permanent morphological characters, as well as genetic correlations between deciduous traits, between permanent traits, and between deciduous and permanent homologues. Patterns of heritability and genetic correlation within and across dentitions are evaluated with a

focus on biodistance applications, specifically with respect to refining data collection standards and analytical approaches.

Summary of Results

In Chapter 3 "performance" was introduced as an alternative to narrow-sense heritability as a gauge of character utility in genealogy reconstruction. The chapter focused specifically on deciduous crown morphology in a sample of subadults of documented pedigree (Burlington Grown Study sample). I evaluated performance as the degree to which close biological relatives were phenotypically similar with respect to the entire sample, referencing pairwise Euclidean distances and multidimensional scaling output (via distance ordination). Pairwise phenotypic distances were averaged across nuclear families and sibling pairs and compared to non-relative distance averages via bootstrap resampling. Results indicate that the average phenotypic distance between siblings is significantly smaller than the average phenotypic distance between non-relatives ($p<0.001$) and smaller than expected by chance ($p<0.001$). However, a number of family-specific results deviate from this trend. MDS output indicates fairly strong aggregation of biological relatives, as families occupy 3.9% of available multidimensional sample space, on average. The results affirm the value of multivariate deciduous morphology datasets for identifying biological relatives within broader samples of unrelated individuals.

In Chapter 4, the performance of deciduous and permanent morphology was directly compared in a matched set of pedigreed individuals (Burlington Growth Study sample). The same analytical procedures employed in Chapter 3 were applied to a permanent morphological dataset and results were compared. Average inter-sibling distances generated from the permanent dataset are smaller than phenotypic distances between non-relatives (p<0.001) and smaller than expected by chance (p<0.001). Again, family-specific distance results vary. However, most families (~75%) are more widely dispersed across multidimensional sample space when represented by permanent morphological distances. While Mantel test results confirm significant positive relationships between genetic distances and a) deciduous phenotypic distances and b) permanent phenotypic distances, the magnitude of correlation is greater for the deciduous dataset. Therefore, all informal metrics indicate that deciduous crown morphology reflects underlying genetic information with greater fidelity than permanent crown morphology. The findings suggests that in-utero development leads to diminished environmental intervention in phenotypic character expression and/or overall greater conservation of underlying genetic signals in the deciduous teeth. The results encourage the integration of these characters into biodistance data collection protocols.

Chapter 5 presented quantitative genetic analyses of the human diphyodont dental complex—specifically, crown morphology—in three distinct samples (Burlington Growth Study sample, University of Adelaide Twin Study sample, and University of Adelaide Yuendumu Aboriginal Growth Study sample). Narrow-sense heritability and genetic correlation estimates were generated for the complete suite of deciduous and permanent crown characters, which facilitated comparisons between samples, traits, dentitions, arcades, antimeres, metameres, scoring standards, and dichotomization breakpoints. Results indicate wide-ranging but moderate heritability estimates for morphological traits, as well as low to moderate integration for characters within (deciduous-deciduous; permanent-permanent) and between (deciduous-permanent) dentitions. In Chapter 5, specific heritability estimate comparisons were interpreted with respect to biodistance methodology and prescribed “best practices”. Importantly, the deciduous and permanent canines are characterized by a relatively high degree of within-element, within-class, and cross-arcade genetic integration; this may suggest that the canine plays a stabilizing role in the anterior dentition, despite delayed development and eruption sequences relative to the incisors. On average, deciduous and permanent homologues are more strongly genetically correlated than characters within the same tooth row, which indicates a strong degree of morphological conservation between succedaneous elements in the human diphyodont dentition.

Future Directions

Ultimately, the dissertation empirically validates the use of dental morphology as a proxy for underlying genetic information, including deciduous crown characters. Still, the findings raise a number of questions related to the biological foundations of dental variation and encourage continued study of pedigreed cast samples. Building upon the results presented in this dissertation, four avenues of future research are envisioned.

The first avenue of research centers on distance statistic calculation and refining biodistance methodology. This involves an integration of the quantitative genetic findings into biodistance data collection and analytical protocols. The author is currently in the process of developing a centralized deciduous morphology data collection protocol and reference plaque system that incorporates mixed deciduous standards and ASUDAS standards based on insights from quantitative genetic analyses. Increasing the visibility of deciduous morphology scoring standards might encourage researchers to incorporate subadults into ancient kinship research. The results of the quantitative genetic analyses presented in this dissertation can also be applied to exploratory research focused on refining phenotypic distance calculation. For example, heritability estimates and genetic correlations can be used to improve preanalysis data treatment procedures. This dissertation prescribes "best practices" based on comparative heritability results (e.g., antimeric data selection, optimized dichotomization breakpoints, intercorrelated trait removal); an important next step is to adopt these standards in simulated biodistance analyses to determine if/how they improve the performance of dental datasets in identifying known relatives. Further, newly-generated heritability estimates can be used as weighting factors in multivariate dental datasets, potentially allowing for the calculation of more sensitive distance metrics. An important next step is testing this hypothesis in performance analyses of dental datasets collected from samples of known pedigree. These research initiatives are essential to addressing the disconnect between genome- and phenome-level analyses, as phenotypic datasets have yet to approach the resolution offered by genetic kinship studies that exploit variation at numerous polymorphic loci (Rogers and Harpending, 1983; Edge and Rosenberg, 2015a, 2015b).

A second area of continuing research is quantitative genetic validation work. Because morphological trait frequencies vary between distinct bioregional samples, it is important to confirm patterns of heritability and genetic correlation in several samples prior to identifying patterns unique to the human species. Further, previous research has shown Cercopithecoid and human patterns of tooth size integration to differ (e.g., Hlusko et al., 2011; Stojanowski et al., nd). For this reason, additional quantitative genetic studies of primate dental characters are required before order-wide patterns can be elucidated. This research initiative will shed light on the foundations of primate dental variation and the conservation of genetic signals across (regions of) the dentition and, more broadly, across primate taxa.

A third avenue of future research focuses on determinants of dental variation beyond additive genetic effects (i.e., genes/sets of genes), including environment, development, and epigenetics. In quantitative genetic models, error variance is almost certainly correlated across individuals, because relatives often develop within similar environments and full siblings share similar uterine/maternal effects. However, quantitative genetic research rarely probes the "black box" of environment; specific environmental factors are almost never identified in the course of these analyses. Future research might apply documented environmental, behavioral, and medical history data in quantitative genetic analyses of dental phenotypes (i.e., via structural equation modeling/genetic covariance structure models) to estimate the relative contribution of genetic and environmental variables to character variation within large pedigreed samples. Shared and unique environmental influence can thus be directly modeled using empirical data (Rosa et al., 2011; Franić et al., 2012) to identify specific factors/sets of factors that contribute to dental trait expression. For example, family and individual health history data were curated as part of the Burlington Growth Study, but sample size/structure preclude the estimation of these more nuanced models as part of the dissertation. Beyond genes and environment, the field of epigenetics provides insight into the developmental and "mechanical" gene expression foundations of human variation. An important next step in outlining the determinants of tooth crown variation involves broad-scale genome-wide association studies (GWAS) for human crown morphology in pedigreed collections that also include cheek swabs/genetic samples, as well as the exploration of epigenetic modifications at implicated quantitative trait loci (QTLs). These data can be applied to quantitative and wet-lab based studies exploring the epigenetic bases of dental variation (for reviews of emerging research see Townsend and Brook, 2014; Williams et al., 2014; Yong et al., 2014; Seo et al., 2015). Results have the potential to refine models of the human dental complex and to impact the fields of dental anthropology, clinical dentistry, and the evolutionary sciences.

The last critical avenue of future research involves real-world biodistance application. Now that a number of foundational biodistance assumptions have been empirically validated, deciduous dental data can be more fully integrated into bioarchaeological and forensic research. Incorporating deciduous phenotypes into biodistance datasets will facilitate the representation of children, a critical demographic subsample of most bioarchaeological assemblages, in reconstructions of ancient community structure and social group composition. This marks a crucial next step in operationalizing a bioarchaeology of children and childhood (see Perry, 2005, 2006; Lewis, 2007; Halcrow and Tayles, 2011; Tompson et al., 2014)—an emerging area of broader anthropological interest (Lancy, 2008; Montgomery, 2009)—as well as in enhancing the visibility of this crucial period of the human (biological) life course and (social) lived experience in deep time. The results presented in this dissertation might also impact forensic anthropology by helping to refine methods for identifying child victims where physical remains are badly degraded and only dental material preserves. Young children rarely undergo durable corrective procedures; therefore identification based upon deciduous dental matches relies on the morphology of the tooth crowns (e.g., Schuller-Götzburg and Suchanek, 2007). Future research will focus on improving forensic efforts to identify missing children through the establishment of crown variants that are accurate markers of biological affiliation in additional human samples, as well as by improving analytical approaches for estimating positive identification.

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APPENDIX A

AUTHOR CONTRIBUTIONS

Chapter 2 of the dissertation was adapted from the publication “Bioarchaeology and Kinship: Integrating Theory, Social Relatedness, and Biology in Ancient Family Research”, which was published in the Journal of Archaeological Research (2016). This paper was coauthored by the author of this dissertation and Kent M. Johnson. Dr. Johnson has granted his permission for a modified version of the paper to be included as a chapter in this dissertation.

Chapters 3 and 4 of this dissertation were adapted from the publications “Performance Analysis of Deciduous Morphology for Detecting Biological Siblings” and “Comparative Performance of Deciduous and Permanent Dental Morphology in Detecting Biological Relatives”, which were published in the American Journal of Physical Anthropology (2015 and 2017, respectively). These papers were coauthored by the author of this dissertation and Christopher M. Stojanowski. Dr. Stojanowski has granted his permission for a modified version of the paper to be included as a chapter in this dissertation.

APPENDIX B

IRB AND RESEARCH ETHICS STATEMENT

All research protocols were reviewed and granted exemption by Arizona State University's Institutional Review Board (Study 00002779) pursuant to Federal Regulation 45CFR46 (4). Research protocols were also approved by Dr. Bryan Tompson and the Burlington Growth Centre (University of Toronto, Faculty of Dentistry) and University of Adelaide's Human Research Ethics Committee and the Craniofacial Biology and Dental Education Research Group (Project H-27-1990). To ensure subject anonymity, all individuals in the dissertation sample were recoded using a unique numbering system, and all sensitive information was suppressed.

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APPENDIX C

MORPHOLOGICAL TRAIT ABBREVIATION KEY

Morphological trait abbreviation key.

Abbreviation	Trait	Notes
WING	Winging	
L(AB) CVX/ LCURVE (CV)	Labial Convexity	Or *Labial Curvature*
SHOV/ SHV	Shoveling	
DSHOV/DSHV	Double Shoveling	
TD	Tuberculum Dentale	
MES RIDGE/ MRIDGE	Mesial Ridge	Extreme, *Bushman Canine*
DAR	Distal Accessory Ridge	
UTO AZ	Uto-Aztecan Premolar	Or *Distosagittal Ridge*
ODONT	Odontome	
META	Metacone	
HYPO	Hypocone	
CARABELLI/ CTRAIT	Carabelli's Trait	Or *Carabelli's Cusp*
PARA	Parastyle	
DOUBLE	Double Teeth	Due to fusion or gemination
DELTA FORM	Delta form	
LING CUSP	Lingual Cusp Variation	
ANT FOVEA/AFOV	Anterior Fovea	
DWRINK	Deflecting Wrinkle	
PSTYLID	Protostylid	
GROOVE	Groove Pattern	
DTCREST	Distal Trigonid Crest	
CNO	Cusp Number	Or *Cusp Number* (dm^1) Or *Crown Pattern* (dm^2)
C5	Cusp 5	Or *Metaconule* (maxillary) Or *Hypoconulid* (mandibular)
C6	Cusp 6	Or *Entoconulid* Or *Tuberculum Sextum*
C7	Cusp 7	Or *Metaconulid* Or *Tuberculum Intermedium*
PEG	Peg-Shaped	Minimal expression, *reduced*
CONG ABS	Congenital Absence	

APPENDIX D

DECIDUOUS PERFORMANCE ANALYSIS:

TRAIT REMOVAL TABLE

Deciduous morphological variables removed from the performance analysis, scoring standards, and reason for removal.

Morphological Variables[a]	Primary Standards	Secondary Standards[b]	Reason for Omission[c]
SHOVEL i^1	Hanihara (1963)	Turner et al. (1991)	< 40 Observations
SHOVEL i^2	Hanihara (1963)	Turner et al. (1991)	Inter-trait Correlation
SHOVEL c^1	Hanihara (1963)	Turner et al. (1991)	Inter-trait Correlation
DOUBLE SHOVEL i^1	Sciulli (1998)	Turner et al. (1991)	Sex Correlation
TUBERCULUM DENTALE i^1	Grine (1986)	Turner et al. (1991)	<40 Observations
TUBERCULUM DENTALE i^2	Grine (1986)	Turner et al. (1991)	<40 Observations
TUBERCULUM DENTALE c^1	Grine (1986)	Turner et al. (1991)	Error; Sex Correlation
MESIAL RIDGE c^1	Irish and Morris (1996)	Turner et al. (1991)	Inter-trait Correlation
HYPOCONE m^1	Hanihara (1963)[d]	Turner et al. (1991)	Inter-trait Correlation
PARASTYLE m^1	Turner et al. (1991)		Inter-trait Correlation
PEG/REDUCED i^2	Turner et al. (1991)		Monomorphic
SHOVEL i_1	Hanihara (1963)	Turner et al. (1991)	<40 Observations
SHOVEL i_2	Hanihara (1963)	Turner et al. (1991)	Inter-trait Correlation
DOUBLE TEETH i_1	Sciulli (1998)		Monomorphic
DOUBLE TEETH i_2	Sciulli (1998)		Monomorphic
DOUBLE TEETH c	Sciulli (1998)		Monomorphic
DISTAL ACCESSORY RIDGE c_1	Turner et al. (1991)		Sex Correlation
DELTA FORM m_1	Dahlberg (1949)		Monomorphic
CUSP NUMBER m_1	Lease (2003)	Turner et al. (1991)	Inter-trait Correlation
PROTOSTYLID m_1	Turner et al. (1991)		Inter-trait Correlation
CUSP 6 m_1	Turner et al. (1991)		Monomorphic
CUSP 7 m_1	Turner et al. (1991)		Inter-trait Correlation
ANTERIOR FOVEA m_1	Turner et al. (1991)[e]		Error
ANTERIOR FOVEA m_2	Turner et al. (1991)		Inter-trait Correlation
DISTAL TRIGONID CREST m_2	Turner et al. (1991)		Sex Correlation
CUSP 5 m_2	Sciulli (1998)[f]	Turner et al. (1991)	Sex Correlation

[a] Maxillary and mandibular arcades are indicated by superscripts and subscripts, respectively. [b] A number of morphological variables were scored according to multiple published standards. Here, the standards listed as “primary” are those designed for observation and data recording on deciduous teeth. The standards listed as “secondary” are those adapted from permanent dental morphology observation and data recording standards. [c] Reason for omission through pre-analysis data treatment. [d] Augmented from Dahlberg (1949) and referred to as “crown pattern of the deciduous upper second molar” in Hanihara (1961) or “cusp number, hypocone of maxillary first deciduous molar” in Hanihara (1963). [e] Original trait standards augmented for observation on the first molar, but removed due to a lack of precision in data recording. [f] Trait expression dichotomized and referred to as “hypoconulid of the mandibular second deciduous molar” in Sciulli (1998).

APPENDIX E

DECIDUOUS PERFORMANCE ANALYSIS:

FAMILY-SPECIFIC MDS PLOTS (DECIDUOUS MORPHOLOGY)

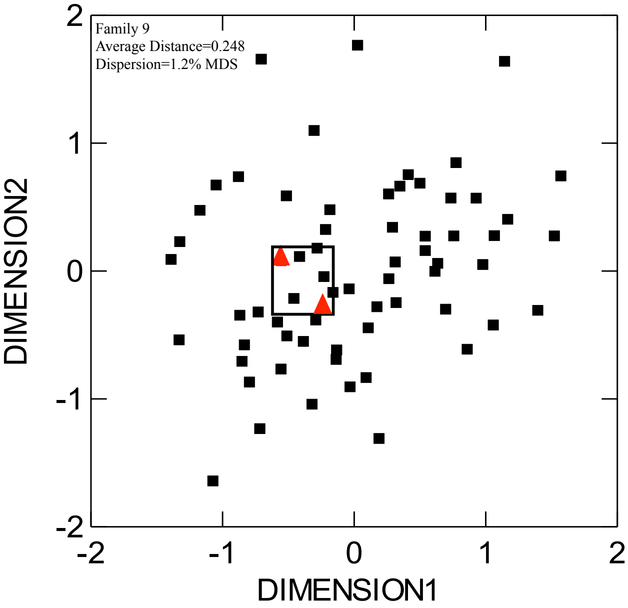


Figure 1. Family 9 MDS plot, with siblings marked in red and multidimensional space occupied (Family 9 Area) enclosed in a rectangle (relative dispersion = 1.2%).

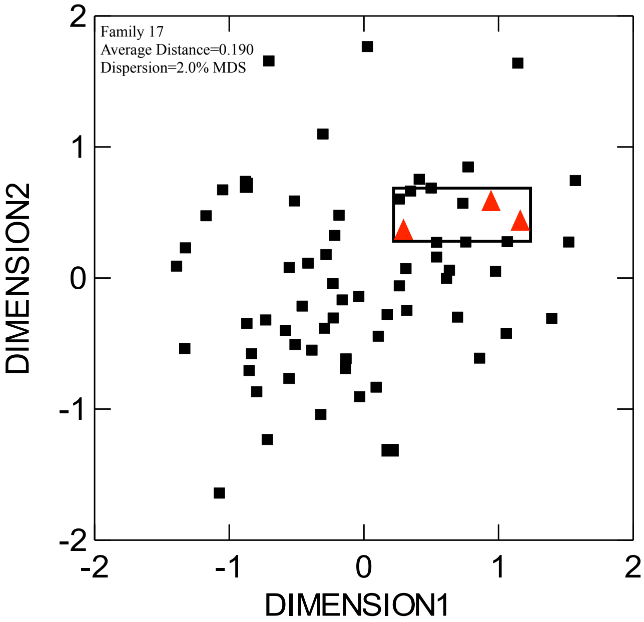


Figure 2. Family 17 MDS plot, with siblings marked in red and multidimensional space occupied (Family 17 Area) enclosed in a rectangle (relative dispersion = 2.0%).

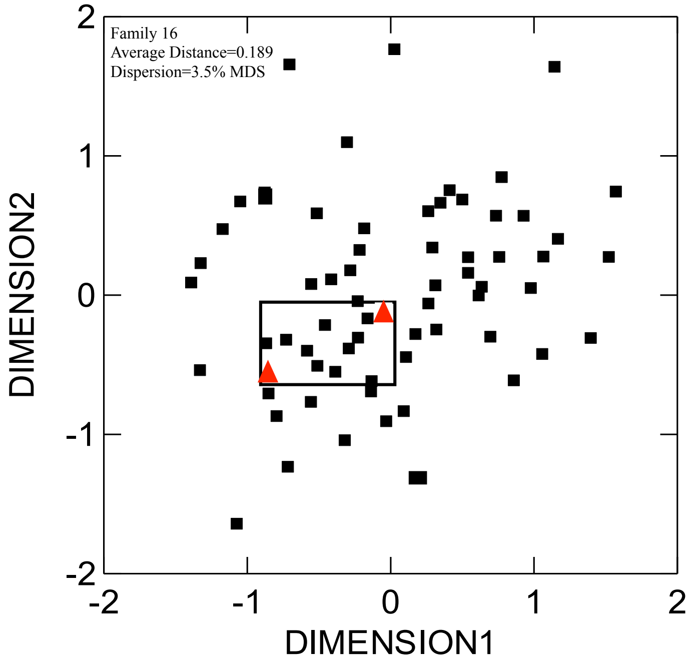


Figure 3. Family 16 MDS plot, with siblings marked in red and multidimensional space occupied (Family 16 Area) enclosed in a rectangle (relative dispersion = 3.5%).

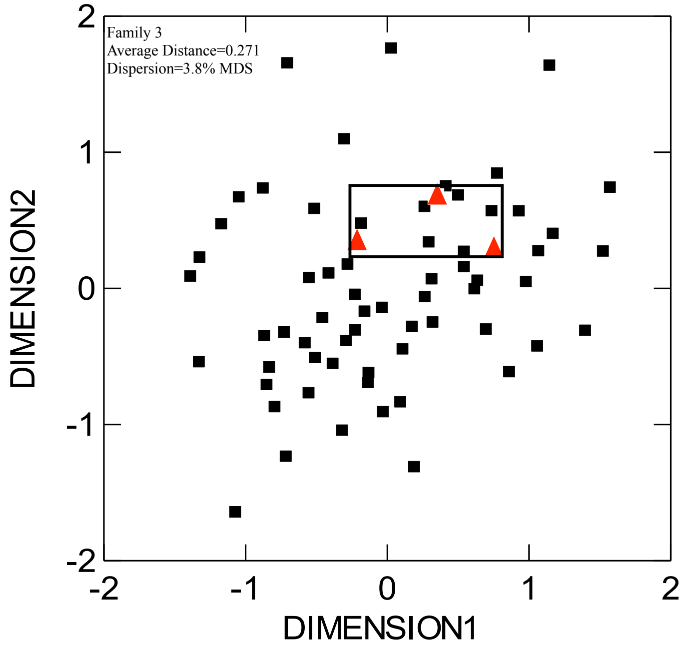


Figure 4. Family 3 MDS plot, with siblings marked in red and multidimensional space occupied (Family 3 Area) enclosed in a rectangle (relative dispersion = 3.8%).

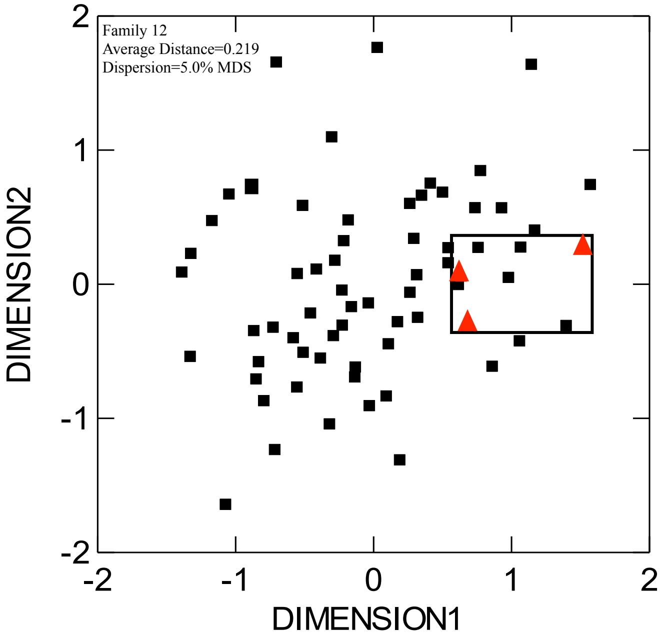


Figure 5. Family 12 MDS plot, with siblings marked in red and multidimensional space occupied (Family 12 Area) enclosed in a rectangle (relative dispersion = 5.0%).

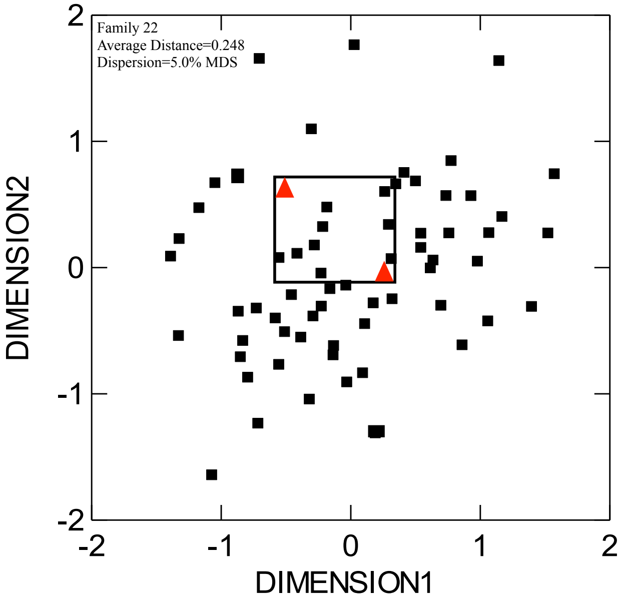


Figure 6. Family 22 MDS plot, with siblings marked in red and multidimensional space occupied (Family 22 Area) enclosed in a rectangle (relative dispersion = 5.0%).

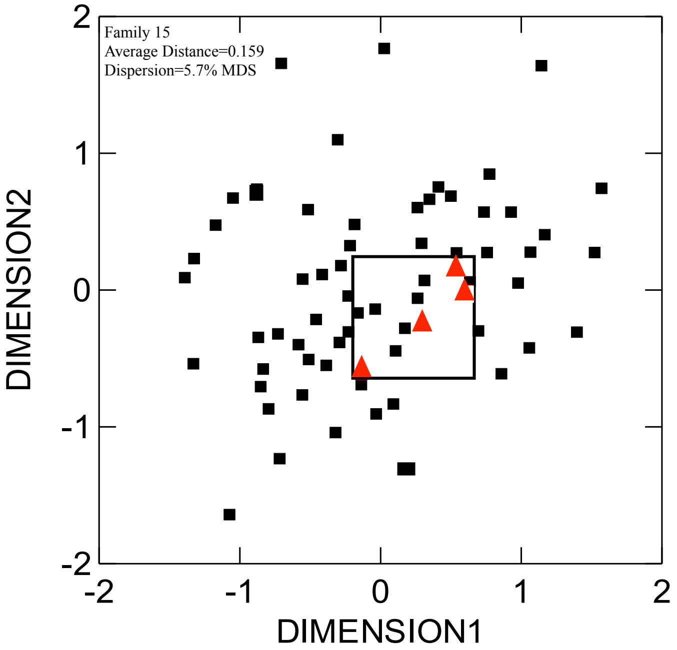


Figure 7. Family 15 MDS plot, with siblings marked in red and multidimensional space occupied (Family 15 Area) enclosed in a rectangle (relative dispersion = 5.7%).

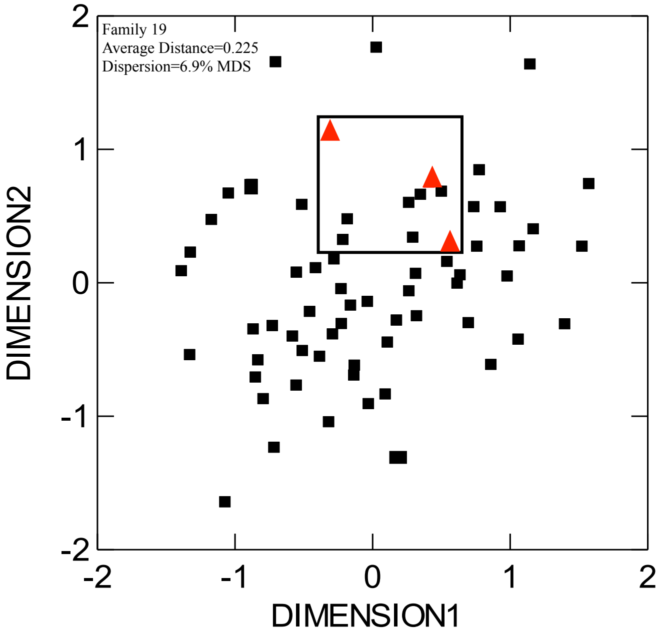


Figure 8. Family 19 MDS plot, with siblings marked in red and multidimensional space occupied (Family 19 Area) enclosed in a rectangle (relative dispersion = 6.9%).

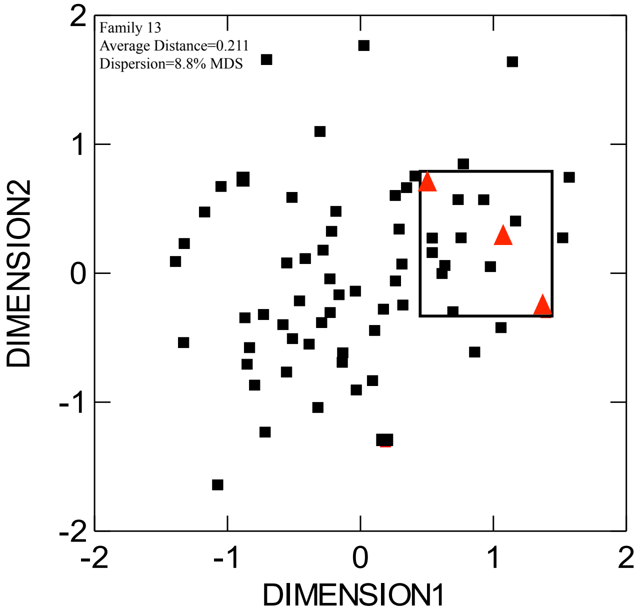


Figure 9. Family 13 MDS plot, with siblings marked in red and multidimensional space occupied (Family 13 Area) enclosed in a rectangle (relative dispersion = 8.8%).

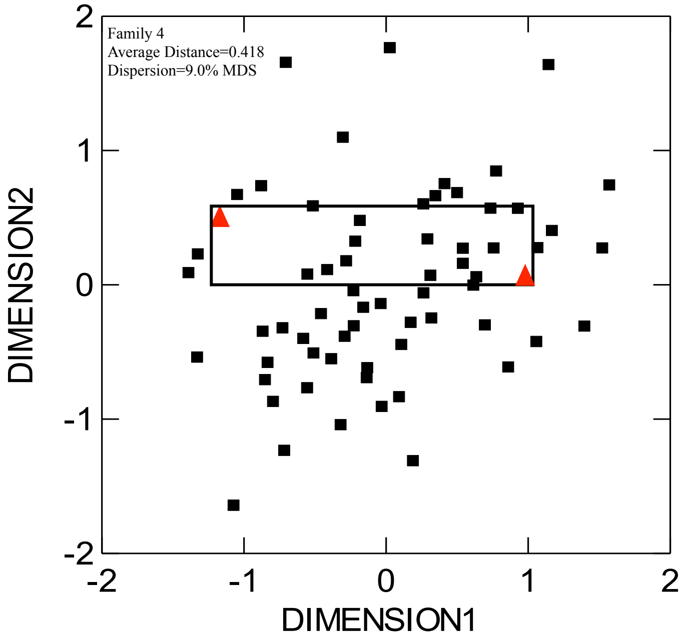


Figure 10. Family 4 MDS plot, with siblings marked in red and multidimensional space occupied (Family 4 Area) enclosed in a rectangle (relative dispersion = 9.0%).

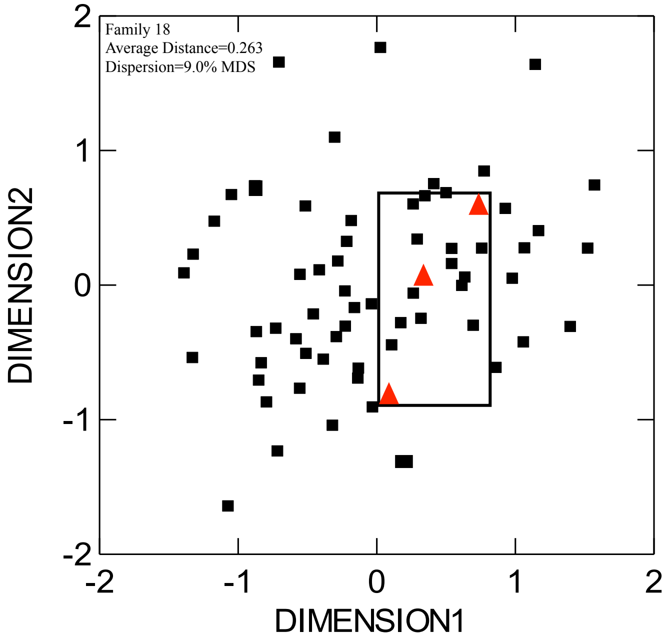


Figure 11. Family 18 MDS plot, with siblings marked in red and multidimensional space occupied (Family 18 Area) enclosed in a rectangle (relative dispersion = 9.0%).

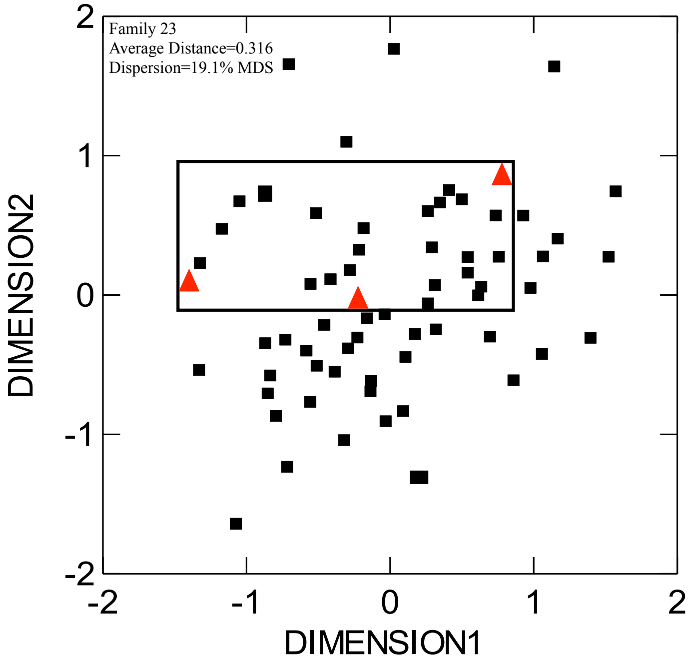


Figure 12. Family 23 MDS plot, with siblings marked in red and multidimensional space occupied (Family 23 Area) enclosed in a rectangle (relative dispersion = 19.1%).

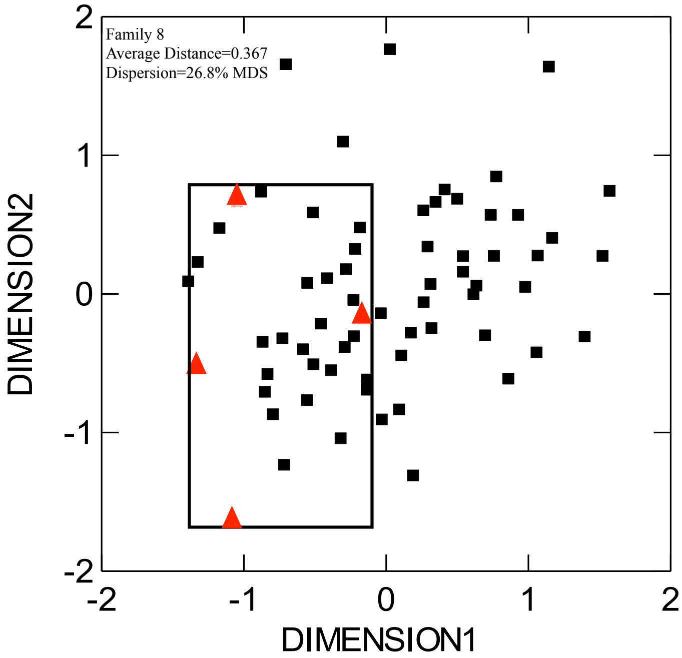


Figure 13. Family 8 MDS plot, with siblings marked in red and multidimensional space occupied (Family 8 Area) enclosed in a rectangle (relative dispersion = 26.8%).

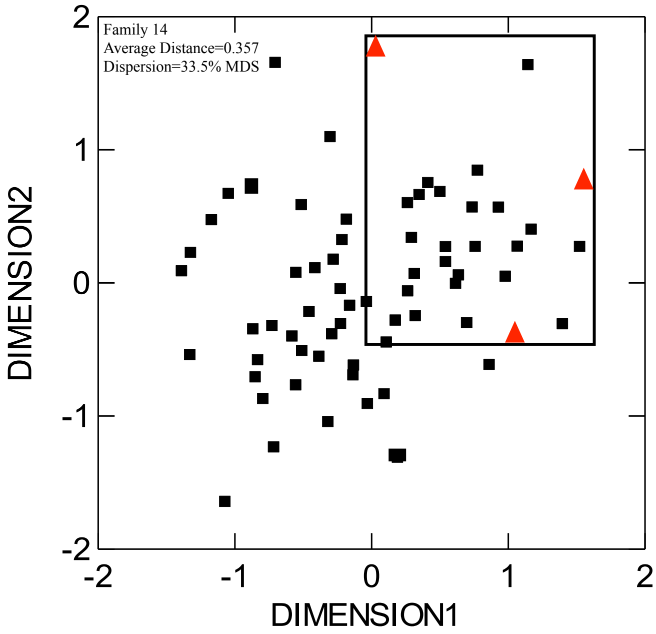
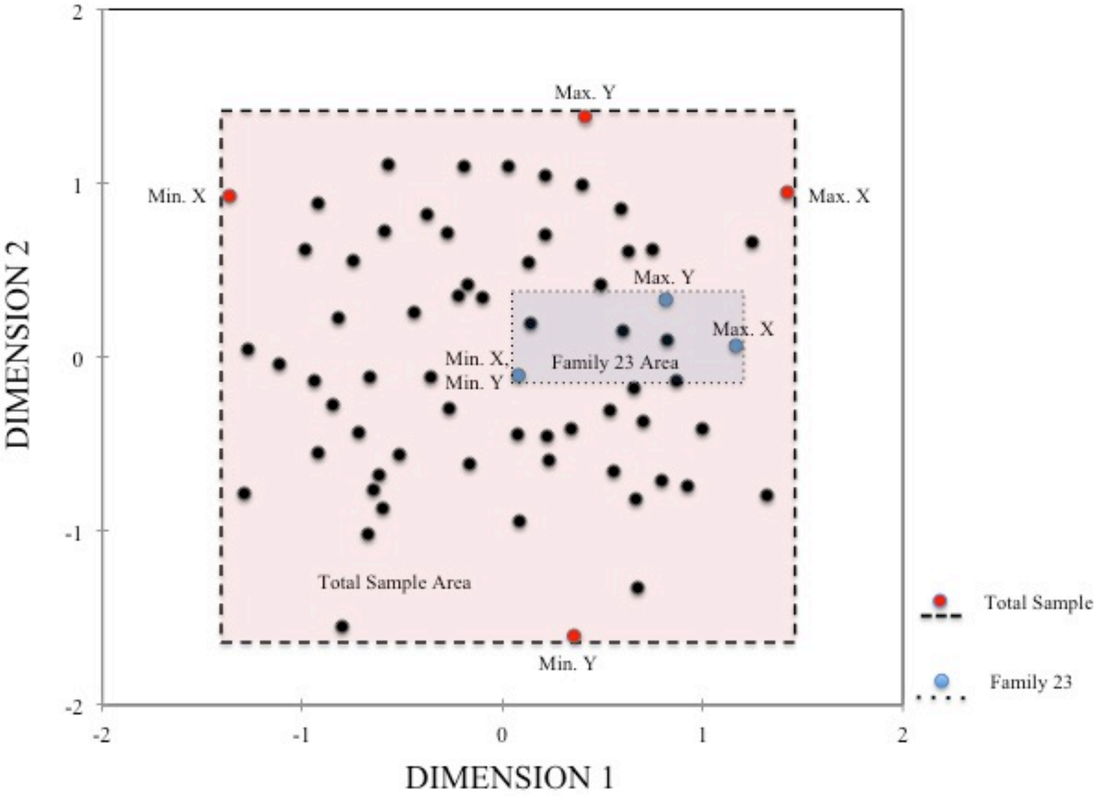


Figure 14. Family 14 MDS plot, with siblings marked in red and multidimensional space occupied (Family 14 Area) enclosed in a rectangle (relative dispersion = 33.5%).

APPENDIX F

COMPARATIVE PERFORMANCE ANALYSIS:

SAMPLE MDS PLOT



Sample MDS plot highlighting Family 23's (blue) dispersion or multidimensional space occupied relative to the multidimensional space occupied by the total Burlington Growth Study sample (red). Points in color represent those peripheral MDS coordinates used to calculate the multidimensional space occupied (area) for both Family 1 and the total sample.

APPENDIX G

COMPARATIVE PERFORMANCE ANALYSIS:

MORPHOLOGY SCORE CONVERSION GUIDELINES

Traits scaled for deciduous and permanent comparison and associated conversion guidelines.

Morphological Trait *Elements Compared*[a]	Deciduous Grades[b]	Permanent Grades[c]	Scaled Grades
SHOVEL			
i^1 *versus* I^1	0	0	0
i^2 *versus* I^2	1	1, 2	1
c^1 *versus* C^1	2	3, 4	2
i_1 *versus* I_1	3	5, 6	3
i_2 *versus* I_2		7 (omitted)	
DOUBLE SHOVEL			
i^1 *versus* I^1	0	0	0
i^2 *versus* I^2	1, 2, 3	1, 2, 3, 4, 5, 6	1
c^1 *versus* C^1			
TUBERCULUM DENTALE			
i^2 *versus* I^2	0	0	0
c^1 *versus* C^1	1, 2, 3	1, 2, 3, 4, 5-	1
	4	5, 6	2
DISTAL ACCESSORY RIDGE			
c^1 *versus* C^1	0	0	0
c_1 *versus* C_1	1	1	1
	2	2	2
	3	3	3
	4	4, 5	4
HYPOCONE (CUSP NUMBER)			
m^2 *versus* M^1	0	0	0
	3+A	1	1
	3+B	2	2
	4-	3, 3.5	3
	4	4, 5	4
CUSP 5			
m^2 *versus* M^1	0	0	0
	1	1, 2, 3, 4, 5	1
CARABELLI'S TRAIT			
m^2 *versus* M^1	0	0	0
	1	1, 2	1
	2	3, 4	2
	3	5, 6	3
	4	7	4

CUSP NUMBER			
m_2 versus M_1	4	4	1
	5	5	2
	6	6	3
	7	7	4
	8	8	5
HYPOCONULID			
m_2 versus M_1	0	0	0
	1	1, 2, 3, 4, 5	1
DEFLECTING WRINKLE			
m_2 versus M_1	0	0	0
		1 (omitted)	
	1	2, 3	1
PROTOSTYLID			
m_2 versus M_1	0	0	0
		1, 2 (omitted)	
	1	3, 4, 5	1
	2	6, 7	2
CUSP 7			
m_2 versus M_1	0	0	0
	1	1	1
	2	1A	2
	3	2	3
	4	3	4
	5	4	5

---

[a] Maxillary and mandibular arcades are indicated by superscripts and subscripts, respectively. Deciduous elements are denoted by lowercase script; permanent elements are capitalized.

[b] Deciduous morphological traits were scored according to various published standards (Hanihara, 1963; Grine, 1986; Sciulli, 1998; Lease 2003; see Paul and Stojanowski, 2015 Supplemental Table 1 for a list of scoring standards by trait). The scoring standards yielding data that corresponded to less within-sample variation for a given trait (i.e. that were excluded from the analysis) are listed in the final column of the table.

[c] Permanent morphological traits scored according to Arizona State University Dental Anthropology System standards (Turner et al., 1991). Certain expression grades were omitted where no equivalent variants exist in the deciduous homologues.

APPENDIX H

COMPARATIVE PERFORMANCE ANALYSIS:

FAMILY-SPECIFIC MDS PLOTS (PERMANENT MORPHOLOGY)

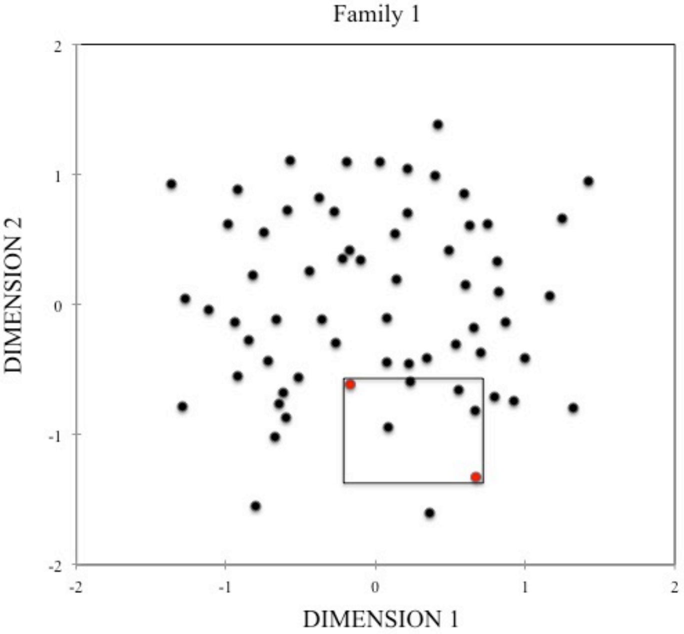


Figure 1. Family 1 MDS plot, with siblings marked in red and multidimensional space occupied (Family 1 Area) enclosed in a rectangle (relative dispersion = 7.3%).

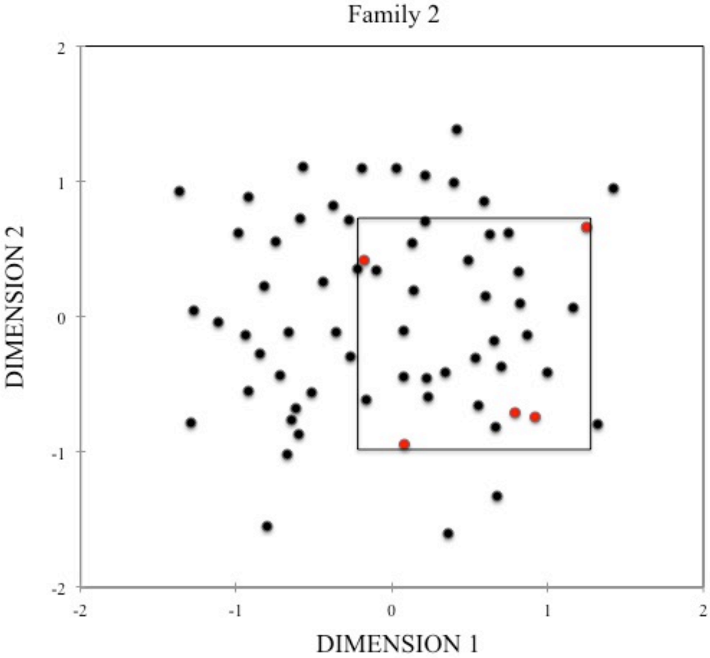


Figure 2. Family 2 MDS plot, with siblings marked in red and multidimensional space occupied (Family 2 Area) enclosed in a rectangle (relative dispersion = 27.7%).

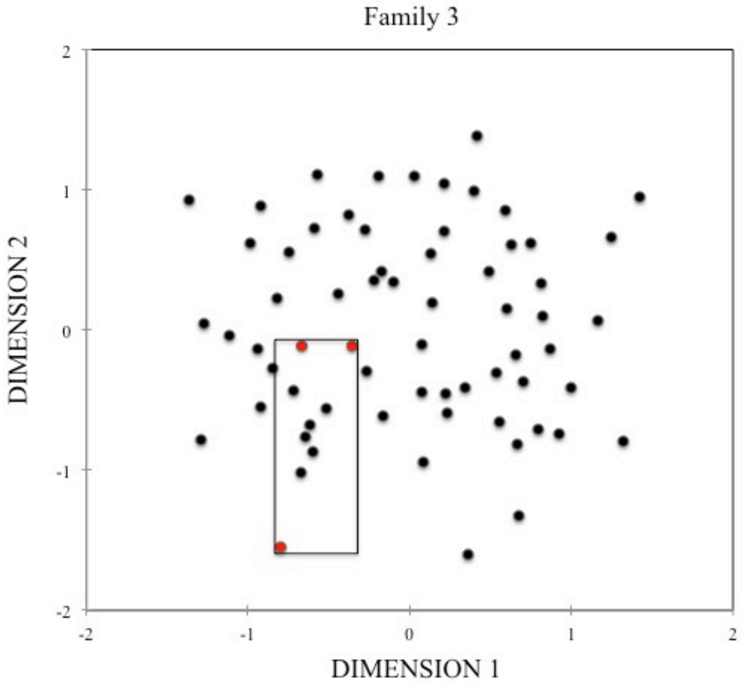


Figure 3. Family 3 MDS plot, with siblings marked in red and multidimensional space occupied (Family 3 Area) enclosed in a rectangle (relative dispersion = 7.7%).

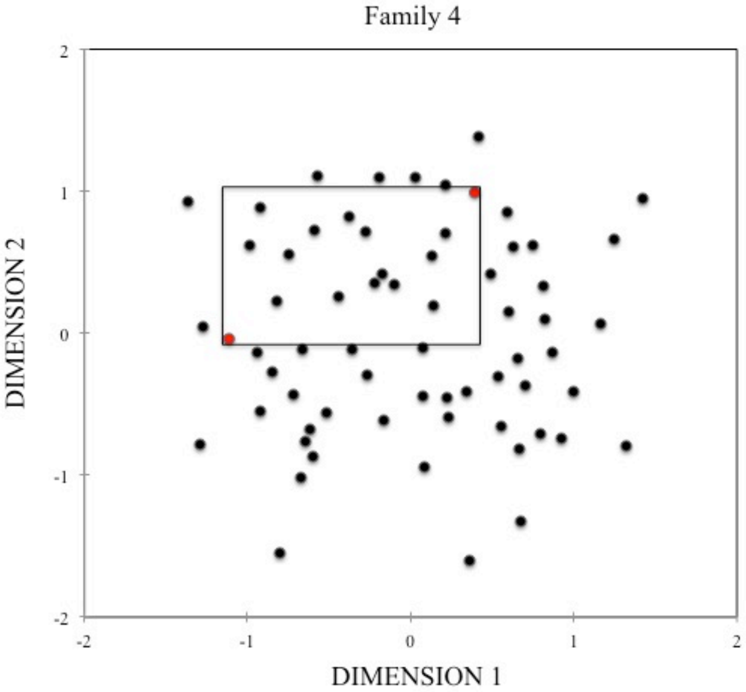


Figure 4. Family 4 MDS plot, with siblings marked in red and multidimensional space occupied (Family 4 Area) enclosed in a rectangle (relative dispersion = 18.7%).

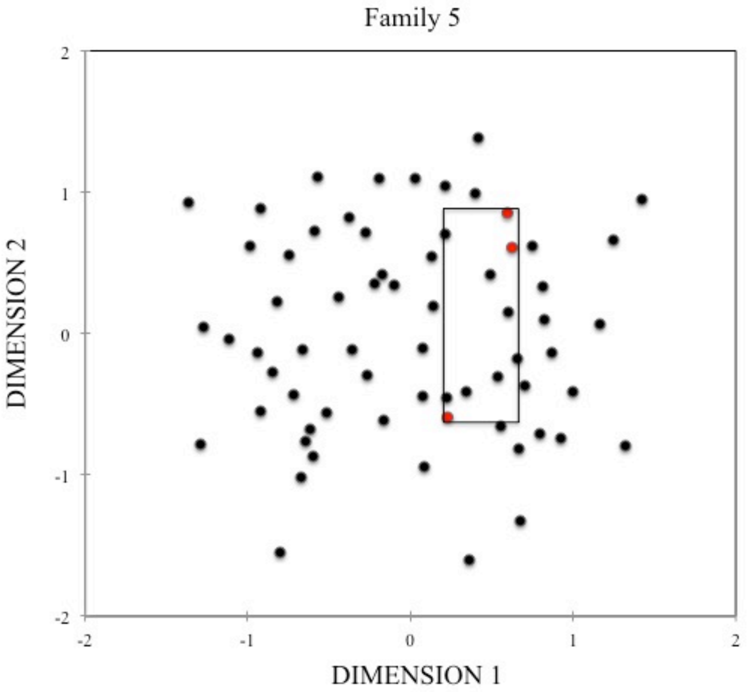


Figure 5. Family 5 MDS plot, with siblings marked in red and multidimensional space occupied (Family 5 Area) enclosed in a rectangle (relative dispersion = 6.8%).

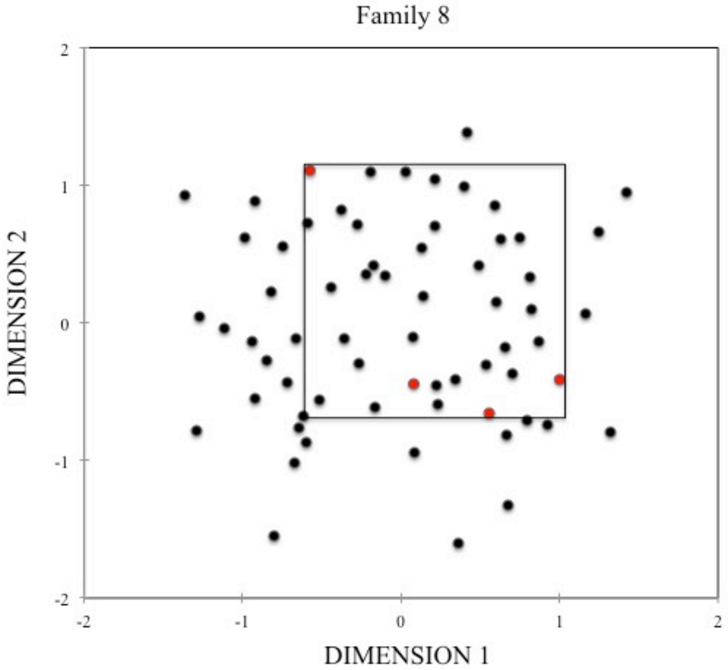


Figure 6. Family 8 MDS plot, with siblings marked in red and multidimensional space occupied (Family 8 Area) enclosed in a rectangle (relative dispersion = 33.4%).

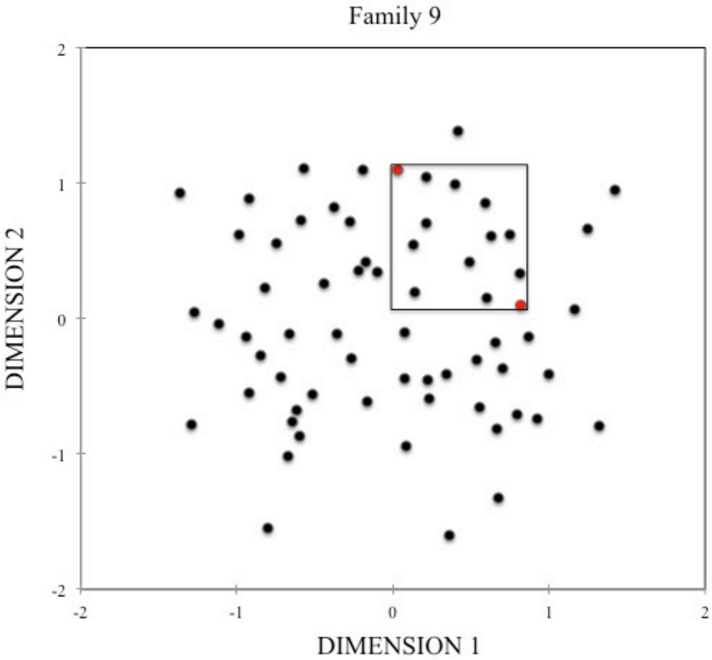


Figure 7. Family 9 MDS plot, with siblings marked in red and multidimensional space occupied (Family 9 Area) enclosed in a rectangle (relative dispersion = 9.5%).

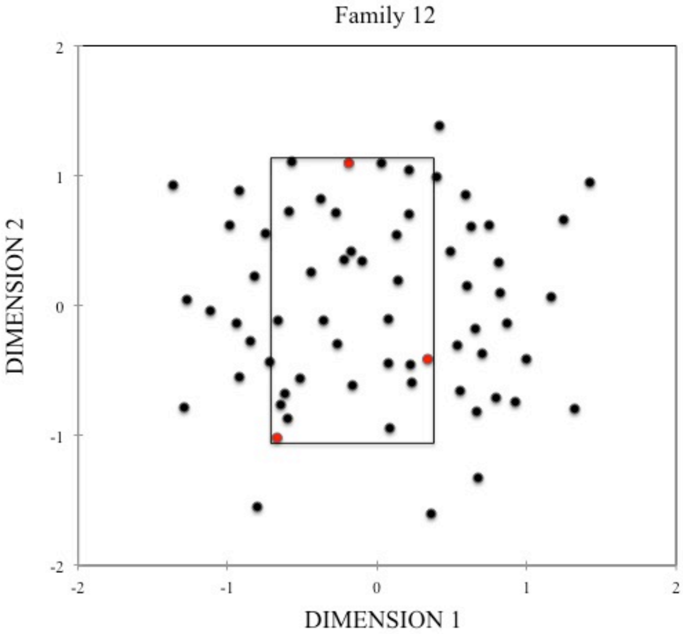


Figure 8. Family 12 MDS plot, with siblings marked in red and multidimensional space occupied (Family 12 Area) enclosed in a rectangle (relative dispersion = 25.7%).

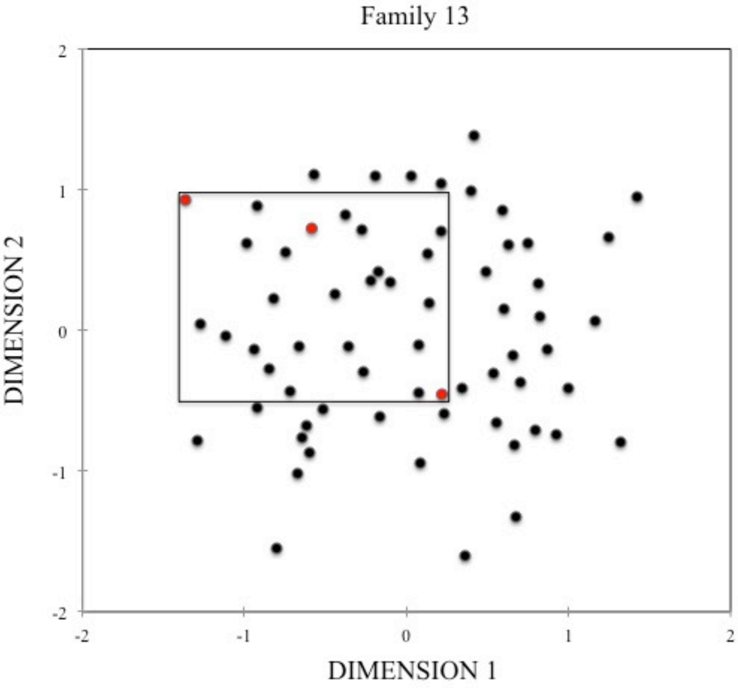


Figure 9. Family 13 MDS plot, with siblings marked in red and multidimensional space occupied (Family 13 Area) enclosed in a rectangle (relative dispersion = 26.5%).

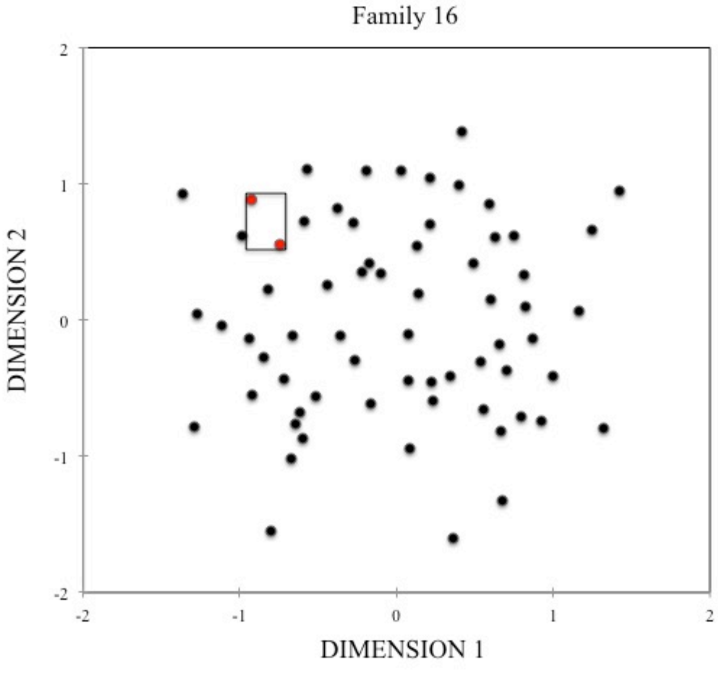


Figure 10. Family 16 MDS plot, with siblings marked in red and multidimensional space occupied (Family 16 Area) enclosed in a rectangle (relative dispersion = 0.7%).

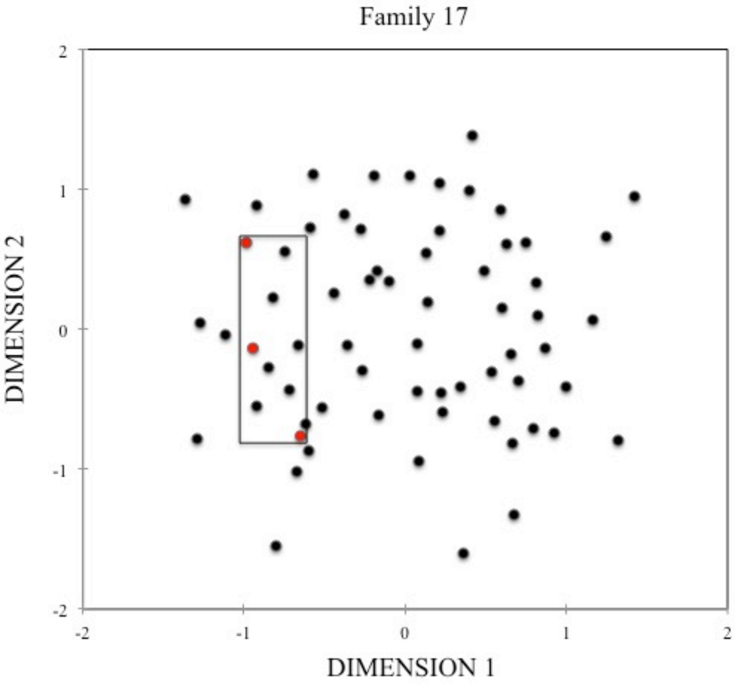


Figure 11. Family 17 MDS plot, with siblings marked in red and multidimensional space occupied (Family 17 Area) enclosed in a rectangle (relative dispersion = 5.6%).

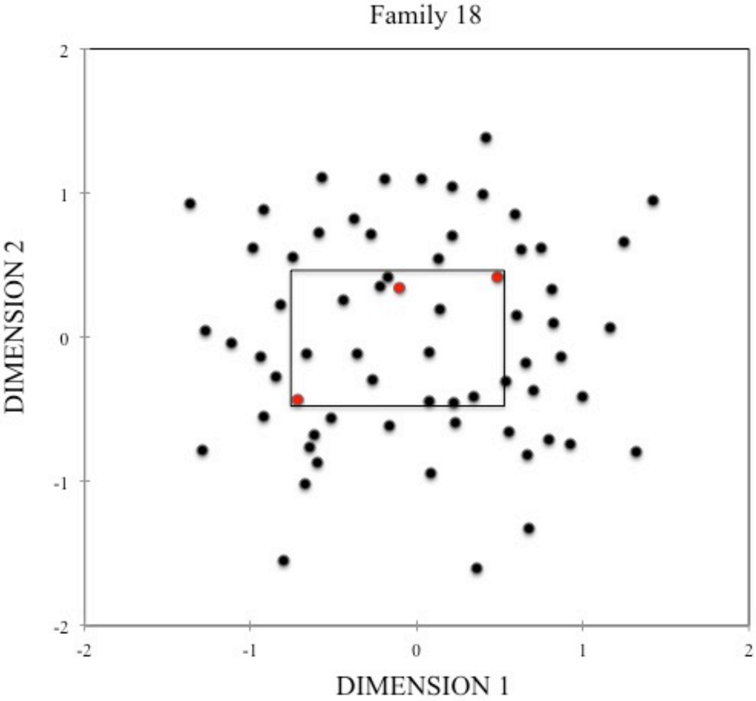


Figure 12. Family 18 MDS plot, with siblings marked in red and multidimensional space occupied (Family 18 Area) enclosed in a rectangle (relative dispersion = 12.5%).

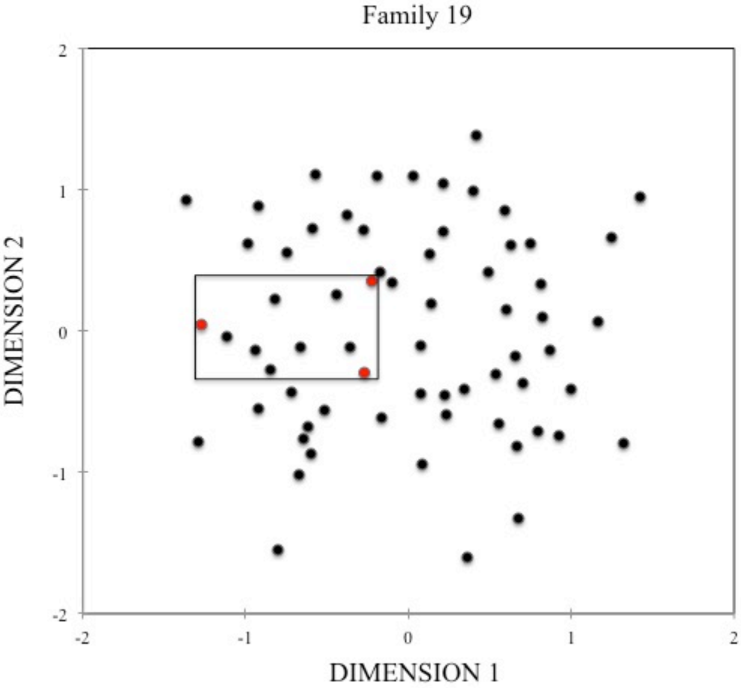


Figure 13. Family 19 MDS plot, with siblings marked in red and multidimensional space occupied (Family 19 Area) enclosed in a rectangle (relative dispersion = 8.2%).

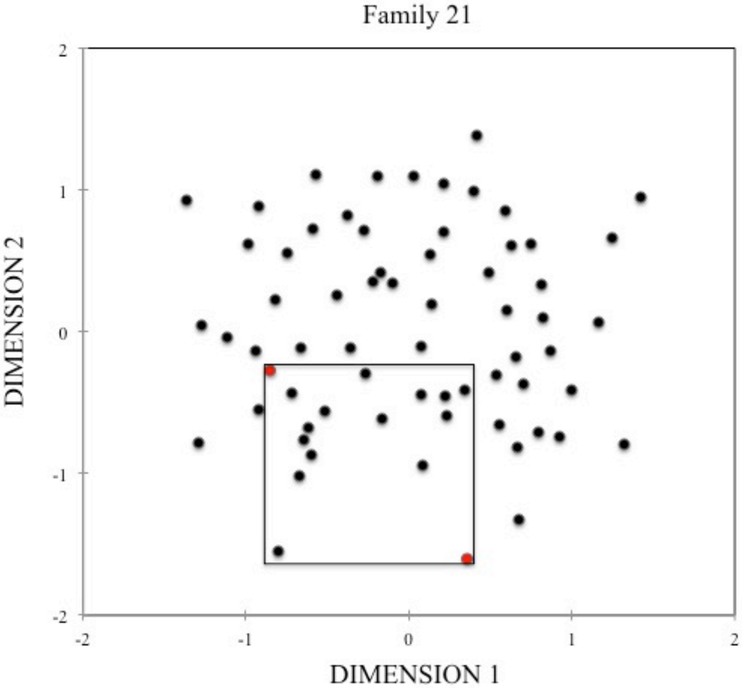


Figure 14. Family 21 MDS plot, with siblings marked in red and multidimensional space occupied (Family 21 Area) enclosed in a rectangle (relative dispersion = 19.3%).

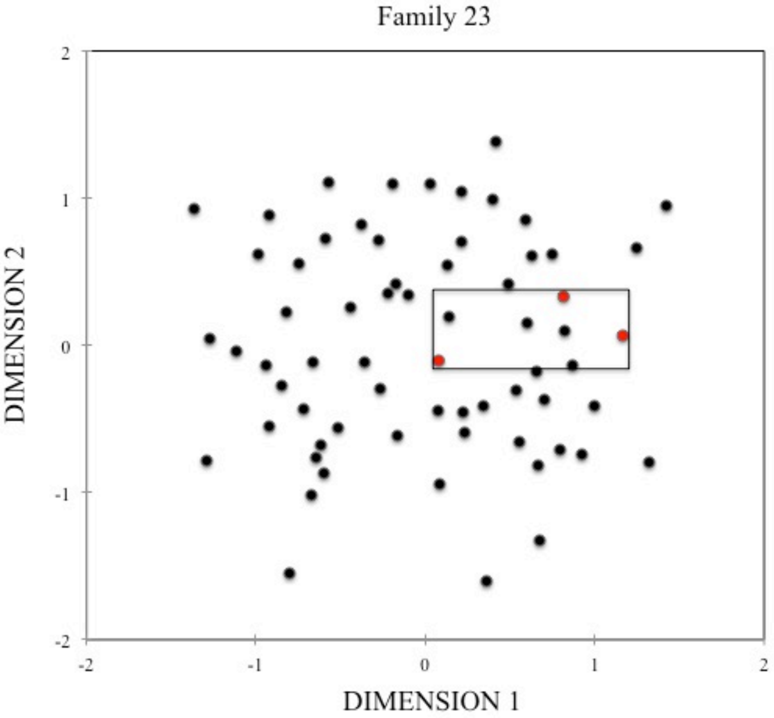


Figure 15. Family 23 MDS plot, with siblings marked in red and multidimensional space occupied (Family 23 Area) enclosed in a rectangle (relative dispersion = 5.7%).

APPENDIX I

BURLINGTON GROWTH STUDY SAMPLE

DECIDUOUS-PERMANENT HOMOLOGUE PHENOTYPIC CORRELATIONS

Table 1. Goodman-Kruskal γ and tetrachoric correlation results for the unscaled traits.

Morphological Trait[a]	N	γ[b]	ASE[b]	Aprx. Sig.[b]	rTet.[c]	ESE[c]
LABIAL CURVE						
li^1 *versus* LI^1	39	0.269	0.215	0.231		
ri^1 *versus* RI^1	40	**0.375**	**0.189**	**0.045**		
i^1 *versus* I^1 *(MAX)*	40	0.089	0.222	0.688		
SHOVEL						
li^1 *versus* LI^1	30	**0.591**	**0.177**	**0.006**		
ri^1 *versus* RI^1	32	0.220	0.286	0.447		
i^1 *versus* I^1 *(MAX)*	32	**0.523**	**0.204**	**0.027**		
li^2 *versus* LI^2	38	0.260	0.253	0.313		
ri^2 *versus* RI^2	35	0.319	0.214	0.166		
i^2 *versus* I^2 *(MAX)*	40	**0.581**	**0.192**	**0.018**		
lc^1 *versus* LC^1	38	0.159	0.240	0.506		
rc^1 *versus* RC^1	43	0.443	0.226	0.059		
c^1 *versus* C^1 *(MAX)*	45	0.166	0.240	0.488		
li_1 *versus* LI_1	30	1.000	0.000	0.292		
ri_1 *versus* RI_1	27	0.875	0.159	0.149		
i_1 *versus* I_1 *(MAX)*	33	0.867	0.165	0.160		
li_2 *versus* LI_2	39	0.116	0.449	0.804		
ri_2 *versus* RI_2[d]	34	0.660	0.363	0.269	0.468	0.325
i_2 *versus* I_2 *(MAX)*	39	0.353	0.367	0.414		

DOUBLE SHOVEL				
li^{1} *versus* LI^{1}	39	0.099	0.331	0.768
ri^{1} *versus* RI^{1}	40	-0.161	0.407	0.691
i^{1} *versus* I^{1} *(MAX)*	41	-0.053	0.337	0.875
li^{2} *versus* LI^{2}	41	-0.319	0.391	0.403
ri^{2} *versus* RI^{2}	41	**-0.722**	**0.217**	**0.040**
i^{2} *versus* I^{2} *(MAX)*	43	-0.341	0.338	0.321
lc^{1} *versus* LC^{1}	47	**0.380**	**0.140**	**0.016**
rc^{1} *versus* RC^{1}	48	**0.414**	**0.160**	**0.013**
c^{1} *versus* C^{1} *(MAX)*	50	**0.571**	**0.137**	**0.001**
TUBERCULUM DENTALE				
li^{2} *versus* LI^{2}	19	-0.160	0.343	0.640
ri^{2} *versus* RI^{2}	23	0.313	0.268	0.268
i^{2} *versus* I^{2} *(MAX)*	25	0.398	0.231	0.100
lc^{1} *versus* LC^{1}	28	**0.320**	**0.148**	**0.038**
rc^{1} *versus* RC^{1}	31	0.199	0.164	0.231
c^{1} *versus* C^{1} *(MAX)*	38	0.203	0.138	0.148
METACONE				
lm^{2} *versus* $LM1^{1}$	64	0.057	0.207	0.784
rm^{2} *versus* RM^{1}	64	**0.298**	**0.170**	**0.012**
m^{2} *versus* M^{1} *(MAX)*	66	**0.518**	**0.172**	**0.011**
HYPOCONE				
lm^{2} *versus* LM^{1}	60	**0.488**	**0.176**	**0.017**
rm^{2} *versus* RM^{1}	61	0.409	0.192	0.070

m^2 versus M^1 (MAX)	64	**0.454**	**0.179**	**0.022**
CUSP 5				
lm^2 versus LM^1	55	-1.000	0.000	0.316
rm^2 versus RM^1	57	0.552	0.399	0.458
m^2 versus M^1 (MAX)	61	-0.116	0.508	0.809
CARABELLI'S TRAIT				
lm^2 versus LM^1	62	**0.562**	**0.086**	**<0.001**
rm^2 versus RM^1	62	**0.394**	**0.111**	**<0.001**
m^2 versus M^1 (MAX)	63	**0.601**	**0.078**	**<0.001**
ANTERIOR FOVEA				
lm_2 versus LM_1	17	**0.553**	**0.197**	**0.008**
rm_2 versus RM_1[e]	19	**0.352**	**0.152**	**0.019**
m_2 versus M_1 (MAX)	24	**0.524**	**0.161**	**0.001**
DEFLECTING WRINKLE				
lm_2 versus LM_1	21	0.106	0.349	0.764
rm_2 versus RM_1	23	**0.587**	**0.207**	**0.043**
m_2 versus M_1 (MAX)	28	0.242	0.245	0.336
PROTOSTYLID				
lm_2 versus LM_1	52	0.091	0.215	0.675
rm_2 versus RM_1	56	0.278	0.181	0.131
m_2 versus M_1 (MAX)	59	0.127	0.167	0.449
CUSP 5				
lm_2 versus LM_1	50	0.162	0.216	0.462
rm_2 versus RM_1	50	**0.458**	**0.176**	**0.021**
m_2 versus M_1 (MAX)	57	0.259	0.205	0.225

CUSP 6				
lm_2 versus LM_1	51	0.796	0.166	0.179
rm_2 versus RM_1	52	0.743	0.226	0.204
m_2 versus M_1 (MAX)	57	0.447	0.344	0.374
CUSP 7				
lm_2 versus LM_1	59	**0.679**	**0.144**	**0.011**
rm_2 versus RM_1	61	**0.606**	**0.179**	**0.050**
m_2 versus M_1 (MAX)	64	**0.743**	**0.124**	**0.002**

---

[a] Maxillary and mandibular arcades are indicated by superscripts and subscripts, respectively. Deciduous elements are denoted by lowercase script; permanent elements are capitalized. All morphological traits scored according to Arizona State University Dental Anthropology System standards (Turner et al., 1991). R=right, L=left, and MAX = maximum expression. [b] Goodman-Kruskal γ output accompanied by ASE (asymptotic error) and an approximate significance value (Aprx. Sig.). Results bolded where approximate significance values are less than 0.050. [c] Tetrachoric correlation results include a correlation coefficient (rTet.) and estimated standard error (ESE); values obtained via maximum likelihood estimation. [d] Trait scored on an ordinal scale but expression across the sample limited to two ordinal grades for both the deciduous and permanent elements of interest. For this reason, the trait was also treated as a binary variable, and a tetrachoric correlation coefficient was estimated. [e] Either the deciduous or permanent character was associated with high levels of intra-observer error. Results should be accepted with caution.

Table 2. Goodman-Kruskal γ and tetrachoric correlation results for the scaled traits.

Morphological Trait[a]	N	γ[b]	ASE[b]	Aprx. Sig.[b]	rTet.[c]	ESE[c]
SHOVEL						
li^1 *versus* LI^1	30	**0.675**	**0.227**	**0.022**		
ri^1 *versus* RI^1	32	-0.246	0.319	0.470		
i^1 *versus* I^1 *(MAX)*	32	0.132	0.325	0.668		
li^2 *versus* LI^2	38	0.200	0.266	0.458		
ri^2 *versus* RI^2	35	0.092	0.286	0.749		
i^2 *versus* I^2 *(MAX)*	40	0.399	0.261	0.165		
lc^1 *versus* LC^1	38	0.239	0.258	0.362		
rc^1 *versus* RC^1	43	**0.558**	**0.221**	**0.027**		
c^1 *versus* C^1 *(MAX)*	45	0.166	0.240	0.488		
li_1 *versus* LI_1^{***}	30	1.000	0.000	0.294		
ri_1 *versus* RI_1[d]	27	0.867	0.171	0.155	0.721	0.251
i_1 *versus* I_1 *(MAX)*	33	0.857	0.177	0.165	0.693	0.253
li_2 *versus* LI_2	41	-0.170	0.430	0.686		
ri_2 *versus* RI_2	32	0.152	0.488	0.765		
i_2 *versus* I_2 *(MAX)*	41	0.008	0.402	0.983		
DOUBLE SHOVEL						
li^1 *versus* LI^{1***}	39					
ri^1 *versus* RI^1	40				-0.409	0.385
i^1 *versus* I^1 *(MAX)*	41				0.936	0.237

li^2 versus LI^2	41				-0.988	0.252
ri^2 versus RI^2	40				-0.458	0.293
i^2 versus I^2 (MAX)	43				-0.453	0.256
lc^1 versus LC^1	47				-0.271	0.230
rc^1 versus RC^1	48				-0.062	0.287
c^1 versus C^1 (MAX)	50				0.177	0.361
TUBERCULUM DENTALE						
li^2 versus LI^{2d}	20	-0.167	0.446	0.714	-0.130	0.352
ri^2 versus RI^2	23	0.546	0.338	0.164		
i^2 versus I^2 (MAX)	26	0.667	0.261	0.052		
lc^1 versus LC^{1e}	28	0.221	0.318	0.506		
rc^1 versus RC^1	31	0.208	0.345	0.558		
c^1 versus C^1 (MAX)	38	0.433	0.217	0.076		
DISTAL ACCESSORY RIDGE						
lc^1 versus LC^1	35	0.291	0.189	0.130		
rc^1 versus RC^{1e}	35	0.000	0.249	1.000		
c^1 versus C^1 (MAX)	45	0.119	0.177	0.505		
lc_1 versus LC_1	33	**0.714**	**0.120**	**<0.001**		
rc_1 versus RC_1	31	0.352	0.262	0.243		
c_1 versus C_1 (MAX)	37	**0.625**	**0.133**	**<0.001**		
HYPOCONE (CUSP NUMBER)						
lm^2 versus LM^1	58	0.700	0.309	0.399		
rm^2 versus RM^1	60	0.508	0.476	0.512		
m^2 versus M^1 (MAX)	63	0.967	0.056	0.315		

CUSP 5						
*lm^2 versus LM^1******	54					
rm^2 versus RM^1	56				0.389	0.367
m^2 versus M^1 (MAX)	60				0.120	0.358
CARABELLI'S TRAIT						
lm^2 versus LM^1	63	**0.735**	**0.075**	**<0.001**		
rm^2 versus RM^1	59	**0.675**	**0.099**	**<0.001**		
m^2 versus M^1 (MAX)	63	**0.742**	**0.077**	**<0.001**		
CUSP NUMBER						
lm_2 versus LM_1	52	0.874	0.149	0.153		
rm_2 versus RM_1	50	0.822	0.199	0.162		
m_2 versus M_1 (MAX)	59	0.593	0.315	0.254		
DEFLECTING WRINKLE						
lm_2 versus LM_1	21				0.319	0.450
rm_2 versus RM_1	23				0.221	0.433
m_2 versus M_1 (MAX)	28				0.076	0.353
PROTOSTYLID						
*lm_2 versus LM_1******	52					
*rm_2 versus RM_1******	56					
*m_2 versus M_1 (MAX)******	60					
CUSP 5						
lm_2 versus LM_1	50				-0.900	0.168
*rm_2 versus RM_1******	50					
*m_2 versus M_1 (MAX)******	57					

CUSP 7				
lm_2 versus LM_1	56	**0.720**	**0.146**	**0.016**
rm_2 versus RM_1	59	**0.816**	**0.106**	**0.008**
m_2 versus M_1 (MAX)	62	**0.760**	**0.122**	**0.003**

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[a]Maxillary and mandibular arcades are indicated by superscripts and subscripts, respectively. Deciduous elements are denoted by lowercase script; permanent elements are capitalized. R=right, L=left, and MAX = maximum expression. [b]Goodman-Kruskal γ output accompanied by ASE (asymptotic error) and an approximate significance value (Aprx. Sig.). Results bolded where approximate significance values are less than 0.050. [c]Tetrachoric correlation results include a correlation coefficient (rTet.) and estimated standard error (ESE); values obtained via maximum likelihood estimation. [d]Trait scored on an ordinal scale but expression across the sample limited to two ordinal grades for both the deciduous and permanent elements of interest. For this reason, the trait was also treated as a binary variable, and a tetrachoric correlation coefficient was estimated. [e]Either the deciduous or permanent character was associated with high levels of intra-observer error. Results should be accepted with caution. ***Correlation between traits marked with asterisks could not be estimated due to computational error. Either the permanent or deciduous character (or both) was converted to a constant in the process of scaling, and therefore cross tabulation associations could not be assessed.

APPENDIX J

BURLINGTON GROWTH STUDY SAMPLE

HERITABILITY ESTIMATES

Table 1. Burlington Growth Study sample heritability estimates: deciduous crown morphology (mixed deciduous standards).

Trait[a]	N[b] *Count*	K[c]	Heritability			Covariates			
			h2[d]	p-value[e]	SE[f]	c2[g]	age[h] p-value	sex[h] p-value	age*sex[h] p-value
lxi1 wing*	52	8.1149	0.360	0.182	0.392	0.000	0.771	0.110	0.854
bp1	*5*	---------	0.886	0.186	0.865	0.094	0.483	**0.037**	0.486
bp2	*4*	---------	0.000	0.500	-------	0.085	0.818	**0.084**	0.345
lxi1 shov	41	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*21*	---------	**1.000**	**0.031**	-------	0.000	0.571	0.808	0.381
bp2	*5*	---------	1.000	0.056	-------	0.000	0.779	0.402	0.639
bp3	*0*								
lxi2 shov	52	-0.4534	0.053	0.450	0.431	0.000	0.123	0.426	0.233
bp1	*37*	---------	0.817	0.100	0.457	0.000	0.300	0.318	0.425
bp2	*6*	---------	1.000	0.214	-------	0.146	**0.030**	**0.050**	**<0.001**
bp3	*0*								
lxc shov	60	-0.6375	0.000	0.500	-------	0.000	0.204	0.818	0.381
bp1	*41*	---------	0.552	0.128	0.445	0.000	0.288	0.613	0.467
bp2	*2*	---------	0.000	0.500	-------	0.000	0.289	0.496	0.521
bp3	*0*								
lxi1 dshov*	49	13.5403	0.000	0.500	-------	0.000	0.651	0.270	0.130
bp1	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*1*	---------	0.000	0.500	-------	0.000	0.480	0.230	0.997
bp3	*0*								
lxi2 dshov*	56	15.1697	0.466	0.104	0.370	0.000	0.690	0.870	0.503
bp1	*5*	---------	0.952	0.168	0.846	0.066	0.455	0.704	**0.010**
bp2	*3*	---------	0.000	0.500	-------	0.000	0.940	0.878	0.859
bp3	*0*								

lxc dshov	69	-1.1057	**0.743**	**0.002**	0.178	0.000	0.996	0.927	0.496
bp1	*53*	---------	0.611	0.083	0.404	0.000	0.963	0.612	0.470
bp2	*29*	---------	0.697	0.051	0.457	0.000	0.905	0.517	0.418
bp3	*14*	---------	**1.000**	**0.004**	-------	0.000	0.778	0.709	0.813
lxi2 td	44	-0.9370	0.166	0.395	0.591	0.000	0.702	0.127	0.350
bp1	*17*	---------	0.000	0.500	-------	0.000	0.713	0.367	0.274
bp2	*6*	---------	1.000	0.123	-------	0.216	0.997	**0.007**	1.000
bp3-bp4	*0*								
lxc td	54	-0.5360	0.436	0.167	0.441	0.000	0.648	0.866	0.200
bp1	*49*	---------	1.000	0.091	-------	0.000	0.233	0.814	0.223
bp2	*42*	---------	**1.000**	**0.001**	-------	0.000	0.336	0.344	0.844
bp3	*25*	---------	0.000	0.500	-------	0.133	0.273	0.727	**0.076**
bp4	*3*	---------	0.000	0.500	-------	0.000	0.424	0.481	1.000
lxm1 cno	66	-0.6424	**0.557**	**0.030**	0.286	0.000	0.471	0.732	0.200
bp3m	*55*	---------	**1.000**	**0.023**	-------	0.000	0.990	0.148	0.104
bp3h	*33*	---------	0.571	0.055	0.347	-------	0.296	0.247	0.829
bp4-	*31*	---------	0.557	0.058	-------	0.000	0.285	0.402	0.939
bp4	*3*	---------	0.000	0.500	-------	0.000	0.361	0.311	0.995
lxm2 cno*	79	6.1097	0.142	0.329	0.325	0.088	0.102	**0.004**	0.155
bp3a/b	*79*								
bp4-	*79*	---------	0.000	0.500	-------	0.000	0.999	0.314	1.000
bp4	*72*	---------	0.512	0.326	1.090	0.172	0.219	**0.003**	0.391
lxm2 c5	78	---------	-------	-------	-------	-------	-------	-------	-------
	4								
lxm2 Carab	83	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*81*	---------	0.000	0.500	-------	0.125	1.000	**0.048**	0.999
bp2	*57*	---------	**0.716**	**0.039**	0.421	0.040	**0.057**	0.334	**0.086**
bp3	*35*	---------	**1.000**	**0.004**	-------	0.044	**<0.001**	**0.006**	0.136
bp4	*13*	---------	**1.000**	**0.003**	-------	0.074	0.921	**<0.001**	0.797
lni1 shov	41	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	0.000	0.500	-------	0.000	0.526	0.192	0.996

bp2-bp3	*0*								
lni2 shov	56	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*26*	---------	**1.000**	**0.009**	-------	0.000	0.954	0.348	0.992
bp2	*1*	---------	0.000	0.500	-------	0.000	1.000	0.448	0.766
bp3	*0*								
lnc shov	70	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*43*	---------	0.454	0.130	0.433	0.000	0.608	0.439	0.699
bp2	*8*	---------	0.715	0.182	1.999	0.000	0.433	0.314	0.689
bp3	*0*								
lni1 double	47	---------	-------	-------	-------	-------	-------	-------	-------
	0								
lni2 double	58	---------	0.000	0.500	-------	0.000	0.970	0.404	0.997
	1								
lnc double	76	---------	-------	-------	-------	-------	-------	-------	-------
	0								
lnc td*	65	1.3303	0.000	0.500	-------	0.000	0.804	0.659	0.830
bp1	*16*	---------	0.000	0.500	-------	0.000	0.766	0.926	0.669
bp2	*3*	---------	1.000	0.257	-------	0.000	1.000	0.112	0.998
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------
lnm2 dwrink	66	---------	0.380	0.255	0.584	0.047	0.755	**0.061**	0.613
	19								
lnm2 pstylid	77	-0.5053	**0.517**	**0.022**	0.217	0.028	0.153	**0.088**	0.308
bp1	*55*	---------	**0.725**	**0.033**	0.326	0.000	0.117	0.138	0.233
bp2	*1*	---------	1.000	0.329	-------	0.000	0.897	0.160	1.000
lnm2 c7	75	-0.8469	0.131	0.310	0.276	0.000	0.450	0.592	0.378
bp1	*31*	---------	0.000	0.500	-------	0.000	0.061	0.331	0.117
bp2	*14*	---------	0.497	0.225	0.630	0.000	0.818	0.897	0.641
bp3	*1*	---------	0.000	0.500	-------	0.000	0.905	0.170	1.000
bp4-bp5	*0*								
lnm2 delta	77	---------	-------	-------	-------	-------	-------	-------	-------

	0								
rxi1 wing*	54	7.2144	0.000	0.500	-------	0.000	0.320	0.308	0.890
bp1	*5*	---------	0.000	0.500	-------	0.000	0.263	0.326	0.773
bp2	*4*	---------	0.000	0.500	-------	0.000	0.780	0.227	0.599
rxi1 shov	42	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*20*	---------	1.000	0.099	-------	0.232	0.392	**0.021**	0.487
bp2	*2*	---------	1.000	0.274	-------	0.000	0.405	0.579	0.878
bp3	*0*								
rxi2 shov	49	0.4285	0.000	0.500	-------	0.000	0.118	0.162	0.233
bp1	*41*	---------	0.008	0.496	-------	0.074	**0.071**	0.658	0.368
bp2	*7*	---------	0.000	0.500	-------	0.000	0.490	0.139	0.364
bp3	*0*								
rxc shov	64	-0.8283	0.000	0.500	-------	0.109	0.227	**0.030**	**0.060**
bp1	*39*	---------	0.000	0.500	-------	0.072	0.198	**0.034**	**0.059**
bp2	*2*	---------	0.000	0.500	-------	0.000	1.000	0.230	0.997
bp3	*0*								
rxi1 dshov*	51	13.9699	0.000	0.500	0.454	0.000	0.682	0.278	0.860
bp1	*3*	---------	0.000	0.500	-------	0.188	0.784	**0.064**	**<0.001**
bp2	*2*	---------	0.000	0.500	-------	0.000	0.477	0.209	0.293
bp3	*0*								
rxi2 dshov*	54	9.9469	0.000	0.500	-------	0.000	0.638	0.131	0.432
bp1	*4*	---------	0.000	0.500	-------	0.155	0.525	**0.095**	0.296
bp2	*3*	---------	0.000	0.500	-------	0.088	0.944	**0.071**	0.370
bp3	*0*								
rxc dshov	71	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*54*	---------	**1.000**	**0.001**	-------	0.000	0.748	0.625	0.636
bp2	*36*	---------	**1.000**	**0.013**	-------	0.000	0.853	0.492	0.480
bp3	*17*	---------	0.826	0.074	0.529	0.062	0.218	**0.019**	0.238
rxi2 td	46	-1.0625	0.167	0.321	0.347	0.075	0.628	**0.062**	0.934
bp1	*21*	---------	0.292	0.330	0.636	0.054	0.356	**0.066**	0.647
bp2	*8*	---------	0.000	0.500	-------	0.000	0.808	0.166	0.560

bp3-bp4	*0*								
rxc td	57	-0.6185	**0.798**	**0.008**	0.174	0.000	0.379	0.993	0.190
bp1	*53*	---------	**1.000**	**0.011**	-------	0.000	0.255	0.410	0.110
bp2	*43*	---------	**1.000**	**0.020**	-------	0.000	0.581	0.615	0.458
bp3	*26*	---------	0.408	0.190	0.472	0.000	0.968	0.327	0.763
bp4	*5*	---------	0.000	0.500	-------	0.000	0.844	0.478	0.426
rxm1 cno	70	---------	-------	-------	-------	-------	-------	-------	-------
bp3m	*60*	---------	**1.000**	**0.005**	-------	0.000	0.207	0.750	0.316
bp3h	*34*	---------	**1.000**	**<0.001**	-------	0.000	0.429	0.672	0.974
bp4-	*27*	---------	**1.000**	**0.006**	-------	0.000	0.645	0.707	0.434
bp4	*3*	---------	0.000	0.500	-------	0.000	0.455	0.222	1.000
rxm2 cno	79	---------	-------	-------	-------	-------	-------	-------	-------
bp3a/b	*79*								
bp4-	*74*	---------	**1.000**	**0.013**	-------	0.000	0.343	0.669	0.520
bp4	*68*	---------	0.934	0.048	2.264	0.000	0.132	0.396	0.604
rxm2 c5	76	---------	0.000	0.500	-------	0.000	0.274	0.896	0.325
	2								
rxm2 Carab	81	-0.6594	**0.723**	**0.001**	0.182	0.000	0.741	0.605	0.941
bp1	*81*	---------	0.000	0.500	-------	0.000	1.000	0.361	1.000
bp2	*64*	---------	**0.954**	**0.010**	0.220	0.000	0.880	0.741	0.229
bp3	*42*	---------	**1.000**	**0.001**	-------	0.000	0.916	0.459	0.997
bp4	*13*	---------	0.536	0.142	0.477	0.000	0.393	0.353	0.148
rni1 shov	39	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*4*	---------	0.000	0.499	-------	0.213	0.383	**0.029**	**0.025**
bp2-bp3	*0*								
rni2 shov	53	-1.2589	0.581	0.082	0.461	0.000	0.112	0.495	0.201
bp1	*29*	---------	1.000	0.055	-------	0.018	**0.092**	0.306	0.250
bp2	*1*	---------	0.000	0.500	-------	0.000	1.000	0.467	0.988
bp3	*0*								
rnc shov	67	-0.5949	**0.694**	**0.001**	0.148	0.045	**0.021**	0.100	0.144
bp1	*30*	---------	**0.973**	**0.011**	0.279	0.158	**0.001**	**0.060**	**0.011**

bp2	*6*	---------	0.884	0.130	0.710	0.000	0.875	0.210	0.957
bp3	*0*								
rni1 double	60 *0*	---------	-------	-------	-------	-------	-------	-------	-------
rni2 double	58 *1*	---------	0.000	0.500	-------	0.000	0.995	0.400	0.997
rnc double	58 *1*	---------	0.000	0.500	0.007	0.000	1.000	0.400	0.963
rnc td	62	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*13*	---------	**1.000**	**0.039**	-------	0.000	0.624	0.604	0.677
bp2	*2*	---------	1.000	0.368	-------	0.247	0.398	0.559	**0.001**
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------
rnm2 dwrink	67 *20*	---------	0.534	0.143	0.529	0.000	0.675	0.552	0.697
rnm2 pstylid	79	-0.2639	**0.418**	**0.025**	0.209	0.000	0.899	0.362	0.839
bp1	*55*	---------	**0.691**	**0.027**	0.328	0.039	0.640	**0.057**	0.650
bp2	*5*	---------	**0.691**	**0.027**	0.322	0.039	0.640	**0.057**	0.650
rnm2 c7	80	---------	0.394	0.087	0.321	0.000	0.549	0.131	0.721
bp1	*28*	---------	0.360	0.213	0.481	0.037	0.940	**0.052**	1.000
bp2	*13*	---------	0.309	0.309	0.654	0.000	0.521	0.453	0.683
bp3-bp5	*0*								
rnm1 delta	77 *1*	---------	-------	-------	-------	-------	-------	-------	-------
xi1 wing max*	54	5.1691	0.392	0.152	0.379	0.000	0.459	0.257	0.938
bp1	*6*	---------	0.808	0.165	0.752	0.000	0.374	0.174	0.587
bp2	*4*	---------	0.000	0.500	-------	0.091	0.818	**0.074**	0.349
xi1 shov max	44	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*25*	---------	0.000	0.500	-------	0.076	0.919	**0.095**	0.941
bp2	*6*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*0*								

xi2 shov max	56	0.5369	0.325	0.238	0.482	0.051	**0.038**	0.392	0.119
bp1	*51*	---------	0.604	0.216	0.705	0.000	0.238	0.688	0.836
bp2	*11*	---------	0.000	0.500	-------	0.067	**0.042**	0.334	**0.053**
bp3	*0*								
xc shov max	66	0.1960	0.000	0.500	-------	0.006	0.107	0.315	**0.086**
bp1	*51*	---------	0.000	0.500	-------	0.052	0.129	**0.096**	0.133
bp2	*3*	---------	0.000	0.500	-------	0.000	0.303	0.995	0.373
bp3	*0*								
xi1 dshov max*	52	9.7500	0.000	0.500	-------	0.000	0.701	0.556	0.487
bp1	*4*	---------	0.000	0.500	-------	0.000	0.785	0.312	0.262
bp2	*2*	---------	0.000	0.500	-------	0.085	0.459	0.200	**<0.001**
bp3	*0*								
xi2 dshov max*	58	6.3388	0.516	0.080	0.368	0.000	0.595	0.676	0.307
bp1	*6*	---------	0.859	0.146	0.733	0.000	0.567	0.401	0.185
bp2	*4*	---------	0.000	0.500	-------	0.000	1.000	0.430	0.850
bp3	*0*	---------	0.000	0.500	-------	0.000	0.997	0.429	0.996
xc dshov max	72	-1.1202	**0.778**	**0.002**	0.172	0.000	0.792	0.858	0.794
bp1	*61*	---------	**0.770**	**0.026**	0.306	0.000	0.933	0.835	0.769
bp2	*42*	---------	0.404	0.161	0.574	0.000	0.818	0.492	0.849
bp3	*21*	---------	**1.000**	**0.002**	-------	0.000	0.454	0.261	0.712
xi2 td max	49	-1.2140	0.000	0.500	-------	0.093	0.796	**0.036**	0.896
bp1	*27*	---------	0.171	0.394	0.629	0.045	0.738	**0.099**	0.961
bp2	*10*	---------	0.000	0.500	-------	0.091	0.919	**0.041**	0.594
bp3-bp4	*0*								
xc td max	66	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*61*	---------	**1.000**	**0.016**	-------	0.065	**0.006**	0.833	**0.022**
bp2	*52*	---------	**1.000**	**0.001**	-------	0.035	0.534	0.429	**0.021**
bp3	*34*	---------	**0.896**	**0.046**	0.552	0.000	0.859	0.967	0.497
bp4	*6*	---------	0.000	0.500	-------	0.000	0.904	0.772	0.483
xm1 cno max	73	---------	-------	-------	-------	-------	-------	-------	-------
bp3m	*66*	---------	**1.000**	**0.018**	-------	0.004	0.108	0.164	**0.003**

bp3h	*42*	---------	**0.734**	**0.029**	0.407	0.000	0.699	0.110	0.571
bp4-	*36*	---------	**0.973**	**0.005**	0.374	0.000	0.800	0.510	0.376
bp4	*3*	---------	0.000	0.500	-------	0.000	0.420	0.271	0.744
xm2 cno max*	82	6.5401	0.108	0.352	0.294	0.046	0.115	**0.035**	0.185
bp3a/b	*82*								
bp4-	*82*	---------	0.000	0.500	-------	0.000	0.997	0.315	1.000
bp4	*75*	---------	0.485	0.326	1.027	0.090	0.205	**0.039**	0.352
xm2 c5 max	78	---------	0.759	0.369	1.574	0.000	0.188	0.759	0.703
	5								
xm2 Carab max	84	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*84*	---------	0.000	0.500	-------	0.000	1.000	0.345	1.000
bp2	*70*	---------	0.653	0.103	0.333	0.000	0.105	0.871	0.694
bp3	*44*	---------	**1.000**	**<0.001**	-------	0.000	0.300	0.242	0.431
bp4	*18*	---------	**1.000**	**0.013**	-------	0.049	0.012	**0.002**	0.143
ni1 shov max	42	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*4*	---------	0.000	0.500	-------	0.198	0.213	**0.028**	**0.002**
bp2-bp3	*0*								
ni2 shov max	56	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*32*	---------	**1.000**	**0.007**	-------	0.037	0.147	**0.002**	0.100
bp2	*1*	---------	0.000	0.500	-------	0.000	1.000	0.448	0.766
bp3	*0*								
nc shov max	71	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*50*	---------	0.411	0.179	0.469	0.000	0.940	0.563	0.493
bp2	*9*	---------	**1.000**	**0.045**	-------	0.000	0.444	0.272	0.869
bp3	*0*								
ni1 double max	47	---------	-------	-------	-------	-------	-------	-------	-------
	0								
ni2 double max	59	---------	0.000	0.500	-------	0.000	1.000	0.410	0.997
	1								
nc double max	74	---------	0.000	0.500	0.001	0.000	0.530	0.504	0.814
	1								

nc td max	67	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*22*	---------	**1.000**	**0.009**	<0.001	0.000	0.967	0.937	0.961
bp2	*4*	---------	1.000	0.199	-------	0.120	1.000	**0.079**	0.320
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------
nm2 dwrink max	72	---------	0.505	0.138	0.498	0.037	0.744	**0.059**	0.911
	27								
nm2 pstylid max*	79	---------	0.263	0.117	0.231	0.000	0.672	0.622	0.573
bp1	*62*	---------	0.523	0.093	0.393	0.000	0.373	0.864	0.337
bp2	*5*	---------	0.609	0.154	0.512	0.000	0.601	0.257	0.778
nm2 c7 max	80	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*36*	---------	0.220	0.201	0.276	0.000	0.622	0.389	0.713
bp2	*19*	---------	**1.000**	**0.014**	-------	0.000	0.716	0.829	0.515
bp3	*1*	---------	0.000	0.500	-------	0.000	0.971	0.166	1.000
bp4-bp5	*0*								
nm1 delta max	78	---------	-------	-------	-------	-------	-------	-------	-------
	1								

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[a] l=left; r=right; x=maxillary; n=mandibular; max=maximum of the left and right antimeric expressions; bp=breakpoint. All morphological trait abbreviations outlined in Appendix C. Ordinal traits were normalized and treated as continuous for the purpose for heritability estimation. Breakpoints indicate presence/absence dichotomization cutoffs for ordinal traits; each of these breakpoints was treated as an individual binary character for heritability estimation. Kurtosis is not estimated for binary character models. Certain breakpoints were omitted from the heritability analysis because expression was monomorphic across the sample. Traits marked with asterisks are associated with less stable heritability estimates because other model parameters could not be estimated, because sample size was too small, or because kurtosis values were too high after normalization. These results should be accepted with caution. Dashes are associated with incalculable parameter estimates. Traits marked with dashes for all parameters represent models that failed to converge. [b] N=sample size for heritability estimation; Count=count for dichotomized trait expression (presence) at the denoted breakpoint (bp). Count values are italicized. If a trait is binary (i.e., its original scoring standards do not include ordinal scale scoring) this value is marked on a blank row beneath the sample size “N”. [c] K=model kurtosis value. [d] h2= maximum likelihood heritability estimate. [e] All significant heritability estimates (p-value<0.05) and associated

probability value estimates are bolded. [f]SE= maximum likelihood standard error estimate; this parameter estimate is typically omitted when heritability estimated equal 0.000 or 1.000. [g]c2= maximum likelihood total covariate estimate. [h]All significant probability value estimates for the covariates of age, sex, and age/sex interaction are bolded.

Table 2. Burlington Growth Study sample heritability estimates: deciduous crown morphology (ASUDAS standards).

			Heritability			Covariates			
Trait[a]	N[b] *Count*	K[c]	h2[d]	p-value[e]	SE[f]	c2[g]	age[h] p-value	sex[h] p-value	age*sex[h] p-value
lxi1 wing[i]	52	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*5*	---------	0.886	0.186	0.865	0.094	0.483	**0.037**	0.486
bp2	*0*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*48*	---------	1.000	0.083	-------	0.000	0.481	0.292	0.661
bp4	*1*	---------	1.000	0.351	-------	0.000	0.988	0.995	0.954
lxi lab cvx	46	---------	-------	-------	-------	-------	-------	-------	-------
bp1-bp2	*46*								
bp3	*18*	---------	0.000	0.500	-------	0.000	0.927	0.983	0.994
bp4	*3*	---------	0.000	0.500	-------	0.000	1.000	0.946	0.868
lxi1 shov	40	-0.9340	0.000	0.500	-------	0.000	0.854	0.592	0.314
bp1	*19*	---------	0.000	0.500	-------	0.000	1.000	1.000	0.670
bp2	*4*	---------	0.000	0.500	-------	0.000	0.722	0.785	0.403
bp3-bp7	*0*								
lxi2 shov	51	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*36*	---------	1.000	0.079	-------	0.095	0.776	**0.097**	0.841
bp2	*6*	---------	1.000	0.135	-------	0.139	0.999	**0.036**	0.999
bp3	*1*	---------	1.000	0.396	-------	0.264	1.000	0.540	**0.043**
bp4-bp7	*0*								
lxc shov	60	-0.6096	0.106	0.347	0.268	0.000	0.287	0.811	0.317
bp1	*40*	---------	0.436	0.187	0.477	0.000	0.254	0.663	0.299
bp2	*5*	---------	0.000	0.500	-------	0.000	0.597	0.558	0.571
bp3-bp7	*0*								
lxi1 dshov*	49	10.0769	0.000	0.500	-------	0.121	0.709	0.410	**0.086**
bp1	*3*	---------	-------	-------	-------	-------	-------	-------	-------

bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4-bp6	*0*								
lxi2 dshov	56	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*7*	---------	0.495	0.298	0.913	0.050	0.383	0.194	**0.091**
bp2-bp6	*0*								
lxc dshov	65	-0.3516	**0.682**	**0.003**	0.182	0.000	0.867	0.652	0.416
bp1	*53*	---------	0.134	0.406	2.390	0.000	0.959	0.725	0.302
bp2	*18*	---------	**1.000**	**0.011**	-------	0.000	0.465	0.789	0.962
bp3	*8*	---------	**1.000**	**0.002**	-------	0.000	0.991	0.764	0.795
bp4	*1*	---------	0.000	0.500	-------	0.206	**0.062**	0.505	0.991
bp5-bp6	*0*								
lxi2 td	42	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*14*	---------	0.523	0.289	0.916	0.000	0.592	0.647	0.335
bp2	*2*	---------	0.213	0.485	4.527	0.000	1.000	0.123	0.986
bp3	*1*	---------	0.000	0.500	-------	0.000	0.998	0.360	0.688
bp4-bp6	*0*								
lxc dar	49	-0.0910	0.500	0.052	0.277	0.000	0.395	0.668	0.295
bp1	*14*	---------	0.627	0.095	0.088	0.000	0.590	0.512	0.392
bp2	*4*	---------	-------	-------	-------	-------	-------	-------	-------
bp3-bp5	*0*								
lxm1 meta	67	-0.6963	0.360	0.123	0.310	0.000	0.830	0.859	0.195
bp1	*54*	---------	**1.000**	**0.008**	-------	0.000	0.984	0.144	0.345
bp2	*53*	---------	**1.000**	**0.017**	-------	0.087	0.965	**0.099**	0.437
bp3	*16*	---------	0.423	0.207	3.145	0.000	0.912	0.262	0.248
bp3.5-bp5	*0*								
lxm2 meta	80	-0.6869	**0.555**	**0.006**	0.208	0.000	0.858	0.812	0.720
bp1-bp3	*80*								
bp3.5	*47*	---------	**0.618**	**0.044**	0.406	0.000	0.692	0.938	0.826
bp4	*9*	---------	**1.000**	**0.031**	-------	0.000	0.945	0.951	0.886
bp5	*1*	---------	0.000	0.500	-------	0.000	1.000	0.348	1.000

lxm1 hypo	71	-0.7158	0.133	0.270	0.229	0.000	0.582	0.319	0.344
bp1	*33*	---------	0.531	0.052	0.379	0.000	0.478	0.402	0.494
bp2	*14*	---------	0.000	0.500	-------	0.000	0.529	0.787	0.525
bp3	*4*	---------	0.000	0.500	-------	0.000	1.000	0.445	0.964
bp3.5-bp5	*0*								
lxm2 hypo	83	---------	0.139	0.279	0.244	0.000	0.953	0.671	0.932
bp1-bp2	*83*								
bp3	*82*	---------	0.000	0.500	-------	0.000	1.000	0.346	1.000
bp3.5	*75*	---------	0.378	0.314	0.775	0.075	0.980	**0.054**	0.671
bp4	*24*	---------	0.155	0.357	0.449	0.000	0.851	0.713	0.801
bp5	*4*	---------	0.000	0.500	-------	0.000	0.408	0.660	0.706
lxm2 c5*	78	13.4968	0.332	0.218	0.438	0.067	**0.011**	0.810	**0.086**
bp1	*5*	---------	0.000	0.500	-------	0.000	0.132	0.900	0.591
bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4-bp5	*0*								
lxm2 Carab	84	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*83*	---------	0.000	0.500	-------	0.000	1.000	0.351	1.000
bp2	*74*	---------	0.000	0.756	0.102	0.000	0.173	0.393	0.270
bp3	*61*	---------	**0.882**	**0.019**	0.450	0.130	**0.009**	**0.083**	**0.096**
bp4	*43*	---------	**1.000**	**0.001**	-------	0.000	**0.060**	**0.039**	0.138
bp5	*33*	---------	**1.000**	**0.004**	-------	0.130	0.458	**<0.001**	0.825
bp6	*19*	---------	**1.000**	**0.021**	-------	0.141	0.755	**0.030**	0.716
bp7	*8*	---------	**1.000**	**0.002**	-------	0.000	0.951	0.181	0.598
lxm1 para^j	78	---------	0.000	0.500	-------	0.000	0.989	0.170	0.974
	2								
lxm2 para^j	83	---------	-------	-------	-------	-------	-------	-------	-------
	0								
lni1 shov	41	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	0.000	0.500	-------	0.000	0.526	0.192	0.996
bp2-bp7	*0*								

lni2 shov	55	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*23*	---------	**1.000**	**0.004**	-------	0.000	0.254	0.543	0.500
bp2	*1*	---------	1.000	0.351	-------	0.000	0.995	0.389	0.652
bp3-bp7	*0*								
lnc dar*	49	0.8658	0.000	0.500	-------	0.063	0.351	**0.061**	0.132
bp1	*13*	---------	0.000	0.500	-------	0.069	0.428	**0.041**	0.129
bp2	*3*	---------	1.000	0.359	-------	0.000	1.000	0.977	0.932
bp3	*1*	---------	0.100	0.500	0.707	0.000	1.000	1.000	1.000
bp4-bp5	*0*								
lnm2 ant fovea	55	-0.7015	**0.672**	**0.010**	0.299	0.000	0.621	0.716	0.945
bp1	*52*	---------	1.000	0.082	-------	0.000	0.287	0.562	0.277
bp2	*38*	---------	**0.931**	**0.040**	0.511	0.000	0.514	0.916	0.813
bp3	*17*	---------	**0.839**	**0.048**	0.500	0.000	0.421	0.308	0.818
bp4	*0*								
lnm1 cno	60	-2.0262	0.275	0.179	0.344	0.000	0.693	0.598	0.463
bp5	*27*	---------	0.425	0.179	0.485	0.000	0.699	0.589	0.463
bp6	*0*								
lnm2 cno*	72	11.9866	0.000	0.500	-------	0.000	0.400	0.293	0.667
bp5	*72*	---------	0.000	0.500	-------	0.000	0.228	0.440	0.988
bp6	*4*	---------	0.000	0.500	-------	0.199	0.824	0.346	**0.069**
bp7	*0*								
lnm2 groove[i]	36	---------	-------	-------	-------	-------	-------	-------	-------
y	*32*	---------	0.000	0.500	-------	0.000	0.586	0.746	0.387
x	*0*								
+	*4*	---------	0.000	0.500	-------	0.000	0.588	0.742	0.388
lnm2 dwrink	62	-1.0129	0.079	0.371	0.250	0.000	0.648	0.173	0.860
bp1	*35*	---------	0.241	0.300	0.475	0.000	0.535	0.595	0.947
bp2	*18*	---------	0.352	0.218	0.473	0.000	0.454	0.109	0.850
bp3	*3*	---------	1.000	0.079	-------	0.000	0.632	0.323	0.928
lnm2 pstylid	77	-0.5646	**0.834**	**<0.001**	0.081	0.000	0.239	0.357	0.367
bp1	*60*	---------	**1.000**	**0.001**	-------	0.000	0.171	0.499	0.506

bp2	*28*	---------	**0.902**	**0.003**	0.236	0.000	0.332	0.595	0.427
bp3	*16*	---------	**1.000**	**<0.001**	-------	0.000	0.661	0.306	0.921
bp4	*14*	---------	**1.000**	**<0.001**	-------	0.000	0.818	0.725	0.764
bp5	*4*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*2*	---------	1.000	0.238	-------	0.104	0.852	**<0.001**	0.178
bp7	*0*								
lnm1 c5	56	-0.5273	0.052	0.444	0.376	0.049	**0.093**	0.330	0.379
bp1	*22*	---------	0.450	0.150	0.452	0.000	0.160	0.697	0.481
bp2	*16*	---------	0.082	0.443	0.593	0.000	0.151	0.495	0.730
bp3	*4*	---------	0.000	0.500	-------	0.000	0.161	0.252	0.192
bp4	*1*	---------	0.000	0.500	-------	0.199	0.784	**0.066**	0.998
bp5	*1*	---------	0.000	0.500	-------	0.199	0.784	**0.066**	0.998
lnm2 c5*	70	1.1982	0.000	0.500	-------	0.000	0.903	0.375	0.437
bp1	*69*	---------	0.000	0.500	-------	0.181	0.628	**0.075**	1.000
bp2	*69*	---------	0.000	0.500	-------	0.182	0.616	**0.076**	0.997
bp3	*68*	---------	0.000	0.500	-------	0.306	0.771	**0.010**	0.999
bp4	*57*	---------	0.321	0.313	0.613	0.000	0.854	0.541	0.379
bp5	*6*	---------	0.562	0.243	0.834	0.000	0.726	0.172	0.386
lnm1 c6	64	---------	-------	-------	-------	-------	-------	-------	-------
	0								
lnm2 c6*	69	14.1888	0.000	0.500	0.462	0.000	0.930	0.528	0.160
bp1	*4*	---------	0.000	0.500	-------	0.194	0.830	0.339	**0.071**
bp2	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*0*								
lnm2 c7	75	-0.8469	0.131	0.310	0.276	0.000	0.450	0.592	0.378
bp1	*31*	---------	0.000	0.500	-------	0.000	0.207	0.328	0.116
bp1a	*14*	---------	0.497	0.225	0.364	0.000	0.818	0.897	0.641
bp2	*1*	---------	0.000	0.500	-------	0.000	0.909	0.171	1.000
bp3-bp4	*0*								

lnm2 dtcrest	69	---------	0.000	0.500	-------	0.280	0.512	**0.003**	0.995
	4								
rxi1 wing[i]	54	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*5*	---------	0.896	0.183	-------	0.100	0.482	**0.034**	0.648
bp2	*2*	---------	**1.000**	**0.038**	-------	0.000	1.000	0.159	1.000
bp3	*49*	---------	**1.000**	**0.047**	-------	0.000	0.252	0.480	0.555
bp4	*1*	---------	1.000	0.351	-------	0.000	0.989	0.994	0.953
rxi1 lab cvx	50	-0.1398	0.491	0.083	0.387	0.000	0.351	0.923	0.718
bp1	*49*	---------	1.000	0.087	-------	0.357	**<0.001**	**0.069**	**<0.001**
bp2	*43*	---------	**1.000**	**0.033**	-------	0.000	0.407	0.465	0.741
bp3	*18*	---------	0.000	0.500	-------	0.000	0.699	0.606	1.000
bp4	*2*	---------	0.000	0.083	0.500	0.000	1.000	0.217	1.000
rxi1 shov	43	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*20*	---------	**1.000**	**0.018**	-------	0.017	0.135	0.526	**0.090**
bp2	*3*	---------	0.000	0.500	-------	0.000	0.185	0.582	0.474
bp3-bp7	*0*								
rxi2 shov	48	-0.0606	0.138	0.367	0.408	0.000	0.109	0.178	0.375
bp1	*38*	---------	0.102	0.436	1.856	0.000	0.101	0.500	0.318
bp2	*7*	---------	0.000	0.500	-------	0.000	0.410	0.169	0.659
bp3-bp7	*0*								
rxc shov	62	-0.2732	0.000	0.500	-------	0.120	**0.056**	0.442	**0.007**
bp1	*35*	---------	0.000	0.500	-------	0.114	**0.038**	0.715	**0.003**
bp2	*2*	---------	0.000	0.500	-------	0.000	0.980	0.183	0.969
bp3-bp7	*0*								
rxi1 dshov*	50	8.1010	0.000	0.500	0.493	0.054	0.558	**0.010**	0.617
bp1	*4*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*1*	---------	0.000	0.500	-------	0.000	0.479	0.238	0.997
bp3-bp6	*0*								
rxi2 dshov	54	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*5*	---------	0.000	0.500	-------	0.000	0.655	0.128	0.559
bp2-bp6	*0*								

rxc dshov	69	-0.9223	**0.569**	**0.021**	0.267	0.047	0.778	**0.037**	0.571
bp1	*50*	---------	**0.612**	**0.049**	0.365	0.000	0.378	0.337	0.384
bp2	*23*	---------	**1.000**	**0.017**	-------	0.000	0.610	0.202	0.978
bp3	*9*	---------	0.000	0.500	-------	0.121	0.625	**0.009**	0.753
bp4	*2*	---------	0.000	0.500	-------	0.000	0.115	0.236	0.990
bp5-bp6	*0*								
rxi2 td	42	-0.6248	0.000	0.500	-------	0.000	0.286	0.159	0.930
bp1	*16*	---------	0.000	0.500	-------	0.000	0.132	0.209	0.641
bp2	*3*	---------	1.000	0.198	-------	0.000	1.000	0.132	1.000
bp3	*1*	---------	1.000	0.352	-------	0.000	0.902	0.445	0.696
bp4-bp6	*0*								
rxc dar	57	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*17*	---------	0.228	0.230	0.317	0.000	0.177	0.876	0.511
bp2-bp5	*0*								
rxm1 meta	69	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*52*	---------	**1.000**	**0.002**	-------	0.000	0.507	0.936	0.808
bp2	*51*	---------	**1.000**	**0.001**	-------	0.000	0.507	0.936	0.808
bp3	*25*	---------	**1.000**	**<0.001**	-------	0.000	0.499	0.520	0.628
bp3.5-bp5	*0*								
rxm2 meta	79	-0.5363	**0.426**	**0.020**	0.211	0.000	0.260	0.605	0.708
bp1-bp2	*79*								
bp3	*78*	---------	0.000	0.500	-------	0.000	1.000	0.217	0.997
bp3.5	*56*	---------	**0.684**	**0.041**	0.411	0.000	0.239	0.954	0.848
bp4	*17*	---------	0.252	0.282	0.385	0.000	0.490	0.575	0.466
bp5	*0*								
rxm1 hypo	71	-0.9470	**0.688**	**0.007**	0.269	0.056	**0.099**	0.750	0.622
bp1	*34*	---------	**1.000**	**0.002**	-------	0.000	0.309	0.625	0.812
bp2	*15*	---------	0.544	0.154	0.488	0.150	**0.002**	0.110	**0.049**
bp3	*4*	---------	-------	-------	-------	-------	-------	-------	-------
bp3.5	*1*	---------	0.000	0.500	-------	0.000	-------	0.129	1.000
bp4-bp5	*0*								

rxm2 hypo	80	0.4191	0.130	0.267	0.223	0.085	**0.008**	0.352	**0.031**
bp1	*79*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*78*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	78	---------	-------	-------	-------	-------	-------	-------	-------
bp3.5	*67*	---------	0.930	0.073	0.581	0.042	**0.027**	0.894	0.114
bp4	*18*	---------	0.000	0.500	-------	0.051	**0.031**	0.466	**0.080**
bp5	*2*	---------	0.000	0.500	-------	0.000	1.000	0.171	1.000
rxm2 c5	77	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*2*	---------	0.000	0.500	-------	0.001	0.262	0.973	**0.038**
bp2-bp5	*0*								
rxm2 Carab	81	-0.4706	**0.747**	**0.001**	0.302	0.000	0.792	0.485	0.597
bp1	*80*	---------	0.000	0.500	-------	0.000	1.000	0.178	1.000
bp2	*73*	---------	0.000	0.500	-------	0.000	0.391	0.821	0.207
bp3	*60*	---------	0.398	0.162	0.432	0.000	0.678	0.518	0.498
bp4	*49*	---------	**1.000**	**<0.001**	-------	0.000	0.912	0.141	0.635
bp5	*32*	---------	**1.000**	**0.005**	-------	0.000	0.911	0.304	0.496
bp6	*16*	---------	0.515	0.101	0.412	0.000	0.496	0.427	0.605
bp7	*7*	---------	**1.000**	**0.030**	-------	0.000	0.879	0.823	0.785
rxm1 para^{j}	77	---------	0.000	0.500	-------	0.000	0.427	0.496	0.976
	3								
rxm2 para^{j}	81	---------	-------	-------	-------	-------	-------	-------	-------
	0								
rni1 shov	39	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*3*	---------	0.000	0.500	-------	0.312	0.383	**0.013**	1.000
bp2-bp7	*0*								
rni2 shov	52	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*23*	---------	**1.000**	**0.023**	-------	0.175	**0.001**	0.797	<0.001
bp2-bp7	*0*								
rnc dar*	45	1.0020	0.255	0.332	0.589	0.101	0.944	**0.036**	0.645
bp1	*12*	---------	0.544	0.294	0.897	0.096	0.909	**0.031**	0.671
bp2	*3*	---------	0.130	0.490	3.554	0.000	0.503	0.594	0.235

bp3-bp5	*0*								
rnm2 ant fovea	58	-0.4755	0.386	0.077	0.258	0.000	0.316	0.300	0.926
bp1	*53*	---------	0.000	0.500	-------	0.196	0.768	**0.006**	0.735
bp2	*39*	---------	0.293	0.254	0.311	0.000	0.952	0.175	0.892
bp3	*18*	---------	**0.970**	**0.039**	-------	0.000	0.183	0.746	0.618
bp4	*3*	---------	-------	-------	-------	-------	-------	-------	-------
rnm1 cno	56	-1.9842	0.178	0.272	0.322	0.000	0.351	0.277	0.942
bp5	*24*	---------	0.281	0.272	0.489	0.000	0.342	0.292	0.911
bp6	*0*								
rnm2 cno	72	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*72*								
bp6	*5*	---------	0.000	0.500	-------	0.119	0.383	0.227	**0.013**
bp7	*0*								
rnm2 groove[i]	43	---------	-------	-------	-------	-------	-------	-------	-------
y	*33*	---------	**1.000**	**0.004**	-------	0.000	0.653	0.147	0.358
x	*8*	---------	**1.000**	**0.006**	-------	0.072	0.602	0.288	**0.025**
+	*2*	---------	0.000	0.500	-------	0.000	0.824	0.821	0.920
rnm2 dwrink	61	-0.9667	0.349	0.144	0.333	0.062	**0.080**	0.748	0.371
bp1	*27*	---------	0.391	0.183	0.454	0.000	0.327	0.767	0.960
bp2	*16*	---------	0.763	0.081	0.546	0.000	0.136	0.594	0.404
bp3	*6*	---------	0.000	0.500	-------	0.079	**0.037**	0.273	0.202
rnm2 pstylid	78	-0.6559	**0.795**	**<0.001**	0.111	0.000	0.618	0.324	0.696
bp1	*59*	---------	**0.837**	**0.004**	0.222	0.039	0.965	**0.079**	0.990
bp2	*29*	---------	**1.000**	**0.001**	-------	0.000	0.658	0.464	0.628
bp3	*22*	---------	**1.000**	**<0.001**	-------	0.000	0.427	0.899	0.407
bp4	*15*	---------	**1.000**	**0.003**	-------	0.000	0.488	0.854	0.436
bp5	*8*	---------	1.000	0.066	-------	0.000	0.315	0.628	0.610
bp6	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp7	*0*								
rnm1 c5	55	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*23*	---------	0.472	0.160	0.514	0.000	0.177	0.424	0.887

	bp2	*17*	---------	0.000	0.500	-------	0.000	0.132	0.499	0.424
	bp3	*5*	---------	0.296	0.442	0.031	0.000	0.656	0.931	0.924
	bp4-bp5	*0*								
rnm2 c5		75	0.5748	**0.592**	**0.003**	0.180	0.097	0.180	0.331	**0.003**
	bp1-bp2	*75*								
	bp3	*74*	---------	1.000	0.452	-------	0.403	**0.015**	0.992	0.970
	bp4	*55*	---------	**0.774**	**0.022**	0.287	0.100	0.477	0.656	**0.012**
	bp5	*4*	---------	1.000	0.076	-------	0.000	0.998	0.531	0.548
rnm1 c6		62	---------	-------	-------	-------	-------	-------	-------	-------
		0								
rnm2 c6*		71	9.8359	0.000	0.500	0.484	0.048	0.371	0.961	**0.062**
	bp1	*4*	---------	0.000	0.500	-------	0.150	0.383	0.245	**0.014**
	bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
	bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
	bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------
	bp5	*0*								
rnm2 c7		79	-0.9026	0.394	0.087	0.321	0.000	0.549	0.131	0.721
	bp1	*28*	---------	0.373	0.205	0.485	0.033	0.678	**0.065**	0.764
	bp1a	*13*	---------	0.315	0.306	0.632	0.000	0.338	0.467	0.471
	bp2-bp4	*0*								
rnm2 dtcrest		73	---------	**1.000**	**0.043**	-------	0.067	**0.038**	0.335	0.467
		4								
xi1 lab cvx max		50	---------	-------	-------	-------	-------	-------	-------	-------
	bp1	*50*								
	bp2	*48*	---------	**1.000**	**0.009**	-------	0.133	**<0.001**	**<0.001**	0.482
	bp3	*24*	---------	0.931	0.118	0.784	0.000	0.653	0.631	0.534
	bp4	*3*	---------	-------	-------	-------	-------	-------	-------	-------
xi1 shov max		44	-0.8789	0.369	0.282	0.704	0.031	0.182	0.257	**0.062**
	bp1	*25*	---------	1.000	0.083	-------	0.000	0.516	0.307	0.236
	bp2	*5*	---------	0.000	0.500	-------	0.032	0.161	0.915	**0.080**
	bp3-bp7	*0*								

xi2 shov max	54	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*48*	---------	0.566	0.238	0.778	0.000	0.208	0.436	0.911
bp2	*11*	---------	0.000	0.500	-------	0.078	0.358	**0.044**	0.584
bp3	*1*	---------	1.000	0.378	-------	0.157	0.874	0.467	**0.091**
bp4-bp7	*0*								
xc shov max	66	-0.2249	0.000	0.500	-------	0.053	**0.073**	0.837	**0.060**
bp1	*47*	---------	0.230	0.327	0.508	0.059	**0.037**	0.691	**0.030**
bp2	*5*	---------	0.000	0.500	-------	0.000	0.801	0.651	0.645
bp3-bp7	*0*								
xi1 dshov max*	52	9.9959	0.000	0.500	-------	0.000	0.528	0.151	0.506
bp1	*4*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4-bp6	*0*								
xi2 dshov max	57	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*7*	---------	0.486	0.301	0.906	0.051	0.337	0.221	**0.079**
bp2-bp6	*0*								
xc dshov max	69	-0.5388	**0.590**	**0.012**	0.237	0.038	0.587	**0.055**	0.952
bp1	*58*	---------	0.240	0.321	9.609	0.000	0.943	0.675	0.532
bp2	*25*	---------	**1.000**	**0.020**	-------	0.053	0.261	**0.084**	0.632
bp3	*14*	---------	**1.000**	**0.042**	-------	0.000	0.195	0.105	0.654
bp4	*2*	---------	0.000	0.500	-------	0.000	0.236	0.115	0.990
bp5-bp6	*0*								
xi2 td max	49	-0.8588	0.000	0.500	-------	0.000	0.751	0.108	0.515
bp1	*22*	---------	0.000	0.500	-------	0.000	0.521	0.218	0.338
bp2	*3*	---------	1.000	0.210	-------	0.156	1.000	**0.071**	0.998
bp3	*1*	---------	0.000	0.500	-------	0.000	0.953	0.372	0.673
bp4-bp6	*0*								
xc dar max	59	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*23*	---------	**1.000**	**0.001**	-------	0.000	0.173	0.222	0.428
bp2	*4*	---------	-------	-------	-------	-------	-------	-------	-------

bp3-bp5	*0*								
xm1 meta max	72	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*60*	---------	**0.999**	**0.031**	0.472	0.000	0.369	0.117	0.916
bp2	*59*	---------	**1.000**	**0.006**	-------	0.038	**0.097**	0.207	0.946
bp3	*25*	---------	**1.000**	**0.011**	-------	0.000	0.169	0.261	0.579
bp3.5-bp5	*0*								
xm2 meta max	82	-0.5206	**0.446**	**0.022**	0.231	0.000	0.734	0.893	0.954
bp1-bp3	*82*								
bp3.5	*64*	---------	0.132	0.384	3.607	0.000	0.959	0.511	0.569
bp4	*19*	---------	**0.745**	**0.021**	0.536	0.000	0.674	0.528	0.643
bp5	*1*	---------	0.000	0.500	-------	0.000	1.000	0.340	1.000
xm1 hypo max	74	0.8319	0.339	0.103	0.293	0.000	0.142	0.309	0.951
bp1	*41*	---------	**0.912**	**0.008**	0.344	0.000	0.525	0.185	0.634
bp2	*21*	---------	0.000	0.500	-------	0.000	0.730	0.704	0.346
bp3	*6*	---------	-------	-------	-------	-------	-------	-------	-------
bp3.5	*1*	---------	1.000	0.334	-------	0.203	-------	**0.058**	1.000
bp4-bp5	*0*								
xm2 hypo max	84	0.1100	0.088	0.351	0.237	0.000	0.631	0.284	0.910
bp1-bp2	*84*								
bp3	*83*	---------	0.000	0.500	-------	0.000	1.000	0.340	1.000
bp3.5	*78*	---------	0.000	0.500	-------	0.099	0.884	**0.005**	0.798
bp4	*31*	---------	0.000	0.500	-------	0.000	0.410	0.551	0.776
bp5	*5*	---------	0.000	0.500	-------	0.000	0.640	0.979	0.491
xm2 c5 max	79	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*6*	---------	0.591	0.384	1.535	0.000	0.422	0.381	0.969
bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4-bp5	*0*								
xm2 Carab max	85	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*84*	---------	0.00	0.500	-------	0.000	1.000	0.345	1.000
bp2	*81*	---------	0.000	0.500	-------	0.203	**0.012**	0.472	**0.084**

bp3	*69*	---------	0.350	0.256	0.556	0.072	**0.009**	0.128	0.717
bp4	*52*	---------	**1.000**	**<0.001**	0.028	0.106	0.562	**0.001**	0.905
bp5	*41*	---------	**1.000**	**<0.001**	-------	0.060	0.683	**0.013**	0.620
bp6	*23*	---------	**1.000**	**0.007**	-------	0.104	0.472	**0.001**	0.848
bp7	*10*	---------	**1.000**	**0.003**	-------	0.048	0.741	0.483	**0.047**
xm1 para max^j	81*5*	---------	0.000	0.500	-------	0.134	1.000	**0.054**	0.996
xm2 para max^j	84*0*	---------	-------	-------	-------	-------	-------	-------	-------
ni1 shov max	42	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*3*	---------	0.000	0.500	-------	0.286	0.240	**0.018**	1.000
bp2-bp7	*0*								
ni2 shov max	55	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*26*	---------	**1.000**	**0.021**	-------	0.120	**0.009**	**0.072**	**0.066**
bp2	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp3-bp7	*0*								
nc dar max	52	0.4868	0.168	0.340	0.413	0.128	0.738	**0.014**	0.853
bp1	*17*	---------	0.132	0.428	0.390	0.115	0.972	**0.005**	0.547
bp2	*4*	---------	0.000	0.500	-------	0.000	0.447	0.808	0.660
bp3	*1*	---------	0.100	0.500	0.707	0.000	1.000	1.000	1.000
bp4-bp5	*0*								
nm2 ant fovea max	65	-0.4064	**0.672**	**0.007**	0.238	0.000	0.130	0.687	0.627
bp1	*63*	---------	0.000	0.500	-------	0.239	0.843	**0.038**	0.999
bp2	*48*	---------	**0.814**	**0.012**	0.257	0.000	0.256	0.407	0.773
bp3	*22*	---------	0.472	0.164	0.504	0.000	0.575	0.535	0.597
bp4	*3*	---------	-------	-------	-------	-------	-------	-------	-------
nm1 cno max	65	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*35*	---------	0.552	0.085	0.228	0.000	0.985	0.509	0.674
bp6	*0*								
nm2 cno max	78	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*78*								

bp6	*5*	---------	0.000	0.500	-------	0.128	0.304	0.190	**0.012**
bp7	*0*								
nm2 dwrink max	67	-1.1203	0.237	0.191	0.280	0.059	0.119	**0.088**	0.425
bp1	*39*	---------	0.514	0.101	0.439	0.000	0.319	0.243	0.810
bp2	*25*	---------	**0.818**	**0.027**	0.384	0.000	0.189	0.115	0.602
bp3	*9*	---------	0.068	0.460	0.587	0.000	0.162	0.111	0.240
nm2 pstylid max	79	-0.5296	**0.965**	**<0.001**	0.034	0.000	0.928	0.929	0.877
bp1	*67*	---------	**1.000**	**0.001**	-------	0.000	0.344	0.140	0.617
bp2	*37*	---------	**1.000**	**0.004**	-------	0.000	0.853	0.595	0.879
bp3	*25*	---------	**0.931**	**0.001**	0.204	0.000	0.171	0.365	0.236
bp4	*17*	---------	**1.000**	**0.001**	-------	0.000	0.682	0.880	0.725
bp5	*9*	---------	1.000	0.093	-------	0.017	**0.040**	0.862	0.558
bp6	*4*	---------	-------	-------	-------	-------	-------	-------	-------
bp7	*0*								
nm1 c5 max	61	-0.8942	0.102	0.349	0.278	0.000	0.110	0.975	0.429
bp1	*29*	---------	0.140	0.376	0.538	0.039	**0.099**	0.524	0.414
bp2	*24*	---------	0.271	0.298	0.503	0.045	**0.091**	0.900	0.435
bp3	*8*	---------	0.000	0.500	-------	0.000	0.442	0.533	0.667
bp4	*1*	---------	0.000	0.500	-------	0.194	0.853	**0.068**	1.000
bp5	*1*	---------	0.000	0.500	-------	0.194	0.853	**0.068**	0.999
nm2 c5 max	77	1.7151	0.334	0.052	0.221	0.000	0.971	0.394	0.211
bp1-bp3	*77*								
bp4	*70*	---------	0.747	0.057	0.333	0.114	0.493	0.656	**0.066**
bp5	*9*	---------	0.622	0.163	0.632	0.000	0.783	0.410	0.676
nm1 c6 max	82	---------	-------	-------	-------	-------	-------	-------	-------
	0								
nm2 c6 max*	75	10.8674	0.000	0.500	0.477	0.045	0.387	0.929	**0.073**
bp1	*5*	---------	0.000	0.500	-------	0.123	0.396	0.213	**0.013**
bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------

bp5	*0*								
nm2 c7 max	80	-0.8550	0.065	0.403	0.271	0.000	0.399	0.399	0.538
bp1	*51*	---------	0.000	0.500	-------	0.000	0.290	0.222	0.393
bp1a	*21*	---------	0.000	0.500	-------	0.000	0.274	0.244	0.454
bp2	*1*	---------	0.218	0.346	0.852	0.000	0.694	0.759	0.649
bp3-bp4	*0*								
nm2 dtcrest max	73	---------	0.306	0.339	0.764	0.156	0.592	**0.016**	0.781
	6								

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[a] l=left; r=right; x=maxillary; n=mandibular; max=maximum of the left and right antimeric expressions; bp= breakpoint. All morphological trait abbreviations outlined in Appendix C. Ordinal traits were normalized and treated as continuous for the purpose for heritability estimation. Breakpoints indicate presence/absence dichotomization cutoffs for ordinal traits; each of these breakpoints was treated as an individual binary character for heritability estimation. Kurtosis is not estimated for binary character models. Certain breakpoints were omitted from the heritability analysis because expression was monomorphic across the sample. Traits marked with asterisks are associated with less stable heritability estimates because other model parameters could not be estimated, because sample size was too small, or because kurtosis values were too high after normalization. These results should be accepted with caution. Dashes are associated with incalculable parameter estimates. Traits marked with dashes for all parameters represent models that failed to converge. The traits xc tuberculum dentale and nm1 cusp 7 were removed due to high levels of intra-observer error. [b] N=sample size for heritability estimation; Count=count for dichotomized trait expression (presence) at the denoted breakpoint (bp). Count values are italicized. If a trait is binary (i.e., its original scoring standards do not include ordinal scale scoring) this value is marked on a blank row beneath the sample size "N". [c] K=model kurtosis value. [d] h2= maximum likelihood heritability estimate. [e] All significant heritability estimates (p-value<0.05) and associated probability value estimates are bolded. [f] SE= maximum likelihood standard error estimate; this parameter estimate is typically omitted when heritability estimated equal 0.000 or 1.000. [g] c2= maximum likelihood total covariate estimate. [h] All significant probability value estimates for the covariates of age, sex, and age/sex interaction are bolded. [i] As the winging and groove pattern data are categorical and not ordinal, each category was treated as a separate binary variable. [j] Parastyle for deciduous molars was scored only as a binary variable at the breakpoint of ASUDAS grade 3.

Table 3. Burlington Growth Study sample heritability estimates: permanent crown morphology (ASUDAS standards).

			Heritability			Covariates			
Trait[a]	N[b] *Count*	K[c]	h2[d]	p-value[e]	SE[f]	c2[g]	age[h] p-value	sex[h] p-value	age*sex[h] p-value
LXI1 WING[i]	121	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*1*	---------	0.000	0.500	-------	0.000	0.301	0.406	0.994
bp3	*85*	---------	0.234	0.151	0.124	0.000	0.866	0.309	0.656
bp4	*32*	---------	0.433	0.067	0.318	0.000	0.802	0.254	0.813
LXI1 LAB CVX	121	-0.3305	0.247	0.053	0.171	0.091	**0.006**	0.206	0.869
bp1	*111*	---------	**1.000**	**0.035**	-------	0.196	**0.001**	0.268	**0.094**
bp2	*67*	---------	**0.436**	**0.033**	0.246	0.000	0.194	0.666	0.699
bp3	*11*	---------	1.000	0.067	-------	0.655	**0.001**	**0.010**	**<0.001**
bp4	*3*	---------	0.000	0.500	-------	0.118	**0.068**	0.221	0.381
LXI1 SHOV	117	-0.7442	**0.751**	**<0.001**	0.154	0.000	0.151	0.198	0.444
bp1	*80*	---------	**0.963**	**<0.001**	0.233	0.067	**0.006**	0.433	0.226
bp2	*30*	---------	**1.000**	**0.001**	-------	0.000	0.831	0.241	0.773
bp3	*6*	---------	0.643	0.061	0.383	0.000	0.176	0.453	0.278
bp4-bp7	*0*								
LXI2 SHOV	109	-0.6821	**0.365**	**0.017**	0.182	0.000	0.251	0.719	0.141
bp1	*70*	---------	0.308	0.143	0.299	0.000	0.218	0.494	0.345
bp2	*26*	---------	**0.607**	**0.035**	0.340	0.000	0.636	0.177	0.174
bp3	*12*	---------	0.744	0.076	16.753	0.018	0.195	0.261	**0.081**
bp4	*3*	---------	0.000	0.500	-------	0.197	0.916	1.000	**0.020**
bp5	*1*	---------	0.000	0.500	-------	0.000	0.221	0.432	0.995
bp6-bp7	*0*								
LXC SHOV	99	-0.4462	0.206	0.121	0.190	0.046	**0.036**	0.846	0.463
bp1	*45*	---------	0.411	0.098	0.342	0.054	**0.017**	0.528	0.421

bp2	*13*	---------	0.000	0.500	-------	0.000	0.279	0.890	0.455
bp3	*5*	---------	0.000	0.500	-------	0.000	0.779	0.335	0.903
bp4-bp7	*0*								
LXI1 DSHOV	121	-0.5214	**0.271**	**0.032**	0.163	0.054	**0.025**	0.958	0.695
bp1	*100*	---------	0.000	0.500	-------	0.074	**<0.001**	1.000	0.404
bp2	*62*	---------	**0.373**	**0.049**	0.232	0.000	0.147	0.543	0.699
bp3	*11*	---------	0.275	0.215	0.097	0.000	0.878	0.209	0.434
bp4	*4*	---------	0.000	0.500	-------	0.132	**<0.001**	**0.054**	**0.097**
bp5-bp6	*0*								
LXI2 DSHOV	115	-0.5285	0.143	0.199	0.182	0.047	**0.009**	0.830	0.172
bp1	*57*	---------	0.000	0.500	-------	0.062	**0.003**	0.203	**0.013**
bp2	*16*	---------	**0.953**	**0.008**	0.478	0.000	0.250	0.769	0.749
bp3	*5*	---------	0.000	0.500	-------	0.000	0.303	0.612	0.358
bp4	*1*	---------	0.000	0.500	-------	0.000	0.149	0.855	0.932
bp5-bp6	*0*								
LXC DSHOV*	111	-0.9775	**0.735**	**<0.001**	0.210	0.029	**0.057**	0.648	0.897
bp1	*90*	---------	**1.000**	**<0.001**	-------	0.141	**0.010**	0.859	0.813
bp2	*51*	---------	**0.943**	**<0.001**	0.253	0.000	0.439	0.735	0.431
bp3	*28*	---------	**0.661**	**0.013**	0.298	0.000	0.520	0.903	0.698
bp4	*3*	---------	0.000	0.500	-------	0.167	**0.023**	0.427	0.295
bp5-bp6	*0*								
LXP1 DSHOV	110	-0.7053	0.094	0.269	0.159	0.030	0.313	**0.089**	0.604
bp1	*71*	---------	0.005	0.493	0.260	0.010	**0.075**	0.202	0.320
bp2	*26*	---------	0.104	0.369	0.297	0.000	0.962	0.169	0.897
bp3	*8*	---------	0.429	0.239	0.594	0.000	0.550	0.572	0.659
bp4	*4*	---------	0.882	0.067	0.467	0.000	1.000	0.100	0.410
bp5	*1*	---------	0.000	0.500	-------	0.000	1.000	0.542	0.826
bp6	*0*								
LXP2 DSHOV	94	-0.4682	0.113	0.275	0.119	0.000	0.300	0.692	0.966
bp1	*27*	---------	0.212	0.251	0.345	0.000	0.321	0.491	0.998
bp2	*1*	---------	0.405	0.466	3.461	0.000	0.341	0.450	0.993

bp3-bp6	*0*								
LXI1 TD	100	-0.660	**0.532**	**0.001**	0.173	0.000	0.873	0.921	0.765
bp1	*78*	---------	**0.581**	**0.022**	0.289	0.000	0.445	0.345	0.436
bp2	*51*	---------	0.913	0.001	0.276	0.000	0.445	0.640	0.682
bp3	*27*	---------	0.037	0.456	0.337	0.000	0.506	0.267	0.892
bp4	*7*	---------	0.811	0.159	0.771	0.000	0.167	0.173	0.817
bp5-	*3*	---------	**1.000**	**0.026**	-------	0.003	**0.008**	0.636	0.184
bp5	*2*	---------	0.641	0.432	2.665	0.000	0.926	0.152	0.989
bp6	*1*	---------	0.000	0.500	-------	0.000	0.578	0.566	0.949
LXI2 TD	75	-0.9139	**0.692**	**0.024**	0.323	0.000	0.568	0.189	0.256
bp1	*48*	---------	0.649	0.088	0.413	0.000	0.648	0.267	0.272
bp2	*34*	---------	**0.900**	**0.015**	0.057	0.000	0.215	0.119	0.403
bp3	*20*	---------	**1.000**	**0.005**	-------	0.000	0.400	1.000	0.148
bp4	*14*	---------	**1.000**	**0.036**	-------	0.000	0.634	0.473	0.555
bp5-	*10*	---------	0.000	0.500	-------	0.000	0.722	0.746	0.896
bp5	*6*	---------	0.000	0.500	-------	0.000	0.558	0.449	0.530
bp6	*4*	---------	0.516	0.398	-------	0.157	1.000	**0.029**	1.000
LXC TD	82	-0.8006	0.254	0.115	0.225	0.000	0.572	0.261	0.409
bp1	*69*	---------	0.000	0.500	-------	0.000	0.317	0.326	0.203
bp2	*57*	---------	0.000	0.500	-------	0.000	0.141	0.769	0.175
bp3	*46*	---------	**0.847**	**0.007**	0.331	0.000	0.106	0.991	0.125
bp4	*37*	---------	0.399	0.111	0.337	0.000	0.126	0.432	0.109
bp5-	*27*	---------	0.236	0.258	0.001	0.000	0.318	0.293	0.401
bp5	*16*	---------	0.000	0.500	-------	0.000	0.228	0.470	0.483
bp6	*1*	---------	-------	-------	-------	-------	-------	-------	-------
LXC MES RIDGE*	110	53.2324	0.000	0.500	-------	0.000	0.395	0.676	0.733
bp1	*2*	---------	0.000	0.500	-------	0.000	0.343	0.935	0.714
bp2	*1*	---------	0.000	0.500	-------	0.000	0.343	0.530	0.992
bp3	*0*								
LXC DAR	103	-0.8650	0.329	0.057	0.221	0.141	**<0.001**	0.966	**0.005**
bp1	*74*	---------	0.000	0.500	-------	0.110	**<0.001**	0.165	**<0.001**

bp2	*52*	---------	0.617	**0.033**	0.383	0.037	**0.010**	0.159	0.974
bp3	*36*	---------	**0.766**	**0.010**	0.313	0.081	**0.002**	0.524	**0.049**
bp4	*19*	---------	0.592	0.100	0.481	0.103	**0.004**	0.858	**0.009**
bp5	*1*	---------	0.000	0.500	-------	0.000	0.129	0.853	1.000
LXP1 UTO AZ	96	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LXP1 ODONT	96	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LXP2 ODONT	62	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LXM1 META	113	0.1597	0.037	0.393	0.140	0.068	**0.033**	**0.008**	0.119
bp1-bp3	*113*								
bp3.5	*112*	---------	0.000	0.500	-------	0.000	1.000	1.000	0.669
bp4	*84*	---------	0.045	0.436	0.296	0.076	**0.014**	**0.024**	**0.020**
bp5	*5*	---------	0.000	0.500	-------	0.075	0.695	**<0.001**	0.467
LXM2 META	93	-0.7190	0.165	0.218	0.225	0.148	**<0.001**	0.424	**0.010**
bp1-bp2	*93*								
bp3	*92*	---------	0.100	0.500	0.707	0.767	**0.010**	0.997	0.987
bp3.5	*72*	---------	0.214	0.244	0.332	0.045	**0.008**	0.196	0.159
bp4	*23*	---------	0.165	0.347	0.669	0.098	**0.001**	0.165	**0.002**
bp5	*1*	---------	-------	-------	-------	-------	-------	-------	-------
LXM3 META*	7	3.0000	0.000	0.500	-------	0.000	0.507	0.489	0.489
bp1-bp2	*7*								
bp3	*6*	---------	0.000	0.500	-------	0.000	0.276	0.997	0.996
bp3.5	*1*	---------	0.000	0.500	-------	0.000	0.309	0.997	0.995
bp4-bp5	*0*								

LXM1 HYPO	107	-0.4880	0.124	0.207	0.165	0.000	0.153	0.433	0.408
bp1	*107*								
bp2	*105*	---------	0.101	0.495	0.730	0.377	**0.008**	**0.093**	**0.019**
bp3	*105*	---------	0.101	0.495	0.730	0.377	**0.008**	**0.093**	**0.019**
bp3.5	*103*	---------	0.000	0.500	-------	0.079	**0.062**	0.416	0.196
bp4	*96*	---------	0.527	0.160	0.584	0.000	0.299	0.824	0.424
bp5	*40*	---------	0.254	0.168	0.283	0.000	0.389	0.268	0.751
LXM2 HYPO	66	-0.6801	**0.431**	**0.025**	0.246	0.020	**0.042**	0.671	0.135
bp1	*65*	---------	0.063	0.500	3.569	0.000	0.209	0.597	0.991
bp2	*51*	---------	0.343	0.215	0.452	0.000	0.850	0.732	0.592
bp3	*45*	---------	**0.900**	**0.015**	0.451	0.017	**0.087**	0.812	0.151
bp3.5	*35*	---------	0.432	0.118	0.583	0.025	**0.060**	0.761	0.293
bp4	*16*	---------	0.319	0.251	0.521	0.000	0.275	0.878	0.264
bp5	*2*	---------	0.000	0.500	-------	0.000	0.228	0.140	0.994
LXM3 HYPO	3	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*3*								
bp2	*2*	---------	0.100	0.499	0.707	1.000	**0.096**	1.000	1.000
bp3	*2*	---------	0.100	0.499	0.707	1.000	**0.096**	1.000	1.000
bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*0*								
LXM1 C5	91	0.5956	0.021	0.445	0.157	0.034	**0.038**	0.187	0.402
bp1	*21*	---------	0.000	0.500	-------	0.040	**0.017**	0.773	0.217
bp2	*6*	---------	0.000	0.500	-------	0.083	0.230	**0.055**	0.494
bp3-bp5	*0*								
LXM2 C5*	64	3.7146	**0.732**	**0.032**	0.262	0.000	0.896	0.803	0.908
bp1	*9*	---------	0.934	0.152	0.726	0.000	0.448	0.946	0.597
bp2	*3*	---------	1.000	0.294	-------	0.022	**0.095**	0.328	0.128
bp3	*3*	---------	1.000	0.294	-------	0.022	**0.095**	0.328	0.128
bp4	*1*	---------	0.000	0.500	-------	0.000	0.100	0.804	0.995
bp5	*1*	---------	0.000	0.500	-------	0.000	0.100	0.804	0.995
LXM3 C5	3	---------	-------	-------	-------	-------	-------	-------	-------

bp1	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4-bp5	*0*								
LXM1 CARABELLI	111	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*90*	---------	**0.952**	**0.018**	0.494	0.034	**0.039**	0.627	0.235
bp2	*71*	---------	**1.000**	**<0.001**	-------	0.000	0.440	0.475	0.613
bp3	*67*	---------	**0.979**	**<0.001**	0.244	0.000	0.159	0.456	0.733
bp4	*58*	---------	**0.783**	**0.001**	0.226	0.000	0.655	0.982	0.327
bp5	*47*	---------	**0.924**	**<0.001**	0.186	0.000	0.971	0.819	0.142
bp6	*28*	---------	**0.960**	**<0.001**	0.740	0.000	0.354	0.567	0.210
bp7	*14*	---------	**0.846**	**0.003**	0.295	0.000	0.278	0.939	0.294
LXM2 CARABELLI	97	0.0875	0.209	0.201	0.269	0.000	0.889	0.683	0.449
bp1	*30*	---------	0.458	0.159	0.487	0.000	0.441	0.537	0.757
bp2	*14*	---------	0.000	0.500	-------	0.066	0.328	0.639	**0.013**
bp3	*12*	---------	0.270	0.336	0.675	0.083	0.112	0.221	**0.001**
bp4	*9*	---------	**1.000**	**0.048**	-------	0.158	**0.084**	**0.035**	**<0.001**
bp5	*8*	---------	0.000	0.500	-------	0.050	0.130	0.108	**0.007**
bp6	*4*	---------	1.000	0.198	-------	0.228	**0.036**	0.736	**0.008**
bp7	*2*	---------	1.000	0.317	-------	0.237	**0.047**	0.775	**0.064**
LXM3 CARABELLI*	9	0.0102	0.000	0.500	-------	0.484	0.373	0.104	**0.004**
bp1	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp7	*0*								
LXM1 PARA*	113	7.3207	**0.312**	**0.010**	0.150	0.024	0.273	**0.028**	0.154
bp1	*10*	---------	**0.689**	**0.031**	0.666	0.040	0.100	**0.034**	0.775
bp2	*2*	---------	0.000	0.500	-------	0.000	0.606	1.000	1.000

bp3	*2*	---------	0.000	0.500	-------	0.000	1.000	0.606	0.954
bp4-bp6	*0*								
LXM2 PARA*	101	101.0000	0.000	0.500	-------	0.000	1.000	0.394	0.733
bp1	*1*	---------	0.000	0.500	-------	0.000	1.000	0.350	0.768
bp2	*1*	---------	0.000	0.500	-------	0.000	1.000	0.340	0.998
bp3-bp6	*0*								
LXM3 PARA	7	---------	-------	-------	-------	-------	-------	-------	-------
bp1-bp6	*0*								
LXI2 PEG[j]	118	---------	-------	-------	-------	-------	-------	-------	-------
	1	---------	0.000	0.500	-------	0.000	1.000	0.701	1.000
LXM3 PEG[j]	8	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LXI2 CONG ABS	120	---------	0.000	0.500	-------	0.000	1.000	0.211	0.997
	2								
LXP2 CONG ABS	112	---------	0.000	0.500	-------	0.026	0.556	**0.074**	0.681
	18								
LXM3 CONG ABS	7	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LNI1 SHOV*	121	0.9887	**0.305**	**0.015**	0.157	0.000	0.533	0.861	0.921
bp1	*24*	---------	**0.509**	**0.027**	0.270	0.000	0.395	0.697	0.958
bp2	*1*	---------	0.000	0.500	-------	0.000	0.457	0.213	0.995
bp3-bp7	*0*								
LNI2 SHOV	121	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*24*	---------	**0.682**	**0.012**	0.381	0.000	0.940	0.788	0.736
bp2-bp7	*0*								
LNC DAR	114	-0.1175	0.066	0.362	0.194	0.268	**<0.001**	**<0.001**	**0.006**
bp1	*49*	---------	0.000	0.500	-------	0.132	**<0.001**	**0.003**	**0.071**
bp2	*23*	---------	0.392	0.235	0.567	0.292	**<0.001**	**<0.001**	**0.067**
bp3	*12*	---------	0.067	0.466	0.519	0.252	**0.003**	**0.080**	0.858
bp4	*5*	---------	0.000	0.500	-------	0.069	**0.089**	0.169	**0.993**
bp5	*0*								

LNP1 LING CUSP^i	108	----------	-------	-------	-------	-------	-------	-------	-------
bp 0	9	----------	0.395	0.246	0.597	0.153	**0.020**	0.972	**0.003**
bp1	*14*	---------	0.000	0.500	-------	0.000	0.445	0.272	0.152
bp2	*18*	---------	0.371	0.084	0.311	0.000	0.455	0.846	0.460
bp3	*20*	---------	0.000	0.500	-------	0.030	**0.079**	0.539	0.787
bp4	*5*	---------	0.000	0.500	-------	0.000	0.301	0.106	0.854
bp5	*6*	---------	0.198	0.356	0.550	0.056	0.313	0.979	**0.071**
bp6	*12*	---------	0.328	0.213	0.427	0.000	0.270	0.396	0.158
bp7	*13*	---------	0.448	0.211	0.525	0.000	0.653	0.636	0.988
bp8	*10*	---------	0.899	0.146	0.685	0.000	0.794	0.478	0.717
bp9	*1*	---------	1.000	0.326	<0.001	0.112	1.000	**0.011**	0.947
LNP1 ODONT	103	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LNP2 ODONT	69	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LNM1 ANT FOVEA	44	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*34*	---------	0.000	0.500	-------	0.000	0.624	0.854	0.190
bp2	*19*	---------	**1.000**	**0.028**	-------	0.000	0.469	0.272	0.166
bp3	*8*	---------	**1.000**	**0.048**	-------	0.132	**0.049**	0.153	0.274
bp4	*2*	---------	1.000	0.271	-------	0.183	0.997	**0.084**	0.998
LNM1 CNO*	91	2.9810	0.034	0.425	0.185	0.000	0.182	0.718	0.760
bp5	*86*	---------	0.000	0.500	-------	0.000	0.784	0.596	1.000
bp6	*12*	---------	0.391	0.242	0.549	0.068	**0.011**	0.176	**0.062**
bp7	*1*	---------	1.000	0.329	-------	0.111	1.000	**0.053**	0.999
bp8	*1*	---------	1.000	0.324	-------	0.000	1.000	0.325	0.999
LNM2 CNO	64	0.4323	**0.544**	**0.008**	0.248	0.106	0.597	**0.006**	0.882
bp5	*14*	---------	**1.000**	**0.008**	-------	0.134	0.557	**0.008**	0.766
bp6	*1*	---------	0.000	0.500	-------	0.000	0.129	0.859	0.925
bp7-bp8	*0*								
LNM3 CNO	4	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*2*	---------	0.100	0.500	0.707	0.946	**0.096**	0.994	0.985

bp6	*1*	---------	0.100	0.500	0.707	0.384	0.991	**<0.001**	0.460
bp7-bp8	*0*								
LNM1 GROOVE	20	---------	-------	-------	-------	-------	-------	-------	-------
y	*15*	---------	0.114	0.468	1.413	0.000	0.309	0.492	0.548
x	*4*	---------	0.000	0.500	-------	0.000	0.309	0.214	0.370
+	*2*	---------	0.000	0.500	-------	0.000	0.909	0.547	0.986
LNM2 GROOVE	46	---------	-------	-------	-------	-------	-------	-------	-------
y	*9*	---------	**1.000**	**0.035**	-------	0.000	0.821	0.440	0.451
x	*18*	---------	0.716	0.177	0.763	0.143	**0.005**	0.850	**0.084**
+	*19*	---------	-------	-------	-------	-------	-------	-------	-------
LNM3 GROOVE	5	---------	-------	-------	-------	-------	-------	-------	-------
y	*2*	---------	0.000	0.500	-------	0.000	0.980	1.000	0.996
x	*1*	---------	-------	-------	-------	-------	-------	-------	-------
+	*2*	---------	-------	-------	-------	-------	-------	-------	-------
LNM1 DWRINK	49	-0.5129	0.000	0.500	-------	0.000	0.237	0.288	0.141
bp1	*18*	---------	0.000	0.500	-------	0.012	0.106	0.516	**0.073**
bp2	*6*	---------	0.000	0.500	-------	0.066	0.384	**0.095**	0.368
bp3	*1*	---------	1.000	0.345	-------	0.000	0.998	0.286	0.991
LNM1 PSTYLID	85	-0.5877	**0.450**	**0.038**	0.228	0.030	0.429	0.868	**0.097**
bp1	*40*	---------	0.093	0.416	0.432	0.027	0.547	0.496	**0.071**
bp2	*25*	---------	0.093	0.416	0.440	0.027	0.547	0.496	**0.071**
bp3	*6*	---------	**1.000**	**0.006**	-------	0.000	0.647	0.755	0.984
bp4	*1*	---------	0.127	0.490	3.555	0.000	0.999	0.374	0.998
bp5-bp7	*0*								
LNM2 PSTYLID	86	0.1107	0.226	0.151	0.243	0.052	**0.018**	0.207	**0.064**
bp1	*29*	---------	0.034	0.462	0.374	0.062	**0.010**	0.821	**0.038**
bp2	*22*	---------	0.137	0.346	0.352	0.042	**0.026**	0.410	0.301
bp3	*2*	---------	0.000	0.500	-------	0.439	1.000	0.931	**<0.001**
bp4-bp7	*0*								
LNM3 PSTYLID	*7*	0.0000	1.000	0.266	-------	0.000	0.760	0.202	0.397
bp1	*1*	---------	1.000	0.382	-------	0.000	1.000	0.204	0.997

bp2	*1*	---------	1.000	0.382	-------	0.000	1.000	0.204	0.997
bp3	*1*	---------	1.000	0.382	-------	0.000	1.000	0.204	0.997
bp4	*1*	---------	1.000	0.382	-------	0.000	1.000	0.204	0.997
bp5	*1*	---------	1.000	0.382	-------	0.000	1.000	0.204	0.997
bp6	*1*	---------	1.000	0.382	-------	0.000	1.000	0.204	0.997
bp7	*0*								
LNM1 C5	91	-0.6078	**0.404**	**0.034**	0.244	0.000	0.434	0.631	0.602
bp1	*86*	---------	0.000	0.500	-------	0.000	0.912	0.104	0.803
bp2	*81*	---------	0.000	0.500	-------	0.000	0.901	0.639	0.685
bp3	*76*	---------	0.000	0.500	-------	0.000	0.374	1.000	0.697
bp4	*59*	---------	0.490	0.093	0.350	0.000	0.577	0.935	0.523
bp5	*21*	---------	**0.723**	**0.019**	0.289	0.000	0.478	0.253	0.678
LNM3 C5	4	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*2*	---------	0.100	0.500	0.707	0.946	**0.096**	0.994	0.985
bp2	*2*	---------	0.100	0.500	0.707	0.946	**0.096**	0.994	0.985
bp3	*2*	---------	0.100	0.500	0.707	0.946	**0.096**	0.994	0.985
bp4	*2*	---------	0.100	0.500	0.707	0.946	**0.096**	0.994	0.985
bp5	*1*	---------	0.100	0.498	0.707	1.000	**0.096**	0.994	0.985
LNM1 C6*	91	4.0835	0.144	0.213	0.193	0.000	0.178	0.845	0.497
bp1	*12*	---------	0.000	0.500	-------	0.000	0.912	0.104	0.803
bp2	*7*	---------	0.847	0.111	0.666	0.075	**0.022**	0.152	**<0.001**
bp3	*1*	---------	0.000	0.500	-------	0.000	1.000	0.313	0.931
bp4-bp5	*0*								
LNM2 C6*	69	69.0000	0.000	0.500	-------	0.000	0.137	0.125	0.322
bp1	*1*	---------	0.000	0.500	-------	0.000	0.128	0.879	0.994
bp2	*1*	---------	0.000	0.500	-------	0.000	0.128	0.881	0.909
bp3-bp5	*0*								
LNM3 C6	6	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	0.100	0.500	0.707	0.000	0.999	0.327	0.998
bp2-bp5	*0*								
LNM1 C7*	104	4.0579	0.000	0.500	-------	0.000	0.403	0.806	0.276

bp1	*14*	---------	0.000	0.500	-------	0.000	0.233	0.995	0.166
bp1a	*11*	---------	0.000	0.500	-------	0.000	0.656	0.826	0.486
bp2	*9*	---------	0.000	0.500	-------	0.000	0.690	0.418	0.503
bp3	*3*	---------	0.000	0.500	-------	0.000	0.544	0.415	0.702
bp4	*2*	---------	0.000	0.499	-------	0.172	0.657	**0.067**	1.000
LNM2 C7*	97	29.7996	0.000	0.500	-------	0.000	1.000	0.138	0.729
bp1	*3*	---------	0.000	0.500	-------	0.153	1.000	**0.081**	0.998
bp1a	*1*	---------	0.000	0.500	-------	0.000	0.997	0.287	1.000
bp2-bp4	*0*								
LNM3 C7*	10	5.0127	0.000	0.500	-------	0.647	1.000	**0.010**	**0.014**
bp1	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp1a	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp3-bp4	*0*								
LNM1 DTCREST	65	---------	0.000	0.500	-------	0.000	1.000	0.317	1.000
	1								
LNM2 DTCREST	82	---------	0.528	0.180	0.503	0.000	0.178	0.656	0.538
	5								
LNM3 DTCREST	11	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LNI1 CONG ABS	124	---------	0.000	0.500	-------	0.000	1.000	0.170	0.510
	2								
LNP2 CONG ABS	111	---------	0.000	0.500	-------	0.000	0.273	0.403	0.716
	14								
LNM3 CONG ABS	9	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RXI1 WING	121	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*1*	---------	0.000	0.500	-------	0.000	0.392	0.388	0.994
bp3	*94*	---------	0.379	0.072	0.281	0.000	0.824	0.245	0.304
bp4	*23*	---------	**0.588**	**0.012**	0.269	0.000	0.524	0.105	0.803

RXI1 LAB CVX	121	-0.1658	0.291	0.075	0.241	0.096	**0.004**	0.443	0.740
bp1	*113*	---------	0.000	0.500	-------	0.242	**0.030**	0.189	0.370
bp2	*66*	---------	0.162	0.283	0.295	0.042	**0.047**	0.925	0.863
bp3	*19*	---------	0.470	0.187	0.560	0.105	**0.001**	**0.052**	0.160
bp4	*1*	---------	0.000	0.500	-------	0.000	1.000	0.610	0.989
RXI1 SHOV	119	-0.5639	**0.718**	**<0.001**	0.176	0.000	0.629	0.177	0.490
bp1	*84*	---------	**0.663**	**0.011**	0.339	0.000	0.429	0.174	0.707
bp2	*24*	---------	**1.000**	**<0.001**	-------	0.052	0.972	0.942	**0.035**
bp3	*3*	---------	0.000	0.449	-------	0.119	1.000	**0.089**	0.981
bp4-bp7	*0*								
RXI2 SHOV	111	-0.7345	**0.541**	**0.001**	0.181	0.000	0.657	0.688	0.283
bp1	*68*	---------	**0.612**	**0.013**	0.281	0.018	0.937	**0.092**	0.471
bp2	*25*	---------	**1.000**	**0.001**	-------	0.000	0.359	0.192	0.233
bp3	*10*	---------	1.000	0.094	-------	0.058	0.241	**0.070**	0.246
bp4	*2*	---------	0.000	0.500	-------	0.175	0.701	**0.073**	1.000
bp5-bp7	*0*								
RXC SHOV	103	-0.7504	0.000	0.500	-------	0.000	0.192	0.668	0.705
bp1	*56*	---------	0.000	0.500	-------	0.000	0.308	0.682	0.957
bp2	*10*	---------	0.546	0.126	0.443	0.081	**0.010**	0.238	**0.054**
bp3	*1*	---------	0.000	0.500	-------	0.000	1.000	0.303	1.000
bp4-bp7	*0*								
RXI1 DSHOV	119	-0.2979	**0.249**	**0.042**	0.162	0.065	**0.034**	0.950	0.974
bp1	*101*	---------	0.118	0.368	0.367	0.000	0.195	0.652	0.410
bp2	*56*	---------	0.330	0.096	0.264	0.026	**0.089**	0.962	0.704
bp3	*16*	---------	0.600	0.065	0.435	0.052	**0.063**	0.654	0.831
bp4	*4*	---------	0.000	0.500	-------	0.000	0.972	0.620	0.885
bp5-bp6	*0*								
RXI2 DSHOV	114	-0.7301	0.000	0.500	-------	0.000	0.104	0.567	0.836
bp1	*60*	---------	0.000	0.500	-------	0.000	0.103	0.322	0.776
bp2	*20*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*6*	---------	-------	-------	-------	-------	-------	-------	-------

bp4	*3*	---------	0.000	0.500	-------	0.078	**<0.001**	0.295	**0.078**
bp5-bp7	*0*								
RXC DSHOV	106	-0.5182	**0.321**	**0.033**	0.199	0.046	**0.075**	0.731	0.820
bp1	*81*	---------	0.244	0.198	0.311	0.000	0.114	0.402	0.731
bp2	*51*	---------	**0.503**	**0.025**	0.272	0.000	0.248	0.252	0.505
bp3	*27*	---------	0.357	0.157	0.375	0.023	**0.039**	0.243	0.274
bp4	*7*	---------	0.000	0.500	-------	0.000	0.946	0.434	0.611
bp5-bp6	*0*								
RXP1 DSHOV	109	-0.6279	**0.289**	**0.028**	0.162	0.032	0.837	**0.069**	0.186
bp1	*73*	---------	0.193	0.185	0.263	0.000	0.647	0.130	0.425
bp2	*27*	---------	0.396	0.137	0.359	0.000	0.867	0.219	0.367
bp3	*9*	---------	0.765	0.145	0.920	0.057	0.569	0.945	**0.078**
bp4	*2*	---------	**1.000**	**0.034**	-------	0.000	0.998	0.298	0.997
bp5-bp6	*0*								
RXP2 DSHOV	93	0.6502	0.067	0.348	0.180	0.000	0.534	0.277	0.457
bp1	*23*	---------	0.000	0.500	-------	0.000	1.000	0.891	1.000
bp2	*5*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*1*	---------	0.000	0.500	-------	0.000	1.000	0.891	1.000
bp4-bp6	*0*								
RXI1 TD	101	-0.7186	**0.504**	**0.006**	0.192	0.000	0.996	0.905	0.901
bp1	*75*	---------	0.469	0.083	0.320	0.000	0.323	0.436	0.897
bp2	*45*	---------	**0.754**	**0.004**	0.295	0.000	0.942	0.773	0.552
bp3	*22*	---------	0.000	0.500	-------	0.000	0.454	0.204	0.775
bp4	*5*	---------	0.000	0.500	-------	0.000	0.224	0.418	0.834
bp5-	*2*	---------	1.000	0.312	-------	0.000	1.000	0.189	0.996
bp5	*1*	---------	1.000	0.325	-------	0.000	0.936	0.331	1.000
bp6	*1*	---------	1.000	0.325	-------	0.000	0.936	0.331	1.000
RXI2 TD	83	-0.8373	**0.680**	**0.009**	0.240	0.000	0.837	0.146	0.766
bp1	*55*	---------	0.395	0.157	0.457	0.000	0.725	0.154	0.967
bp2	*35*	---------	0.484	0.115	0.404	0.000	0.480	0.481	0.556
bp3	*21*	---------	**0.948**	**0.011**	0.332	0.000	0.735	0.470	0.229

bp4	*15*	---------	**1.000**	**0.012**	-------	0.000	0.541	0.319	0.358
bp5-	*12*	---------	1.000	0.073	-------	0.000	0.617	0.732	0.458
bp5	*4*	---------	0.837	0.334	1.413	0.000	0.369	0.953	0.865
bp6	*2*	---------	0.183	0.484	3.829	0.000	0.134	0.334	0.229
RXC TD	88	-0.6287	**0.692**	**0.010**	0.305	0.000	0.576	0.354	0.610
bp1	*76*	---------	0.286	0.310	0.597	0.000	0.165	0.893	0.180
bp2	*60*	---------	0.083	0.420	1.179	0.000	0.356	0.433	0.440
bp3	*43*	---------	0.467	0.091	0.348	0.000	0.705	0.259	0.604
bp4	*35*	---------	**1.000**	**0.001**	-------	0.000	0.440	0.393	0.483
bp5-	*26*	---------	**0.955**	**0.014**	0.391	0.037	0.914	**0.045**	0.483
bp5	*14*	---------	0.000	0.500	-------	0.000	0.503	0.133	0.376
bp6	*3*	---------	-------	-------	-------	-------	-------	-------	-------
RXC MES RIDGE*	110	52.4254	0.000	0.500	-------	0.000	0.419	0.823	0.249
bp1	*2*	---------	0.000	0.500	-------	0.000	0.299	0.940	0.203
bp2	*2*	---------	0.000	0.500	-------	0.000	**0.045**	0.882	0.185
bp3	*0*								
RXC DAR	97	-0.6673	0.208	0.175	0.225	0.019	**0.091**	0.146	0.380
bp1	*78*	---------	0.000	0.500	-------	0.000	0.981	0.947	0.194
bp2	*57*	---------	0.345	0.187	0.446	0.015	**0.052**	0.532	0.197
bp3	*37*	---------	0.382	0.166	0.401	0.007	0.150	0.657	**0.099**
bp4	*14*	---------	0.000	0.500	-------	0.122	**0.070**	**0.005**	0.168
bp5	*3*	---------	0.000	0.500	-------	0.192	0.692	**0.023**	1.000
RXP1 UTO AZ	100	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RXP1 ODONT	98	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RXP2 ODONT	60	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RXM1 META	115	0.9248	0.000	0.500	-------	0.000	0.191	0.417	0.143
bp1-bp3.5	*115*								
bp4	*100*	---------	0.000	0.500	-------	0.000	0.461	0.862	0.476

bp5	*15*	---------	0.000	0.500	-------	0.011	0.289	0.166	**0.064**
RXM2 META	99	-0.5879	0.265	0.051	0.183	0.000	0.277	0.371	0.648
bp1-bp3	*99*								
bp3.5	*84*	---------	**0.733**	**0.042**	0.510	0.063	**0.047**	0.521	0.589
bp4	*42*	---------	0.031	0.453	0.271	0.000	0.435	0.349	0.277
bp5	*2*	---------	**1.000**	**0.030**	<0.001	0.000	0.221	0.457	0.412
RXM3 META	5	-1.3000	0.100	0.500	-------	0.000	0.443	1.000	1.000
bp1-bp3	*5*								
bp3.5	*2*	---------	0.100	0.500	0.707	0.000	0.410	1.000	1.000
bp4	*1*	---------	0.100	0.500	0.707	0.000	1.000	0.989	1.000
bp5	*0*								
RXM1 HYPO	104	0.2463	0.142	0.216	0.196	0.000	0.111	0.808	0.118
bp1	*104*								
bp2	*103*	---------	0.000	0.500	-------	0.000	1.000	0.994	0.911
bp3	*102*	---------	0.000	0.500	-------	0.194	0.120	0.498	**0.005**
bp3.5	*101*	---------	0.120	0.494	4.180	0.479	**0.007**	0.722	0.669
bp4	*88*	---------	0.401	0.124	1.389	0.000	0.493	0.617	0.664
bp5	*21*	---------	0.059	0.432	0.357	0.024	0.276	0.961	**0.058**
RXM2 HYPO	65	-0.7052	0.404	0.071	0.291	0.068	**0.015**	0.814	0.377
bp1	*64*	---------	0.000	0.500	-------	0.000	0.156	0.666	0.996
bp2	*48*	---------	0.427	0.126	0.792	0.000	0.444	0.965	0.804
bp3	*35*	---------	0.472	0.152	0.507	0.045	**0.036**	0.330	0.255
bp3.5	*26*	---------	0.030	0.473	0.456	0.082	**0.006**	0.928	0.276
bp4	*11*	---------	0.646	0.180	0.782	0.000	0.147	0.592	0.662
bp5	*2*	---------	0.943	0.364	1.729	0.000	0.156	0.333	0.988
RXM3 HYPO*	4	-2.5743	1.000	0.152	-------	0.000	0.512	1.000	1.000
bp1	*4*								
bp2	*3*	---------	1.000	0.322	-------	0.000	0.998	0.994	0.958
bp3	*2*	---------	1.000	0.209	-------	0.000	0.146	0.998	0.997
bp4-bp5	*0*								
RXM1 C5*	96	1.9494	0.159	0.118	0.145	0.023	**0.032**	0.450	0.125

bp1	*17*	---------	0.000	0.500	-------	0.093	**0.003**	0.128	**<0.001**
bp2	*3*	---------	0.334	0.303	0.642	0.084	**0.066**	0.284	0.571
bp3	*1*	---------	0.000	0.500	-------	0.108	0.961	**<0.001**	0.965
bp4-bp5	*0*								
RXM2 C5*	66	3.1543	**1.000**	**0.002**	-------	0.017	**0.072**	0.320	0.348
bp1	*10*	---------	1.000	0.107	-------	0.000	0.212	0.470	0.318
bp2	*3*	---------	**1.000**	**0.024**	-------	0.000	0.556	0.431	0.253
bp3	*3*	---------	1.000	**0.024**	-------	0.000	0.556	0.431	0.253
bp4	*1*	---------	0.000	0.500	-------	0.000	0.331	0.361	0.994
bp5	*1*	---------	0.000	0.500	-------	0.000	0.331	0.361	0.994
RXM3 C5	4	-2.5743	1.000	0.243	-------	0.000	0.512	0.961	0.998
bp1	*2*	---------	1.000	0.209	-------	0.000	0.146	0.998	0.997
bp2	*2*	---------	1.000	0.209	-------	0.000	0.146	0.998	0.997
bp3	*1*	---------	0.000	0.500	-------	0.000	0.999	0.994	0.960
bp4-bp5	*0*								
RXM1 CARABELLI	105	-0.8555	**0.687**	**<0.001**	0.141	0.000	0.496	0.862	0.500
bp1	*87*	---------	0.013	0.489	0.418	0.100	**0.011**	0.524	0.767
bp2	*67*	---------	**0.782**	**0.002**	0.251	0.000	0.223	0.128	0.145
bp3	*63*	---------	**0.770**	**<0.001**	0.234	0.000	0.431	0.136	0.105
bp4	*56*	---------	**1.000**	**<0.001**	-------	0.000	0.668	0.394	0.341
bp5	*41*	---------	**0.999**	**<0.001**	0.276	0.000	0.902	0.957	0.370
bp6	*22*	---------	**0.597**	**0.028**	0.327	0.000	0.144	0.866	0.173
bp7	*13*	---------	0.536	0.066	0.340	0.023	**0.066**	0.984	0.144
RXM2 CARABELLI	96	-0.2266	**0.438**	**0.022**	0.254	0.047	0.177	0.271	**0.025**
bp1	*35*	---------	0.477	0.072	0.359	0.049	0.280	0.339	**0.017**
bp2	*14*	---------	**1.000**	**0.027**	-------	0.000	0.121	0.715	0.284
bp3	*8*	---------	**1.000**	**0.012**	-------	0.000	0.638	0.648	0.110
bp4	*6*	---------	**1.000**	**0.004**	-------	0.000	0.769	0.808	0.327
bp5	*4*	---------	1.000	0.059	-------	0.000	0.661	0.603	0.492
bp6	*2*	---------	0.000	0.500	-------	0.000	0.629	0.268	0.285
bp7	*0*								

RXM3 CARABELLI*	8	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*3*		0.000	0.500	-------	0.358	0.862	1.000	**0.079**
bp2-bp7	*0*								
RXM1 PARA*	114	6.5636	0.104	0.311	0.218	0.000	0.169	0.867	0.170
bp1	*11*	---------	0.318	0.285	0.573	0.000	0.164	0.868	0.165
bp2	*1*	---------	0.000	0.500	-------	0.000	0.999	0.398	0.998
bp3-bp6	*0*								
RXM2 PARA*	97	45.9151	0.000	0.500	-------	0.000	0.104	0.766	0.538
bp1	*2*	---------	0.000	0.500	-------	0.000	0.136	0.769	0.637
bp2	*2*	---------	0.000	0.500	-------	0.000	0.136	0.769	0.637
bp3-bp6	*0*								
RXM3 PARA	7	---------	-------	-------	-------	-------	-------	-------	-------
bp1-bp6	*0*								
RXI2 PEG[j]	116	---------	-------	-------	-------	-------	-------	-------	-------
	1	---------	0.000	0.500	-------	0.000	1.000	0.290	0.781
RXM3 PEG[j]	10	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RXI2 CONG ABS	120	---------	0.000	0.500	-------	0.000	1.000	0.401	0.996
	1								
RXP2 CONG ABS	113	---------	**0.668**	**0.046**	0.368	0.000	0.624	0.369	0.517
	20								
RXM3 CONG ABS	10	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RNI1 SHOV	119	0.7096	**0.310**	**0.019**	0.166	0.000	0.546	0.579	0.426
bp1	*25*	---------	**0.523**	**0.031**	0.289	0.000	0.412	0.477	0.553
bp2	*1*	---------	0.000	0.500	-------	0.000	0.433	0.305	0.995
bp3-bp7	*0*								
RNI2 SHOV	120	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*27*	---------	0.439	0.083	0.854	0.000	0.839	0.878	0.670
bp2-bp7	*0*								
RNC DAR	106	0.5366	0.144	0.219	0.203	0.313	**<0.001**	**<0.001**	**0.027**

bp1	*39*	---------	0.459	0.120	0.433	0.196	**0.025**	<**0.001**	0.318
bp2	*18*	---------	0.405	0.212	0.543	0.238	**0.001**	**0.005**	**0.043**
bp3	*8*	---------	0.000	0.500	-------	0.140	0.108	**0.006**	0.855
bp4	*2*	---------	0.000	0.500	-------	0.000	0.216	0.229	0.994
bp5	*0*								
RNP1 LING CUSP[i]	103	---------	-------	-------	-------	-------	-------	-------	-------
bp0	*19*	---------	**0.822**	**0.002**	0.226	0.000	0.698	0.159	0.957
bp1	*8*	---------	0.000	0.500	-------	0.066	0.797	**0.015**	0.100
bp2	*16*	---------	**0.699**	**0.032**	0.985	0.000	0.999	0.907	0.806
bp3	*12*	---------	0.115	0.408	0.433	0.000	0.196	0.380	0.148
bp4	*6*	---------	0.891	0.082	0.655	0.066	**0.090**	0.617	**0.005**
bp5	*3*	---------	0.000	0.500	-------	0.000	0.371	0.560	0.686
bp6	*11*	---------	**0.847**	**0.003**	0.245	0.000	0.442	0.921	0.481
bp7	*15*	---------	0.165	0.335	0.398	0.000	0.858	0.420	0.740
bp8	*9*	---------	**0.704**	**0.049**	0.350	0.000	0.570	0.110	0.919
bp9	*4*	---------	0.000	0.500	-------	0.024	0.134	0.166	**0.082**
RNP1 ODONT	108	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RNP2 ODONT	70	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RNM1 ANT FOV	47	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*38*	---------	0.666	0.190	0.746	0.000	0.500	0.405	0.164
bp2	*30*	---------	**1.000**	**0.009**	-------	0.000	0.519	0.158	0.572
bp3	*19*	---------	**1.000**	**0.013**	-------	0.058	**0.059**	0.110	0.685
bp4	*4*	---------	0.350	0.446	2.182	0.000	0.166	0.171	0.754
RNM1 CNO	91	1.4688	0.018	0.457	0.166	0.000	0.189	0.292	0.791
bp5	*83*	---------	0.000	0.500	-------	0.000	0.856	0.705	0.321
bp6	*13*	---------	0.476	0.171	0.548	0.057	**0.059**	0.464	0.773
bp7-bp8	*0*								
RNM2 CNO*	71	0.8769	0.038	0.416	0.182	0.064	0.377	**0.064**	0.334
bp5	*16*	---------	0.000	0.500	-------	0.060	0.633	**0.042**	0.216

bp6	*3*	---------	1.000	0.069	-------	0.000	0.205	0.273	0.434
bp7-bp8	*0*								
RNM3 CNO*	5	5.0000	0.000	0.500	-------	0.000	1.000	1.000	1.000
bp5	*4*	---------	0.000	0.499	-------	0.101	0.986	**0.070**	0.991
bp6-bp8	*0*								
RNM1 GROOVE	27	---------	-------	-------	-------	-------	-------	-------	-------
y	*18*	---------	0.000	0.500	-------	0.000	0.942	0.845	0.728
x	*6*	---------	0.838	0.285	1.286	0.000	0.548	0.925	0.254
+	*3*	---------	-------	-------	-------	-------	-------	-------	-------
RNM2 GROOVE	46	---------	-------	-------	-------	-------	-------	-------	-------
y	*8*	---------	**1.000**	**0.003**	-------	0.000	0.677	0.126	0.331
x	*15*	---------	0.655	0.193	0.820	0.045	0.305	**0.061**	0.886
+	*23*	---------	1.000	0.018	-------	0.000	0.512	0.386	0.890
RNM3 GROOVE	6	---------	-------	-------	-------	-------	-------	-------	-------
y	*0*								
x	*4*	---------	0.097	0.500	1.063	0.637	**0.050**	**0.078**	0.993
+	*2*	---------	-------	-------	-------	-------	-------	-------	-------
RNM1 DWRINK	54	-0.4141	0.370	0.210	0.472	0.047	0.473	**0.099**	0.259
bp1	*24*	---------	0.490	0.211	0.587	0.056	0.691	**0.033**	0.212
bp2	*6*	---------	1.000	0.275	-------	0.131	0.164	**0.012**	**0.057**
bp3	*1*	---------	1.000	0.331	-------	0.000	0.970	0.281	1.000
RNM1 PSTYLID	96	-0.7641	0.131	0.263	0.218	0.000	0.978	0.919	0.351
bp1	*51*	---------	0.236	0.216	0.316	0.000	0.383	0.631	0.430
bp2	*26*	---------	0.000	0.500	-------	0.000	0.907	0.725	0.339
bp3	*11*	---------	**1.000**	**0.012**	-------	0.117	0.356	0.818	**0.078**
bp4	*6*	---------	**1.000**	**0.041**	-------	0.134	**0.099**	0.481	0.903
bp5	*2*	---------	1.000	0.376	-------	0.078	**0.051**	0.482	0.109
bp6	*1*	---------	0.100	0.499	3.542	0.396	**0.066**	0.802	1.000
bp7	*1*	---------	0.100	0.499	3.542	0.396	**0.066**	0.802	1.000
RNM2 PSTYLID	92	0.1108	0.000	0.500	-------	0.000	0.321	0.720	0.499
bp1	*25*	---------	0.000	0.500	-------	0.000	0.210	1.000	0.493

bp2	*21*	---------	0.000	0.500	-------	0.000	0.205	0.343	0.760
bp3	*2*	---------	0.000	0.500	-------	0.000	0.324	0.674	0.375
bp4	*2*	---------	0.000	0.500	-------	0.000	0.324	0.674	0.375
bp5	*2*	---------	0.000	0.500	-------	0.000	0.324	0.674	0.375
bp6	*1*	---------	0.000	0.500	-------	0.000	0.996	0.674	1.000
bp7	*0*								
RNM3 PSTYLID*	5	-2.2520	0.000	0.500	-------	0.210	**0.062**	0.136	0.105
bp1	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp7	*1*	---------	-------	-------	-------	-------	-------	-------	-------
RNM1 C5*	92	1.2175	0.125	0.261	0.211	0.000	0.361	0.222	0.523
bp1	*85*	---------	0.075	0.348	0.202	0.000	0.574	0.253	0.955
bp2	*83*	---------	0.000	0.500	-------	0.000	0.856	0.485	0.589
bp3	*74*	---------	0.000	0.500	-------	0.000	0.818	0.126	0.631
bp4	*51*	---------	**0.604**	**0.042**	0.382	0.000	0.649	0.938	0.501
bp5	*7*	---------	0.000	0.500	-------	0.167	**0.021**	1.000	**0.032**
RNM3 C5	5	-1.3080	0.000	0.500	-------	0.000	1.000	1.000	0.947
bp1	*4*	---------	0.000	0.499	-------	0.101	0.986	**0.070**	0.991
bp2	*4*	---------	0.000	0.499	-------	0.457	0.988	**0.070**	0.995
bp3	*4*	---------	0.000	0.499	-------	0.457	0.988	**0.070**	0.995
bp4	*3*	---------	0.000	0.500	-------	0.145	**0.025**	0.857	0.998
bp5	*0*								
RNM1 C6*	92	3.3778	0.286	0.092	0.247	0.000	0.129	0.569	0.559
bp1	*13*	---------	0.616	0.125	0.591	0.044	**0.058**	0.576	0.520
bp2	*5*	---------	0.000	0.500	-------	0.000	0.822	0.479	0.589
bp3-bp5	*0*								
RNM2 C6*	75	21.8307	**0.414**	**0.017**	0.224	0.079	**0.065**	0.740	0.711

bp1	*3*	---------	1.000	0.064	-------	0.000	0.166	0.252	0.430
bp2	*3*	---------	1.000	0.064	-------	0.000	0.167	0.253	0.430
bp3	*1*	---------	0.000	0.500	-------	0.000	0.390	0.416	0.993
bp4-bp5	*0*								
RNM3 C6	6	---------	-------	-------	-------	-------	-------	-------	-------
bp1-bp5	*0*								
RNM1 C7*	107	7.4146	0.000	0.500	-------	0.000	0.478	0.701	0.514
bp1	*10*	---------	0.000	0.500	-------	0.000	0.399	0.302	0.368
bp1a	*6*	---------	0.000	0.500	-------	0.000	0.309	0.548	0.813
bp2	*4*	---------	0.000	0.500	-------	0.051	0.400	**0.033**	0.152
bp3	*2*	---------	0.000	0.500	-------	0.172	0.595	**0.068**	0.997
bp4	*2*	---------	0.000	0.500	-------	0.172	0.596	**0.068**	1.000
RNM2 C7	100	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*4*	---------	0.884	0.335	1.383	0.038	0.124	0.427	**0.080**
bp1a	*1*	---------	1.000	0.321	-------	0.000	1.000	0.308	0.947
bp2-bp4	*0*								
RNM3 C7	9	---------	-------	-------	-------	-------	-------	-------	-------
bp1-bp4	*0*								
RNM1 DTCREST	69	---------	**1.000**	**0.030**	-------	0.000	1.000	0.349	0.653
	2								
RNM2 DTCREST	83	---------	0.510	0.186	0.511	0.000	0.636	0.874	0.674
	5								
RNM3 DTCREST	11	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RNI1 CONG ABS	123	---------	0.000	0.500	-------	0.531	1.000	**<0.001**	0.995
	2								
RNP2 CONG ABS	111	---------	1.000	0.094	-------	0.168	**0.001**	**0.058**	**0.062**
	13								
RNM3 CONG ABS	9	---------	-------	-------	-------	-------	-------	-------	-------
	0								
XI LAB CVX	122	-0.0761	0.193	0.118	0.180	0.145	**<0.001**	0.140	0.711

bp1	*117*	---------	0.961	0.279	1.602	0.335	**0.004**	0.866	0.710
bp2	*87*	---------	0.204	0.247	0.313	0.096	**0.006**	0.911	0.741
bp3	*22*	---------	0.194	0.354	0.552	0.113	**0.001**	**0.010**	0.162
bp4	*3*	---------	0.000	0.500	-------	0.118	**0.068**	0.224	0.383
XI1 SHOV	120	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*91*	---------	**0.772**	**0.004**	0.294	0.000	0.191	0.306	0.786
bp2	*2*	---------	**1.000**	**<0.001**	-------	0.000	0.901	0.233	0.565
bp3	*7*	---------	0.585	0.083	0.492	0.000	0.170	0.271	0.526
bp4-bp7	*0*								
XI2 SHOV	112	-0.5288	**0.341**	**0.028**	0.187	0.000	0.291	0.822	0.200
bp1	*84*	---------	0.000	0.500	-------	0.000	0.548	0.366	0.791
bp2	*34*	---------	**0.846**	**0.011**	0.360	0.000	0.422	0.587	0.106
bp3	*14*	---------	0.561	0.136	0.595	0.000	0.140	0.246	0.109
bp4	*3*	---------	0.000	0.500	-------	0.193	0.877	**0.021**	1.000
bp5	*1*	---------	0.000	0.500	-------	0.000	0.237	0.437	0.995
bp6-bp7	*0*								
XC SHOV	106	-0.6442	0.088	0.263	0.145	0.000	0.156	0.940	0.951
bp1	*66*	---------	0.044	0.424	0.235	0.000	0.232	0.960	0.698
bp2	*15*	---------	0.284	0.233	0.114	0.000	0.193	0.863	0.483
bp3	*5*	---------	0.000	0.500	-------	0.000	0.829	0.409	0.849
bp4-bp7	*0*								
XI1 DSHOV	122	-0.2572	0.215	0.070	0.163	0.048	**0.048**	0.529	0.762
bp1	*111*	---------	0.000	0.500	-------	0.050	**0.087**	0.731	0.637
bp2	*72*	---------	0.289	0.101	0.243	0.000	0.123	0.493	0.705
bp3	*20*	---------	0.026	0.464	0.294	0.000	0.301	0.839	0.648
bp4	*7*	---------	0.000	0.500	-------	0.000	0.979	0.509	0.720
bp5-bp6	*0*								
XI2 DSHOV	119	-0.6140	0.035	0.410	0.155	0.032	**0.056**	0.950	0.502
bp1	*75*	---------	0.000	0.500	-------	0.022	**0.095**	0.744	0.528
bp2	*26*	---------	0.206	0.240	0.326	0.000	0.205	0.651	0.971
bp3	*8*	---------	0.484	0.223	0.651	0.028	**0.066**	0.443	0.173

bp4	*3*	---------	0.000	0.500	-------	0.001	**0.034**	0.141	0.282
bp5-bp6	*0*								
XC DSHOV	112	-0.5753	**0.627**	**<0.001**	0.174	0.032	**0.040**	0.682	0.602
bp1	*96*	---------	**0.825**	**0.016**	0.284	0.147	**0.036**	0.485	0.566
bp2	*59*	---------	**0.862**	**0.001**	0.260	0.000	0.351	0.827	0.771
bp3	*39*	---------	**1.000**	**<0.001**	-------	0.000	0.176	0.133	0.310
bp4	*8*	---------	0.000	0.500	-------	0.000	0.450	0.673	0.313
bp5-bp6	*0*								
XP1 DSHOV	114	-0.5514	**0.256**	**0.042**	0.161	0.033	0.997	**0.064**	0.320
bp1	*85*	---------	0.096	0.342	0.198	0.000	0.636	0.341	0.607
bp2	*38*	---------	**0.519**	**0.043**	0.266	0.035	0.648	**0.028**	0.487
bp3	*11*	---------	0.053	0.460	1.435	0.000	0.910	0.922	0.195
bp4	*4*	---------	0.892	0.063	0.459	0.000	0.548	0.112	1.000
bp5	*1*	---------	0.000	0.500	-------	0.000	1.000	0.563	0.997
bp6	*0*								
XP2 DSHOV	99	-0.3113	0.046	0.378	0.156	0.000	0.349	0.791	0.546
bp1	*34*	---------	0.215	0.213	0.284	0.000	0.490	0.795	0.467
bp2	*6*	---------	0.000	0.500	-------	0.105	**0.033**	0.489	0.494
bp3	*1*	---------	0.000	0.500	-------	0.000	1.000	0.913	1.000
bp4-bp6	*0*								
XI1 TD	109	-0.6137	**0.507**	**0.002**	0.176	0.000	0.698	0.895	0.762
bp1	*89*	---------	0.415	0.097	0.318	0.000	0.351	0.265	0.756
bp2	*62*	---------	**0.923**	**<0.001**	0.245	0.000	0.364	0.430	0.660
bp3	*36*	---------	0.085	0.382	1.497	0.000	0.681	0.312	0.936
bp4	*8*	---------	1.000	0.088	-------	0.084	0.357	**0.040**	0.647
bp5-	*3*	---------	**1.000**	**0.023**	-------	0.000	0.374	0.532	0.224
bp5	*2*	---------	0.764	0.412	2.256	0.000	0.960	0.159	0.993
bp6	*2*	---------	0.764	0.412	2.256	0.000	0.960	0.159	0.993
XI2 TD	91	-0.8543	**0.743**	**0.003**	0.237	0.000	0.439	0.109	0.909
bp1	*64*	---------	0.625	0.056	0.389	0.000	0.254	0.165	0.435
bp2	*43*	---------	**0.622**	**0.034**	0.333	0.000	0.858	0.357	0.983

bp3	*26*	---------	**0.995**	**0.003**	0.299	0.000	0.803	0.889	0.239
bp4	*17*	---------	**1.000**	**0.009**	-------	0.000	0.876	0.329	0.701
bp5-	*14*	---------	0.343	0.290	0.632	0.000	0.869	0.712	0.877
bp5	*7*	---------	0.000	0.500	-------	0.000	0.179	0.600	0.265
bp6	*5*	---------	0.000	0.500	-------	0.000	0.179	0.600	0.265
XC TD	97	-0.6471	**0.445**	**0.025**	0.245	0.000	0.545	0.176	0.291
bp1	*85*	---------	0.289	0.281	0.382	0.000	0.310	0.536	0.146
bp2	*71*	---------	0.000	0.500	-------	0.036	**0.059**	**0.051**	**0.030**
bp3	*53*	---------	0.500	0.058	0.229	0.000	0.483	0.241	0.360
bp4	*45*	---------	**0.982**	**0.002**	0.300	0.029	**0.090**	0.373	**0.097**
bp5-	*35*	---------	0.438	0.083	0.246	0.042	0.586	0.493	**0.028**
bp5	*22*	---------	0.000	0.500	-------	0.000	0.241	0.258	0.798
bp6	*3*	---------	-------	-------	-------	-------	-------	-------	-------
XC MES RIDGE*	111	34.2093	0.000	0.500	-------	0.000	0.481	0.799	0.416
bp1	*3*	---------	0.000	0.500	-------	0.000	0.333	0.275	0.316
bp2	*2*	---------	0.000	0.500	-------	0.000	0.333	0.926	0.198
bp3	*0*								
XC DAR	110	-0.6588	0.311	0.064	0.209	0.000	0.117	0.280	0.231
bp1	*93*	---------	0.000	0.500	-------	0.000	0.867	0.882	0.607
bp2	*70*	---------	0.362	0.204	0.469	0.000	0.320	0.954	0.629
bp3	*52*	---------	**0.868**	**0.004**	0.333	0.003	**0.099**	0.873	0.110
bp4	*25*	---------	0.407	0.175	0.457	0.044	**0.041**	0.171	**0.040**
bp5	*4*	---------	0.000	0.499	-------	0.204	0.452	1.000	**0.009**
XP1 UTO AZ	104	---------	-------	-------	-------	-------	-------	-------	-------
	0								
XP1 ODONT	102	---------	-------	-------	-------	-------	-------	-------	-------
	0								
XP2 ODONT	70	---------	-------	-------	-------	-------	-------	-------	-------
	0								
XM1 META*	119	1.6909	0.000	0.500	-------	0.033	0.124	**0.026**	0.422
bp1-bp3	*119*								

bp3.5	*118*	---------	0.000	0.500	-------	0.000	1.000	1.000	0.685
bp4	*112*	---------	0.000	0.500	-------	0.000	0.179	0.228	0.581
bp5	*19*	---------	0.000	0.500	-------	0.036	0.256	**0.049**	0.316
XM2 META	105	-0.2039	0.249	0.052	0.175	0.038	**0.062**	0.645	**0.089**
bp1-bp2	*105*								
bp3	*104*	---------	0.100	0.500	0.707	0.775	**0.008**	0.998	0.987
bp3.5	*95*	---------	**1.000**	**0.003**	-------	0.000	0.101	0.502	0.137
bp4	*47*	---------	0.000	0.500	-------	0.003	**0.088**	0.511	0.216
bp5	*3*	---------	**1.000**	**0.043**	-------	0.000	0.843	0.141	0.909
XM3 META	9	-0.9548	1.000	0.122	-------	0.248	0.400	**0.084**	**0.089**
bp1-bp3	*9*								
bp3.5	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*0*								
XM1 HYPO	116	-0.8961	0.080	0.288	0.152	0.025	**0.038**	0.528	0.270
bp1	*116*								
bp2	*115*	---------	0.000	0.500	-------	0.000	1.000	0.994	0.926
bp3	*114*	---------	0.000	0.500	-------	0.162	0.129	0.513	**0.005**
bp3.5	*113*	---------	0.103	0.497	3.667	0.456	**0.005**	0.784	0.761
bp4	*109*	---------	0.000	0.500	-------	0.090	**0.022**	0.937	0.233
bp5	*49*	---------	0.205	0.179	0.230	0.000	0.306	0.412	0.486
XM2 HYPO	77	-0.6271	0.214	0.115	0.194	0.023	**0.059**	0.359	0.323
bp1	*76*	---------	0.079	0.500	3.551	0.000	0.199	0.606	0.992
bp2	*64*	---------	0.388	0.177	0.428	0.000	0.897	0.724	0.744
bp3	*54*	---------	0.547	0.053	0.438	0.000	0.294	0.943	0.658
bp3.5	*41*	---------	0.065	0.405	0.271	0.019	**0.067**	0.632	0.301
bp4	*19*	---------	0.000	0.500	-------	0.000	0.394	0.643	0.287
bp5	*3*	---------	0.000	0.500	-------	0.000	**0.049**	0.183	0.999
XM3 HYPO	5	-1.6982	1.000	0.175	-------	0.000	0.737	1.000	1.000
bp1	*5*								
bp2	*3*	---------	1.000	0.255	-------	0.000	0.177	1.000	1.000

bp3	*2*	---------	1.000	0.279	-------	0.403	**0.085**	1.000	1.000
bp3.5	*1*	---------	0.000	0.500	-------	0.000	1.000	0.997	0.961
bp4-bp5	*0*								
XM1 C5	106	0.4880	**0.244**	**0.047**	0.167	0.049	**0.014**	0.383	0.352
bp1	*26*	---------	0.083	0.388	0.283	0.055	**0.004**	0.882	0.142
bp2	*9*	---------	**0.729**	**0.013**	0.302	0.053	**0.081**	0.139	0.965
bp3	*1*	---------	0.000	0.500	-------	0.000	0.824	0.407	0.997
bp4-bp5	*0*								
XM2 C5	76	1.6145	**0.709**	**0.005**	0.230	0.000	0.197	0.908	0.397
bp1	*15*	---------	0.904	0.056	0.538	0.015	**0.094**	0.824	0.191
bp2	*4*	---------	**1.000**	**0.043**	-------	0.000	0.490	0.900	0.392
bp3	*4*	---------	**1.000**	**0.043**	-------	0.000	0.490	0.900	0.392
bp4	*2*	---------	**1.000**	**0.028**	-------	0.000	0.497	0.187	1.000
bp5	*2*	---------	**1.000**	**0.028**	-------	0.000	0.497	0.187	1.000
XM3 C5	5	-1.3080	1.000	0.160	-------	0.000	0.335	0.952	1.000
bp1	*2*	---------	1.000	0.279	-------	0.403	**0.085**	1.000	1.000
bp2	*2*	---------	1.000	0.279	-------	0.403	**0.085**	1.000	1.000
bp3	*1*	---------	1.000	0.500	-------	0.000	1.000	0.997	0.968
bp4-bp5	*0*								
XM1 CARABELLI	116	-0.8045	**0.762**	**<0.001**	0.136	0.000	0.661	0.798	0.328
bp1	*102*	---------	0.404	0.216	0.519	0.107	**0.002**	0.239	0.187
bp2	*80*	---------	**0.833**	**<0.001**	0.246	0.000	0.459	0.181	0.645
bp3	*76*	---------	**0.945**	**<0.001**	0.218	0.000	0.467	0.182	0.419
bp4	*69*	---------	**0.947**	**<0.001**	0.241	0.000	0.719	0.403	0.216
bp5	*52*	---------	**0.842**	**<0.001**	0.246	0.000	0.922	0.789	0.220
bp6	*34*	---------	**0.820**	**0.001**	0.250	0.039	**0.078**	0.663	**0.029**
bp7	*17*	---------	**0.743**	**0.003**	0.244	0.061	**0.027**	**0.063**	0.897
XM2 CARABELLI	102	-0.6062	**0.323**	**0.048**	0.217	0.000	0.537	0.433	0.101
bp1	*46*	---------	0.429	0.063	0.304	0.000	0.917	0.450	0.288
bp2	*19*	---------	0.251	0.254	0.569	0.000	0.237	0.553	0.124
bp3	*14*	---------	0.504	0.232	0.780	0.065	0.278	0.870	**0.020**

bp4	*10*	---------	1.000	0.092	-------	0.037	0.212	0.511	**0.040**
bp5	*9*	---------	0.000	0.500	-------	0.035	0.290	0.520	**0.045**
bp6	*5*	---------	0.000	0.500	-------	0.048	0.298	0.403	**0.049**
bp7	*2*	---------	0.000	0.500	-------	0.214	**0.071**	0.336	**0.087**
XM3 CARABELLI	13	-0.8841	0.000	0.500	-------	0.000	0.378	0.498	0.160
bp1	*5*	---------	0.000	0.500	-------	0.000	0.325	0.861	0.352
bp2	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp7	*0*								
XM1 PARA*	117	2.3501	0.244	0.065	0.173	0.016	0.142	**0.069**	0.725
bp1	*19*	---------	**0.674**	**0.036**	0.343	0.054	**0.076**	**0.078**	0.589
bp2	*3*	---------	0.000	0.500	-------	0.000	0.797	0.109	0.975
bp3	*2*	---------	0.000	0.500	-------	0.000	0.953	0.567	0.893
bp4-bp6	*0*								
XM2 PARA*	105	31.5694	**0.234**	**0.050**	0.164	0.000	0.258	0.705	0.619
bp1	*3*	---------	1.000	0.078	-------	0.000	0.182	0.429	0.767
bp2	*3*	---------	1.000	0.078	-------	0.000	0.181	0.429	0.767
bp3-bp6	*0*								
XM3 PARA	10	---------	-------	-------	-------	-------	-------	-------	-------
	0								
XI2 PEG[j]	119	---------	-------	-------	-------	-------	-------	-------	-------
	2	---------	0.000	0.500	-------	0.000	1.000	0.144	0.880
XM3 PEG[j]	14	---------	-------	-------	-------	-------	-------	-------	-------
	0								
XI2 CONG ABS	121	---------	0.000	0.500	-------	0.000	1.000	0.200	0.632
	2								
XP2 CONG ABS	115	---------	0.360	0.132	0.334	0.000	0.674	0.126	0.620
	22								

XM3 CONG ABS	17	---------	-------	-------	-------	-------	-------	-------	-------
	0								
NI1 SHOV	125	0.2520	**0.313**	**0.013**	0.155	0.000	0.954	0.918	0.267
bp1	*29*	---------	**0.501**	**0.023**	0.265	0.000	0.786	0.813	0.330
bp2	*1*	---------	0.000	0.500	-------	0.000	0.457	0.305	0.994
bp3-bp7	*0*								
NI2 SHOV	125	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*33*	---------	0.000	0.500	-------	0.000	0.457	0.305	0.994
bp2-bp7	*0*								
NC DAR	118	-0.3850	0.190	0.155	0.210	0.240	**<0.001**	<**0.001**	**0.055**
bp1	*63*	---------	0.238	0.213	0.323	0.096	**0.041**	<**0.001**	0.664
bp2	*27*	---------	0.197	0.331	0.220	0.254	**<0.001**	**0.005**	**0.007**
bp3	*15*	---------	0.285	0.346	0.707	0.263	**0.005**	**0.001**	0.903
bp4	*6*	---------	0.000	0.500	-------	0.100	**0.043**	0.207	0.893
bp5	*0*								
NP1 ODONT	108	---------	-------	-------	-------	-------	-------	-------	-------
	0								
NP2 ODONT	78	---------	-------	-------	-------	-------	-------	-------	-------
	0								
NM1 ANT FOVEA	57	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*45*	---------	1.000	0.055	-------	0.053	0.213	0.692	**0.026**
bp2	*34*	---------	0.707	0.055	0.469	0.000	0.781	0.378	0.307
bp3	*22*	---------	**1.000**	**0.024**	-------	0.036	0.371	**0.058**	0.938
bp4	*5*	---------	0.000	0.500	-------	0.150	**0.071**	**0.080**	0.994
NM1 CNO*	100	1.5617	0.000	0.500	-------	0.000	0.166	0.868	0.632
bp5	*94*	---------	0.000	0.500	-------	0.000	0.822	0.642	0.301
bp6	*18*	---------	0.073	0.430	0.449	0.053	**0.049**	0.972	0.617
bp7	*1*	---------	1.000	0.318	-------	0.000	0.992	0.365	0.999
bp8	*1*	---------	1.000	0.318	-------	0.000	0.992	0.363	0.999
NM2 CNO	84	0.0683	0.205	0.127	0.195	0.118	0.548	**0.002**	0.434
bp5	*26*	---------	0.282	0.180	0.311	0.100	0.678	**0.002**	0.414

bp6	*4*	---------	0.860	0.119	0.748	0.057	0.629	**0.059**	0.143
bp7-bp8	*0*								
NM3 CNO	8	-0.7967	0.000	0.500	-------	0.000	0.737	0.916	0.898
bp5	*5*	---------	0.000	0.500	-------	0.000	0.636	0.678	0.848
bp6	*1*	---------	0.000	0.500	-------	0.000	1.000	0.397	0.649
bp7-bp8	*0*								
NM1 DWRINK	62	-0.9219	0.000	0.500	-------	0.017	**0.095**	0.495	0.144
bp1	*35*	---------	0.034	0.479	0.572	0.015	0.115	0.416	**0.061**
bp2	*10*	---------	0.000	0.500	-------	0.103	**0.008**	0.128	**0.069**
bp3	*1*	---------	1.000	0.337	-------	0.000	0.989	0.304	0.999
NM1 PSTYLID	105	-0.8052	0.186	0.195	0.229	0.000	0.938	0.497	0.104
bp1	*64*	---------	0.000	0.500	-------	0.014	0.358	0.577	**0.085**
bp2	*41*	---------	0.202	0.282	0.360	0.046	0.843	**0.084**	0.600
bp3	*13*	---------	**1.000**	**0.011**	-------	0.000	0.356	0.645	0.413
bp4	*7*	---------	0.669	0.174	0.734	0.000	0.125	0.272	0.889
bp5	*2*	---------	1.000	0.362	-------	0.074	**0.050**	0.164	0.104
bp6	*1*	---------	0.100	0.499	3.748	0.395	**0.066**	0.846	1.000
bp7	*1*	---------	0.100	0.499	3.748	0.395	**0.066**	0.846	1.000
NM2 PSTYLID	100	-0.3803	0.094	0.276	0.168	0.021	0.047	0.672	0.201
bp1	*40*	---------	0.022	0.468	0.272	0.024	**0.017**	0.932	0.114
bp2	*33*	---------	0.101	0.347	0.268	0.038	**0.026**	0.306	0.476
bp3	*3*	---------	0.000	0.500	-------	0.000	0.109	0.558	0.871
bp4	*2*	---------	0.000	0.500	-------	0.000	0.357	0.673	0.501
bp5	*2*	---------	0.000	0.500	-------	0.000	0.357	0.673	0.501
bp6	*1*	---------	0.000	0.500	-------	0.000	1.000	0.671	0.123
bp7	*0*								
NM3 PSTYLID	10	-0.0073	0.000	0.500	-------	0.000	0.356	0.629	0.393
bp1	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*2*	---------	-------	-------	-------	-------	-------	-------	-------

bp5	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp7	*1*	---------	-------	-------	-------	-------	-------	-------	-------
NM1 C5	100	-0.5681	0.227	0.114	0.211	0.000	0.435	0.369	0.967
bp1	*95*	---------	0.000	0.500	-------	0.000	0.868	0.360	0.128
bp2	*91*	---------	0.000	0.500	-------	0.000	0.908	0.943	0.307
bp3	*87*	---------	0.000	0.500	-------	0.000	0.908	0.317	0.522
bp4	*68*	---------	**0.691**	**0.029**	0.439	0.000	0.919	0.871	0.953
bp5	*24*	---------	0.552	0.059	0.307	0.000	0.142	0.237	0.376
NM3 C5*	8	-0.8046	0.000	0.500	-------	0.300	**0.045**	0.305	0.294
bp1	*5*	---------	0.000	0.500	-------	0.000	0.636	0.678	0.848
bp2	*5*	---------	0.000	0.500	-------	0.000	0.636	0.568	0.768
bp3	*5*	---------	0.000	0.500	-------	0.000	0.595	0.678	0.848
bp4	*4*	---------	0.000	0.500	-------	0.343	**0.051**	0.791	0.247
bp5	*1*	---------	0.000	0.500	-------	0.266	**0.051**	0.998	0.984
NM1 C6*	100	1.7141	0.117	0.260	0.194	0.000	0.124	0.981	0.731
bp1	*19*	---------	0.076	0.430	0.478	0.046	**0.049**	0.832	0.510
bp2	*10*	---------	0.308	0.283	0.562	0.000	0.107	0.534	0.376
bp3	*1*	---------	0.000	0.500	-------	0.000	1.000	0.364	1.000
bp4-bp5	*0*								
NM2 C6*	83	17.7581	0.338	0.059	0.256	0.000	0.609	0.244	0.474
bp1	*4*	---------	0.951	0.114	0.675	0.060	0.587	**0.050**	0.145
bp2	*4*	---------	0.951	0.114	0.679	0.060	0.605	**0.050**	0.145
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4-bp5	*0*								
NM3 C6*	9	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	0.000	0.500	-------	0.000	1.000	0.408	0.455
bp2-bp5	*0*								
NM1 C7*	111	3.1795	0.000	0.500	-------	0.000	0.600	0.813	0.564
bp1	*17*	---------	0.000	0.500	-------	0.000	0.431	0.452	0.495
bp1a	*11*	---------	0.000	0.500	-------	0.000	0.864	0.680	0.401

bp2	*9*	---------	0.000	0.500	-------	0.000	0.950	0.334	0.448
bp3	*3*	---------	0.000	0.500	-------	0.000	0.566	0.401	0.740
bp4	*2*	---------	0.000	0.500	-------	0.174	0.567	**0.067**	0.997
NM2 C7	105	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*6*	---------	**1.000**	**0.026**	-------	0.000	0.196	0.120	0.135
bp1a	*2*	---------	0.000	0.500	-------	0.000	1.000	0.139	1.000
bp2-bp4	*0*								
NM3 C7*	14	4.5628	0.701	0.244	0.787	0.571	0.839	**0.003**	**0.010**
bp1	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp1a	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp3-bp4	*0*								
NM1 DTCREST	72	---------	**1.000**	**0.029**	-------	0.000	1.000	0.353	0.969
	2								
NM2 DTCREST	93	---------	**1.000**	**0.008**	-------	0.000	0.558	0.452	0.211
	8								
NM3 DTCREST	13	---------	-------	-------	-------	-------	-------	-------	-------
	0								
NI2 CONG ABS	124	---------	0.000	0.500	-------	0.120	1.000	**0.066**	0.953
	3								
NP2 CONG ABS	113	---------	0.000	0.500	-------	0.000	0.174	0.382	0.448
	15								
NM3 CONG ABS	17	---------	-------	-------	-------	-------	-------	-------	-------
	0								

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[a] l=left; r=right; traits without a left or right designation represent the maximum of the left and right antimeric expressions; x=maxillary; n=mandibular; bp= breakpoint. All morphological trait abbreviations outlined in Appendix C. Ordinal traits were normalized and treated as continuous for the purpose for heritability estimation. Breakpoints indicate presence/absence dichotomization cutoffs for ordinal traits; each of these breakpoints was treated as an individual binary character for heritability estimation. Kurtosis is not estimated for binary character models. Certain breakpoints were omitted from the heritability analysis because expression was monomorphic across the sample. Traits

marked with asterisks are associated with less stable heritability estimates because other model parameters could not be estimated, because sample size was too small, or because kurtosis values were too high after normalization. These results should be accepted with caution. Dashes are associated with incalculable parameter estimates. Traits marked with dashes for all parameters represent models that failed to converge. The following traits were removed due to high levels of intra-observer error: NM cusp 5 and NP2 lingual cusp variation. [b]N=sample size for heritability estimation; Count=count for dichotomized trait expression (presence) at the denoted breakpoint (bp). Count values are italicized. If a trait is binary (i.e., its original scoring standards do not include ordinal scale scoring) this value is marked on a blank row beneath the sample size "N". [c]K=model kurtosis value. [d]h2= maximum likelihood heritability estimate. [e]All significant heritability estimates (p-value<0.05) and associated probability value estimates are bolded. [f]SE= maximum likelihood standard error estimate; this parameter estimate is typically omitted when heritability estimated equal 0.000 or 1.000. [g]c2= maximum likelihood total covariate estimate. [h]All significant probability value estimates for the covariates of age, sex, and age/sex interaction are bolded. [i]As the winging, premolar lingual cusp, and groove pattern data are categorical and not ordinal, each category was treated as a separate binary variable. [j]Peg-shaped incisor and peg-shaped molar were scored only as binary variables at the breakpoint of ASUDAS grade 2.

APPENDIX K

UNIVERSITY OF ADELAIDE TWIN STUDY SAMPLE

HERITABILITY ESTIMATES

Table 1. University of Adelaide Twin Study sample heritability estimates: deciduous crown morphology (mixed deciduous standards).

			Heritability			Covariates			
Trait[a]	N[b] *Count*	K[c]	h2[d]	p-value[e]	SE[f]	c2[g]	age[h] p-value	sex[h] p-value	age*sex[h] p-value
lxi1 wing	141	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*4*	---------	1.000	0.056	-------	0.165	**0.067**	0.432	0.467
bp2	*4*	---------	1.000	0.056	-------	0.165	**0.067**	0.432	0.467
lxi1 shov*	88	2.6499	0.000	0.500	-------	0.000	0.728	0.253	0.552
bp1	*81*	---------	0.000	0.500	-------	0.000	0.457	0.465	0.248
bp2	*10*	---------	0.524	0.182	0.444	0.000	0.604	0.375	0.720
bp3	*1*	---------	1.000	0.338	-------	0.183	**0.071**	0.988	1.000
lxi2 shov*	122	1.0129	**0.459**	**0.004**	0.143	0.000	0.340	0.127	0.441
bp1	*112*	---------	0.519	0.123	0.385	0.099	0.175	**0.014**	0.459
bp2	*21*	---------	**0.606**	**0.034**	0.200	0.000	0.670	0.642	0.746
bp3	*0*								
lxc shov	209	0.0590	**0.612**	**<0.001**	0.099	0.046	**0.043**	**0.072**	0.258
bp1	*155*	---------	**0.842**	**<0.001**	0.123	0.043	**0.010**	**0.052**	**0.047**
bp2	*12*	---------	0.512	0.135	0.410	0.035	0.652	**0.059**	0.497
bp3	*0*								
lxi2 dshov*	144	25.8467	0.000	0.500	-------	0.000	0.420	0.372	0.745
bp1	*5*	---------	0.000	0.500	-------	0.000	0.383	0.238	0.636
bp2	*4*	---------	0.000	0.500	-------	0.000	0.383	0.422	0.676
bp3	*2*	---------	0.000	0.500	-------	0.000	0.382	0.884	0.780
lxc dshov	225	-0.8807	**0.622**	**<0.001**	0.100	0.000	0.826	0.967	0.686
bp1	*206*	---------	**1.000**	**<0.001**	-------	0.000	0.630	0.957	0.882
bp2	*166*	---------	**0.832**	**<0.001**	0.703	0.000	0.512	0.878	0.822
bp3	*121*	---------	**0.585**	**0.001**	0.177	0.000	0.819	0.932	0.632

lxi2 td	125	-1.2890	**0.679**	**<0.001**	0.092	0.000	0.605	0.397	0.531
bp1	*62*	---------	**0.795**	**<0.001**	0.179	0.000	0.503	0.258	0.248
bp2	*38*	---------	**0.865**	**<0.001**	0.120	0.000	0.666	0.348	0.967
bp3	*1*	---------	1.000	0.359	-------	0.000	0.449	0.175	0.995
bp4	*1*	---------	1.000	0.359	-------	0.000	0.449	0.176	0.995
lxc td	220	-0.7136	**0.643**	**<0.001**	0.096	0.049	**0.030**	**0.080**	0.768
bp1	*185*	---------	**0.725**	**0.003**	0.206	0.038	**0.020**	0.320	0.364
bp2	*129*	---------	**0.812**	**<0.001**	0.135	0.016	0.489	**0.046**	0.928
bp3	*81*	---------	**0.795**	**<0.001**	0.160	0.034	**0.037**	**0.055**	0.452
bp4	*6*	---------	0.546	0.116	0.376	0.000	0.661	0.406	0.128
lxm1 cno	226	-0.9455	**0.534**	**<0.001**	0.086	0.000	0.542	0.366	0.865
bp3m	*145*	---------	**0.634**	**<0.001**	0.130	0.000	0.220	0.540	0.468
bp3h	*85*	---------	**0.650**	**<0.001**	0.095	0.000	0.732	0.218	0.573
bp4-	*50*	---------	**0.777**	**<0.001**	0.113	0.000	0.370	0.817	0.980
bp4	*4*	---------	-------	-------	-------	-------	-------	-------	-------
lxm2 cno*	265	-0.5554	**0.679**	**<0.001**	0.068	0.000	0.509	0.198	0.674
bp3a	*265*								
bp3b	*254*	---------	**0.957**	**<0.001**	0.086	0.000	0.250	0.234	0.289
bp4-	*219*	---------	**0.859**	**<0.001**	0.103	0.000	0.829	0.193	0.766
bp4	*157*	---------	**0.828**	**<0.001**	0.103	0.000	0.297	0.527	0.349
lxm2 c5	252	---------	**0.684**	**0.005**	0.192	0.064	0.426	**0.001**	0.670
	30								
lxm2 Carab	269	-0.4955	**0.591**	**<0.001**	0.077	0.020	0.436	**0.023**	0.303
bp1	*268*	---------	1.000	0.351	-------	0.269	**0.044**	0.973	0.893
bp2	*222*	---------	**0.616**	**<0.001**	0.143	0.019	0.924	**0.034**	0.480
bp3	*115*	---------	**0.766**	**<0.001**	0.103	0.000	0.555	0.134	0.582
bp4	*26*	---------	0.432	0.097	0.104	0.000	0.587	0.369	0.354
lni1 shov	84	0.5904	**0.447**	**0.018**	0.170	0.000	0.732	0.158	0.353
bp1	*16*	---------	**0.665**	**0.037**	0.266	0.000	0.766	0.161	0.462
bp2-bp3	*0*								
lni2 shov	134	-0.9438	**0.373**	**0.030**	0.175	0.099	**0.003**	0.106	0.221

bp1	*71*	---------	0.493	0.051	0.260	0.066	**0.013**	**0.073**	0.518
bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*0*								
lnc shov	224	-0.5773	**0.567**	**<0.001**	0.089	0.000	0.779	0.776	0.276
bp1	*134*	---------	**0.706**	**<0.001**	0.128	0.000	0.815	0.859	0.621
bp2	*10*	---------	**1.000**	**<0.001**	-------	0.000	0.209	0.505	0.290
bp3	*1*	---------	1.000	0.362	-------	0.306	0.972	0.661	**0.010**
lni1 double	105	---------	-------	-------	-------	-------	-------	-------	-------
	0								
lni2 double	153	---------	0.000	0.500	-------	0.000	0.464	0.364	0.941
	3								
lnc double	244	---------	0.000	0.500	-------	0.000	0.548	0.991	0.631
	2								
lnc td*	232	2.5385	**0.660**	**<0.001**	0.105	0.000	0.394	0.537	0.469
bp1	*39*	---------	**0.779**	**0.001**	0.171	0.000	0.334	0.797	0.393
bp2	*10*	---------	**0.809**	**0.004**	0.182	0.000	0.426	0.307	0.707
bp3	*1*	---------	0.113	0.496	3.551	0.000	0.879	0.215	1.000
bp4	*1*	---------	0.113	0.496	3.551	0.000	0.879	0.215	1.000
lnm2 dwrink	231	---------	**0.690**	**<0.001**	0.136	0.000	0.720	0.910	0.404
	78								
lnm2 pstylid	253	-1.5037	**0.871**	**<0.001**	0.029	0.032	0.512	**0.010**	0.400
bp1	*165*	---------	**1.000**	**<0.001**	-------	0.036	0.483	**0.022**	0.331
bp2	*0*								
lnm2 c7	266	-1.2153	**0.592**	**<0.001**	0.083	0.000	0.654	0.703	0.430
bp1	*154*	---------	**0.875**	**<0.001**	0.099	0.000	0.939	0.780	0.903
bp2	*50*	---------	**0.481**	**0.011**	0.192	0.000	0.342	0.911	0.165
bp3-bp5	*0*								
lnm1 delta	250	---------	0.000	0.500	-------	0.246	**0.066**	**0.014**	0.996
	5								
rxi1 wing*	140	5.7588	**0.852**	**<0.001**	0.047	0.000	0.783	0.515	0.495
bp1	*15*	---------	**0.908**	**0.002**	0.149	0.000	0.868	0.277	0.356

bp2	*4*	---------	**1.000**	**0.022**	-------	0.000	0.108	0.421	0.485
rxi1 shov*	89	1.8797	0.366	0.133	0.249	0.041	0.335	**0.045**	0.462
bp1	*80*	---------	0.000	0.500	-------	0.000	0.594	0.287	1.000
bp2	*9*	---------	0.771	0.072	0.313	0.052	0.375	**0.059**	0.102
bp3	*0*								
rxi2 shov	127	0.1512	**0.403**	**0.003**	0.131	0.000	0.505	0.907	0.971
bp1	*116*	---------	0.530	0.075	0.286	0.000	0.193	0.901	0.173
bp2	*30*	---------	**0.742**	**0.002**	0.168	0.000	0.623	0.946	0.224
bp3	*0*								
rxc shov	211	0.7697	**0.599**	**<0.001**	0.079	0.035	**0.094**	**0.056**	0.257
bp1	*165*	---------	**0.862**	**<0.001**	0.097	0.035	0.345	**0.013**	0.541
bp2	*9*	---------	0.388	0.214	0.093	0.000	0.237	0.612	0.531
bp3	*0*								
rxi2 dshov*	144	12.7809	**0.431**	**0.002**	0.125	0.000	0.737	0.868	0.159
bp1	*9*	---------	0.586	0.065	0.615	0.000	0.469	0.737	0.116
bp2	*6*	---------	**1.000**	**0.004**	-------	0.000	0.943	0.936	0.173
bp3	*2*	---------	0.000	0.500	-------	0.000	0.416	0.756	0.579
rxc dshov	225	-0.9630	**0.295**	**0.005**	0.117	0.000	0.981	0.103	0.685
bp1	*202*	---------	**0.731**	**0.003**	0.196	0.000	0.903	0.493	0.616
bp2	*170*	---------	0.280	0.098	0.116	0.022	0.656	**0.020**	0.730
bp3	*116*	---------	**0.339**	**0.020**	0.138	0.000	0.722	0.262	0.532
rxi2 td	133	-1.1528	**0.302**	**0.041**	0.163	0.054	**0.027**	0.703	**0.015**
bp1	*74*	---------	0.417	0.055	0.240	0.026	**0.035**	0.583	**0.037**
bp2	*40*	---------	**0.554**	**0.035**	0.254	0.016	0.162	0.768	**0.040**
bp3	*2*	---------	0.000	0.500	-------	0.000	0.146	0.788	0.301
bp4	*1*	---------	1.000	0.374	-------	0.123	**0.083**	0.394	0.901
rxc td	228	-0.5080	**0.737**	**<0.001**	0.062	0.000	0.282	0.649	0.594
bp1	*203*	---------	0.325	0.119	0.258	0.000	0.499	0.817	0.577
bp2	*140*	---------	**0.862**	**<0.001**	0.097	0.000	0.324	0.300	0.853
bp3	*99*	---------	**0.952**	**<0.001**	0.090	0.000	0.544	0.440	0.377
bp4	*7*	---------	**1.000**	**0.025**	-------	0.164	0.742	0.114	**0.019**

rxm1 cno	221	-1.0497	**0.755**	**<0.001**	0.057	0.000	0.901	0.169	0.781
bp3m	*143*	---------	**0.848**	**<0.001**	0.076	0.000	0.479	0.257	0.544
bp3h	*87*	---------	**0.852**	**<0.001**	0.107	0.000	0.815	0.134	0.598
bp4-	*49*	---------	**0.834**	**<0.001**	0.098	0.000	0.816	0.785	0.747
bp4	*2*	---------	**1.000**	**0.001**	-------	0.000	1.000	0.312	0.999
rxm2 cno	264	-0.5284	**0.799**	**<0.001**	0.047	0.000	0.382	0.754	0.591
bp3a	*264*								
bp3b	*249*	---------	**0.957**	**<0.001**	0.092	0.000	0.794	0.875	0.573
bp4-	*203*	---------	**0.976**	**<0.001**	0.070	0.000	0.661	0.481	0.908
bp4	*144*	---------	**0.830**	**<0.001**	0.107	0.000	0.347	0.940	0.693
rxm2 c5	237	---------	**0.846**	**<0.001**	0.127	0.000	0.732	0.160	0.528
	24								
rxm2 Carab	258	-0.6878	**0.736**	**<0.001**	0.058	0.000	0.870	0.636	0.808
bp1	*258*								
bp2	*214*	---------	**0.790**	**<0.001**	1.490	0.000	0.460	0.530	0.749
bp3	*132*	---------	**0.938**	**<0.001**	0.086	0.000	0.690	0.277	0.747
bp4	*32*	---------	**0.736**	**0.001**	0.006	0.000	0.858	0.952	0.705
rni1 shov	82	-1.0347	**0.538**	**0.004**	0.152	0.000	0.330	0.260	0.756
bp1	*23*	---------	**0.752**	**0.008**	0.207	0.000	0.250	0.201	0.601
bp2-bp3	*0*								
rni2 shov	143	-0.9733	**0.484**	**0.002**	0.133	0.001	**0.009**	0.131	**0.049**
bp1	*83*	---------	**0.639**	**0.003**	0.141	0.022	0.106	**0.065**	0.217
bp2	*4*	---------	1.000	0.174	-------	0.245	**0.003**	0.257	**0.026**
bp3	*0*								
rnc shov	216	-0.5949	**0.426**	**<0.001**	0.109	0.000	0.830	0.816	0.882
bp1	*112*	---------	**0.574**	**0.001**	0.075	0.000	0.893	0.895	0.687
bp2	*7*	---------	**0.773**	**0.026**	0.275	0.023	0.180	0.509	**0.052**
bp3	*0*								
rni1 double	104	---------	-------	-------	-------	-------	-------	-------	-------
	0								
rni2 double	152	---------	0.000	0.500	-------	0.000	1.000	0.344	0.942

	1								
rnc double	239	---------	0.000	0.500	-------	0.000	1.000	0.290	1.000
	1								
rnc td*	224	2.5578	**0.554**	**<0.001**	0.089	0.000	0.352	0.390	0.824
bp1	*38*	---------	**0.740**	**<0.001**	0.146	0.000	0.529	0.368	0.947
bp2	*13*	---------	**0.700**	**0.006**	0.398	0.000	0.201	0.674	**0.862**
bp3	*2*	---------	0.000	0.500	-------	0.153	0.558	**0.087**	0.999
bp4	*1*	---------	0.113	0.497	3.549	0.000	0.861	0.200	1.000
rnm2 dwrink	239	---------	**0.654**	**<0.001**	0.401	0.000	0.341	0.839	0.565
	69								
rnm2 pstylid	250	-0.8022	**0.483**	**<0.001**	0.091	0.042	0.404	0.396	**0.011**
bp1	*171*	---------	**0.686**	**<0.001**	0.128	0.030	0.562	0.880	**0.011**
bp2	*1*	---------	-------	-------	-------	-------	-------	-------	-------
rnm2 c7	273	-0.9836	**0.674**	**<0.001**	0.068	0.000	0.446	0.921	0.957
bp1	*158*	---------	**0.853**	**<0.001**	0.079	0.000	0.538	0.807	0.864
bp2	*56*	---------	**0.858**	**<0.001**	0.102	0.000	0.630	0.996	0.955
bp3	*2*	---------	0.000	0.500	-------	0.138	0.696	**0.029**	1.000
bp4-bp5	*0*								
rnm1 delta	256	---------	0.000	0.500	-------	0.178	0.169	**0.007**	0.996
	5								
xi1 wing max*	147	6.2352	**0.849**	**<0.001**	0.047	0.000	0.879	0.488	0.509
bp1	*15*	---------	**0.909**	**0.001**	0.148	0.000	0.979	0.284	0.364
bp2	*4*	---------	**0.909**	**0.001**	0.148	0.000	0.979	0.284	0.364
xi1 shov max*	101	3.4324	0.285	0.151	0.244	0.000	0.456	0.173	0.448
bp1	*96*	---------	0.000	0.500	-------	0.000	0.544	0.951	0.100
bp2	*12*	---------	0.636	0.116	0.363	0.000	0.302	0.158	0.115
bp3	*1*	---------	1.000	0.336	-------	0.329	**<0.001**	0.787	0.728
xi2 shov max	145	0.4671	**0.400**	**0.005**	0.136	0.000	0.334	0.233	0.975
bp1	*139*	---------	0.000	0.500	-------	0.132	**0.096**	**0.017**	0.855
bp2	*35*	---------	**0.730**	**0.001**	0.159	0.000	0.499	0.543	0.385
bp3	*0*								

xc shov max*	235	1.0849	**0.714**	**<0.001**	0.060	0.039	**0.042**	**0.044**	0.214
bp1	*197*	---------	**0.880**	**<0.001**	0.093	0.043	**0.095**	**0.026**	**0.092**
bp2	*17*	---------	**0.898**	**<0.001**	0.156	0.000	0.217	0.143	0.685
bp3	*0*								
xi2 dshov max*	157	8.7131	**0.268**	**0.033**	0.136	0.000	0.761	0.512	0.298
bp1	*13*	---------	0.412	0.135	0.332	0.000	0.461	0.475	0.233
bp2	*9*	---------	**0.848**	**0.019**	0.221	0.000	0.949	0.423	0.473
bp3	*3*	---------	0.000	0.500	-------	0.000	0.384	0.755	0.998
xc dshov max	244	0.0146	**0.558**	**<0.001**	0.116	0.000	0.863	0.269	0.977
bp1	*231*	---------	**1.000**	**<0.001**	-------	0.000	0.494	0.566	0.831
bp2	*209*	---------	**0.543**	**0.020**	0.229	0.000	0.431	0.196	0.864
bp3	*170*	---------	**0.597**	**0.001**	0.173	0.000	0.901	0.420	0.962
xi2 td max	151	-1.1715	**0.402**	**0.005**	0.138	0.000	0.849	0.797	0.971
bp1	*95*	---------	**0.520**	**0.014**	0.201	0.000	0.594	0.835	0.489
bp2	*56*	---------	**0.704**	**0.001**	0.162	0.000	0.853	0.311	0.600
bp3	*2*	---------	0.000	0.500	-------	0.000	0.425	0.677	0.625
bp4	*1*	---------	1.000	0.357	-------	0.000	0.432	0.200	0.995
xc td max	251	-0.5136	**0.675**	**<0.001**	0.066	0.030	**0.049**	0.287	0.798
bp1	*234*	---------	0.000	0.500	-------	0.000	0.135	0.803	0.540
bp2	*172*	---------	**0.878**	**<0.001**	0.085	0.016	0.481	**0.052**	0.972
bp3	*124*	---------	**0.987**	**<0.001**	0.648	0.000	0.102	0.239	0.904
bp4	*11*	---------	**0.836**	**0.018**	0.223	0.143	0.187	0.259	**0.001**
xm1 cno max	248	-0.9071	**0.596**	**<0.001**	0.075	0.000	0.711	0.198	0.674
bp3m	*184*	---------	**0.650**	**<0.001**	0.145	0.000	0.141	0.246	0.822
bp3h	*118*	---------	**0.754**	**<0.001**	0.114	0.013	0.854	**0.043**	0.927
bp4-	*70*	---------	**0.838**	**<0.001**	0.092	0.000	0.376	0.826	0.823
bp4	*4*	---------	-------	-------	-------	-------	-------	-------	-------
xm2 cno max	278	-0.0382	**0.775**	**<0.001**	0.050	0.000	0.206	0.477	0.470
bp3a	*278*								
bp3b	*270*	---------	**0.803**	**0.004**	0.197	0.000	0.282	0.235	0.730
bp4-	*234*	---------	**0.959**	**<0.001**	0.065	0.000	0.553	0.357	0.922

bp4	*179*	---------	**0.917**	**<0.001**	0.092	0.000	0.111	0.985	0.287
xm2 c5 max	272 *40*	---------	**0.657**	**0.003**	0.182	0.043	0.740	**0.004**	0.516
xm2 Carab max	276	-0.5866	**0.818**	**<0.001**	0.038	0.000	0.758	0.334	0.855
bp1	*276*								
bp2	*251*	---------	**0.782**	**<0.001**	0.144	0.014	0.354	0.398	**0.058**
bp3	*157*	---------	**0.973**	**<0.001**	0.063	0.000	0.907	0.549	0.862
bp4	*38*	---------	**0.883**	**<0.001**	0.120	0.000	0.697	0.775	0.515
ni1 shov max	93	-1.0255	**0.561**	**0.002**	0.147	0.000	0.367	0.242	0.825
bp1	*26*	---------	**0.766**	**0.005**	0.196	0.000	0.316	0.213	0.717
bp2-bp3	*0*								
ni2 shov max	152	-0.3571	**0.443**	**0.004**	0.139	0.080	**0.049**	**0.044**	0.415
bp1	*98*	---------	**0.605**	**0.003**	0.172	0.030	0.317	**0.020**	0.895
bp2	*5*	---------	1.000	0.176	-------	0.140	**<0.001**	0.194	**<0.001**
bp3	*0*								
nc shov max	233	-0.2541	**0.620**	**<0.001**	0.075	0.000	0.826	0.479	0.405
bp1	*156*	---------	**0.743**	**<0.001**	0.104	0.000	0.732	0.663	0.543
bp2	*13*	---------	**1.000**	**<0.001**	-------	0.000	0.199	0.994	0.805
bp3	*1*	---------	1.000	0.377	-------	0.278	1.000	0.600	**0.017**
ni1 double max	110 *0*	---------	-------	-------	-------	-------	-------	-------	-------
ni2 double max	158 *3*	---------	0.000	0.500	-------	0.000	0.481	0.346	0.895
nc double max	247 *2*	---------	0.000	0.500	-------	0.000	0.579	0.975	0.647
nc td max	245	0.6107	**0.569**	**<0.001**	0.084	0.000	0.987	0.517	0.555
bp1	*63*	---------	**0.758**	**<0.001**	0.133	0.000	0.760	0.681	0.498
bp2	*19*	---------	**0.795**	**<0.001**	0.140	0.000	0.271	0.727	0.990
bp3	*2*	---------	0.000	0.500	-------	0.142	0.647	**0.090**	1.000
bp4	*1*	---------	0.303	0.486	5.145	0.000	0.918	0.209	1.000
nm2 dwrink max	262	---------	**0.972**	**<0.001**	0.066	0.000	0.390	0.689	0.467

	101								
nm2 pstylid max	271	0.2518	**0.722**	**<0.001**	0.067	0.000	0.235	0.410	0.103
bp1	*210*	---------	**0.884**	**<0.001**	0.091	0.000	0.411	0.699	0.154
bp2	*1*	---------	-------	-------	-------	-------	-------	-------	-------
nm2 c7 max	283	-1.0691	**0.815**	**<0.001**	0.042	0.000	0.772	0.781	0.603
bp1	*188*	---------	**0.938**	**<0.001**	0.070	0.000	0.497	0.941	0.794
bp2	*81*	---------	**0.973**	**<0.001**	0.069	0.000	0.743	0.938	0.589
bp3	*2*	---------	0.000	0.500	-------	0.137	0.737	**0.080**	0.999
bp4-bp5	*0*								
nm1 delta max	257	---------	0.000	0.499	-------	0.276	**0.022**	**0.009**	0.992
	6								

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[a] l=left; r=right; x=maxillary; n=mandibular; max=maximum of the left and right antimeric expressions; bp= breakpoint. All morphological trait abbreviations outlined in Appendix C. Ordinal traits were normalized and treated as continuous for the purpose for heritability estimation. Breakpoints indicate presence/absence dichotomization cutoffs for ordinal traits; each of these breakpoints was treated as an individual binary character for heritability estimation. Kurtosis is not estimated for binary character models. Certain breakpoints were omitted from the heritability analysis because expression was monomorphic across the sample. Traits marked with asterisks are associated with less stable heritability estimates because other model parameters could not be estimated, because sample size was too small, or because kurtosis values were too high after normalization. These results should be accepted with caution. Dashes are associated with incalculable parameter estimates. Traits marked with dashes for all parameters represent models that failed to converge. The trait xi1 double shovel was removed due to high levels of intra-observer error. [b] N=sample size for heritability estimation; Count=count for dichotomized trait expression (presence) at the denoted breakpoint (bp). Count values are italicized. If a trait is binary (i.e., its original scoring standards do not include ordinal scale scoring) this value is marked on a blank row beneath the sample size “N”. [c] K=model kurtosis value. [d] h2= maximum likelihood heritability estimate. [e] All significant heritability estimates (p-value<0.05) and associated probability value estimates are bolded. [f] SE= maximum likelihood standard error estimate; this parameter estimate is typically omitted when heritability estimated equal 0.000 or 1.000. [g] c2= maximum likelihood total covariate estimate. [h] All significant probability value estimates for the covariates of age, sex, and age/sex interaction are bolded.

Table 2. University of Adelaide Twin Study sample heritability estimates: deciduous crown morphology (ASUDAS standards).

			Heritability			Covariates			
Trait[a]	N[b] *Count*	K[c]	h2[d]	p-value[e]	SE[f]	c2[g]	age[h] p-value	sex[h] p-value	age*sex[h] p-value
lxi1 wing[i]	142	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*4*	---------	**1.000**	**0.022**	-------	0.000	0.108	0.194	0.385
bp2	*0*								
bp3	*133*	---------	**1.000**	**0.048**	-------	0.000	0.995	0.606	0.281
bp4	*5*	---------	-------	-------	-------	-------	-------	-------	-------
lxi1 shov*	87	1.2627	**0.653**	**0.015**	0.166	0.000	0.389	0.115	0.823
bp1	*73*	---------	**0.815**	**0.035**	0.263	0.000	0.484	0.708	0.809
bp2	*7*	---------	0.476	0.346	0.843	0.057	0.883	**0.072**	0.597
bp3-bp7	*0*								
lxi2 shov*	122	0.8043	**0.179**	**0.164**	0.179	0.000	0.615	0.385	0.826
bp1	*101*	---------	0.279	0.245	2.279	0.047	0.448	**0.016**	0.493
bp2	*12*	---------	0.379	0.175	0.383	0.000	0.739	0.177	0.563
bp3-bp7	*0*								
lxc shov	209	-0.3669	**0.689**	**<0.001**	0.076	0.063	**0.052**	**0.009**	0.234
bp1	*143*	---------	**0.900**	**<0.001**	0.096	0.032	**0.075**	**0.034**	0.325
bp2	*22*	---------	0.198	0.312	0.409	0.030	0.396	**0.052**	0.543
bp3	*2*	---------	1.000	0.269	-------	0.174	0.617	**0.064**	0.998
bp4-bp7	*0*								
lxi1 dshov	116	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*6*	---------	**0.661**	**0.050**	0.043	0.000	0.176	0.962	0.820
bp2-bp6	*0*								
lxc dshov	222	-0.2235	**0.619**	**<0.001**	0.094	0.007	0.216	0.281	**0.082**

bp1	*202*	---------	**0.947**	**<0.001**	0.108	0.000	0.563	0.882	0.688
bp2	*145*	---------	0.181	0.197	0.408	0.000	0.290	0.242	0.110
bp3	*48*	---------	**0.693**	**0.001**	0.166	0.009	0.162	0.742	**0.050**
bp4	*7*	---------	**0.858**	**0.012**	0.206	0.000	0.413	0.119	0.494
bp5	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*0*								
lxi2 td	122	-0.5447	**0.673**	**<0.001**	0.094	0.000	0.989	0.308	0.894
bp1	*51*	---------	**0.805**	**<0.001**	0.143	0.000	0.714	0.359	0.546
bp2	*16*	---------	**0.751**	**0.006**	0.214	0.000	0.435	0.151	0.118
bp3	*3*	---------	0.000	0.500	-------	0.000	0.459	0.642	0.112
bp4	*1*	---------	1.000	0.361	-------	0.000	0.455	0.181	0.995
bp5-	*1*	---------	1.000	0.361	-------	0.000	0.455	0.181	0.995
bp5	*1*	---------	1.000	0.361	-------	0.000	0.455	0.181	0.995
bp6	*0*								
lxc td	215	-0.7269	**0.671**	**<0.001**	0.083	0.035	**0.051**	0.511	0.753
bp1	*168*	---------	**0.636**	**0.003**	0.189	0.035	**0.071**	**0.075**	0.511
bp2	*102*	---------	**0.670**	**<0.001**	0.137	0.000	0.360	0.825	0.956
bp3	*35*	---------	**0.833**	**<0.001**	0.135	0.000	0.109	0.728	0.639
bp4	*14*	---------	**0.864**	**0.003**	0.189	0.189	0.110	**0.090**	**<0.001**
bp5-	*8*	---------	0.541	0.129	0.360	0.190	**0.023**	0.381	0.609
bp5	*6*	---------	0.564	0.108	0.261	0.000	0.632	0.406	0.148
bp6	*0*								
lxc dar*	128	3.5412	**0.367**	**0.026**	0.171	0.000	0.745	0.289	0.431
bp1	*17*	---------	**0.601**	**0.047**	0.271	0.000	0.688	0.472	0.612
bp2	*1*	---------	1.000	0.352	-------	0.084	0.775	**<0.001**	0.994
bp3-bp5	*0*								
lxm2 meta	277	0.0207	**0.575**	**<0.001**	0.077	0.000	0.263	0.125	0.272
bp1-bp2	*277*								
bp3	*274*	---------	0.000	0.500	-------	0.000	0.912	0.296	0.328
bp3.5	*193*	---------	**0.650**	**<0.001**	0.122	0.000	0.234	0.904	0.324
bp4	*31*	---------	**0.788**	**<0.001**	0.125	0.044	0.474	**0.006**	0.315

bp5	*1*	---------	0.000	0.500	-------	0.000	0.901	0.204	1.000
lxm1 hypo	234	-0.2745	**0.573**	**<0.001**	0.083	0.000	0.966	0.345	0.807
bp1	*85*	---------	**0.698**	**<0.001**	0.133	0.000	0.720	0.301	0.613
bp2	*38*	---------	**0.783**	**<0.001**	0.129	0.000	1.000	0.816	0.764
bp3	*10*	---------	**0.933**	**<0.001**	0.117	0.000	0.470	0.920	0.654
bp3.5	*1*	---------	0.000	0.500	-------	0.000	0.997	0.300	1.000
bp4-bp5	*0*								
lxm2 hypo	275	0.4551	**0.687**	**<0.001**	0.058	0.000	0.153	0.491	0.286
bp1-bp2	*275*								
bp3	*266*	---------	**1.000**	**<0.001**	<0.001	0.000	0.185	0.128	0.955
bp3.5	*208*	---------	**0.838**	**<0.001**	0.099	0.000	0.337	0.975	0.377
bp4	*33*	---------	**0.717**	**<0.001**	<0.001	0.000	0.118	0.383	0.467
bp5	*1*	---------	0.000	0.500	-------	0.323	**0.025**	0.853	0.918
lxm2 c5*	253	4.4037	0.765	<**0.001**	0.070	0.023	0.646	**0.021**	0.753
bp1	*34*	---------	0.853	**<0.001**	0.135	0.039	0.889	**0.007**	0.855
bp2	*9*	---------	**1.000**	**<0.001**	-------	0.000	0.781	0.680	0.737
bp3	*6*	---------	**0.817**	**0.018**	0.260	0.000	0.440	0.508	0.894
bp4	*1*	---------	0.305	0.485	5.083	0.000	0.936	0.201	0.999
bp5	*0*								
lxm2 Carab	268	-0.4069	**0.690**	**<0.001**	0.071	0.000	0.906	0.199	0.958
bp1	*267*	---------	1.000	0.351	-------	0.271	**0.044**	0.986	0.853
bp2	*260*	---------	0.000	0.500	-------	0.000	0.370	0.610	0.762
bp3	*221*	---------	**0.640**	**<0.001**	0.336	0.000	0.242	0.169	0.494
bp4	*153*	---------	**0.834**	**<0.001**	0.086	0.000	0.968	0.994	0.997
bp5	*87*	---------	**0.752**	**<0.001**	0.092	0.000	0.381	0.130	0.794
bp6	*51*	---------	**0.835**	**<0.001**	0.125	0.000	0.871	0.241	0.995
bp7	*27*	---------	**0.604**	**0.026**	0.264	0.000	0.729	0.506	0.492
lxm2 para[j]	261	---------	0.000	0.500	-------	0.000	0.921	0.204	1.000
	1								
lni1 shov	84	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*15*	---------	**0.783**	**0.015**	0.221	0.000	0.714	0.226	0.523

bp2-bp7	*0*								
lni2 shov	133	-1.1067	**0.568**	**<0.001**	0.135	0.065	**0.008**	0.208	0.149
bp1	*65*	---------	**0.799**	**0.002**	0.175	0.027	**0.025**	0.127	0.297
bp2-bp7	*0*								
lnc dar	145	-0.1490	**0.299**	**0.045**	0.168	0.000	0.356	0.139	0.468
bp1	*46*	---------	**0.475**	**0.030**	0.227	0.000	0.461	0.130	0.766
bp2	*6*	---------	0.000	0.500	-------	0.000	0.349	0.785	0.166
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4-bp5	*0*								
lnm2 ant fovea*	249	0.9334	**0.586**	**<0.001**	0.087	0.000	0.106	0.842	0.324
bp1	*247*	---------	0.000	0.500	-------	0.000	1.000	0.137	0.999
bp2	*224*	---------	**0.827**	**<0.001**	0.147	0.074	0.464	0.850	**0.010**
bp3	*47*	---------	**0.730**	**<0.001**	0.134	0.000	0.120	0.613	0.740
bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------
lnm1 cno	208	-0.9331	**0.568**	**<0.001**	0.111	0.068	0.936	**0.002**	0.247
bp5	*100*	---------	**0.750**	**<0.001**	0.142	0.036	0.815	**0.001**	0.182
bp6	*3*	---------	0.000	0.500	-------	0.000	0.412	0.422	0.668
lnm2 cno	272	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*272*								
bp6	*17*	---------	**1.000**	**<0.001**	-------	0.000	0.605	0.683	0.539
bp7	*2*	---------	0.984	0.384	1.794	0.139	0.913	**0.075**	1.000
lnm2 groove[i]	136	---------	-------	-------	-------	-------	-------	-------	-------
y	*117*	---------	**1.000**	**<0.001**	-------	0.000	0.720	0.552	0.444
x	*16*	---------	**1.000**	**<0.001**	-------	0.000	0.604	0.652	0.654
+	*3*	---------	0.870	0.407	1.975	0.000	0.768	1.000	0.439
lnm2 dwrink	230	-0.9061	**0.745**	**<0.001**	0.065	0.000	0.647	0.601	0.879
bp1	*158*	---------	**0.915**	**<0.001**	0.082	0.000	0.105	0.115	0.236
bp2	*77*	---------	**0.760**	**<0.001**	0.137	0.000	0.661	0.677	0.313
bp3	*5*	---------	0.000	0.500	-------	0.000	0.501	0.850	0.621
lnm1 c5	207	-0.7696	**0.488**	**<0.001**	0.106	0.036	0.452	**0.014**	0.322
bp1	*97*	---------	**0.629**	**0.001**	0.173	0.035	0.617	**0.001**	0.313

bp2	*71*	---------	**0.654**	**<0.001**	0.150	0.014	0.447	**0.027**	0.197
bp3	*30*	---------	0.354	0.081	0.229	0.000	0.789	0.702	0.177
bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*0*								
lnm2 c5*	271	3.9791	**0.197**	**0.028**	0.108	0.028	**0.003**	1.000	**0.037**
bp1-bp2	*271*								
bp3	*268*	---------	1.000	0.270	-------	0.212	0.221	**0.056**	0.996
bp4	*249*	---------	0.514	0.058	0.292	0.038	0.809	**0.014**	0.225
bp5	*18*	---------	**0.449**	**0.034**	0.235	0.006	0.112	0.771	**0.077**
lnm1 c6*	223	72.3744	0.000	0.500	-------	0.000	0.243	0.436	0.771
bp1	*3*	---------	0.000	0.500	-------	0.000	0.467	0.402	0.633
bp2	*2*	---------	0.785	0.429	2.420	0.156	0.464	**0.092**	0.998
bp3	*2*	---------	0.785	0.429	2.420	0.156	0.464	**0.092**	0.998
bp4	*1*	---------	1.000	0.423	-------	0.374	**0.003**	0.759	0.991
bp5	*0*								
lnm2 c6	274	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*17*	---------	**1.000**	**<0.001**	-------	0.000	0.489	0.720	0.556
bp2	*8*	---------	**1.000**	**<0.001**	-------	0.000	0.782	0.834	0.823
bp3	*2*	---------	0.000	0.500	-------	0.136	0.660	**0.077**	0.999
bp4-bp5	*0*								
lnm2 c7	266	-0.9160	**0.688**	**<0.001**	0.068	0.000	0.688	0.838	0.848
bp1	*151*	---------	**0.882**	**<0.001**	0.087	0.000	0.977	0.742	0.854
bp1a	*123*	---------	**0.823**	**<0.001**	0.106	0.000	0.838	0.619	0.514
bp2	*15*	---------	**0.667**	**0.008**	0.242	0.000	0.464	0.657	0.341
bp3-bp4	*0*								
lnm2 dtcrest	214	---------	0.000	0.500	-------	0.022	**0.077**	0.668	0.107
	7								
rxi1 wing[i]	141	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*7*	---------	1.000	0.065	-------	0.000	0.497	0.590	0.613
bp2	*8*	---------	**0.779**	**0.037**	0.804	0.000	0.936	0.287	0.653
bp3	*125*	---------	**0.901**	**0.002**	0.156	0.000	0.875	0.464	0.571

bp4	*1*	---------	0.000	0.500	-------	0.000	0.921	0.653	0.147
rxi1 shov	87	0.0668	0.470	0.080	0.260	0.053	0.804	**0.016**	0.641
bp1	*66*	---------	0.464	0.201	0.453	0.034	0.838	**0.072**	0.688
bp2	*2*	---------	1.000	0.247	-------	0.219	0.770	**0.044**	0.998
bp3-bp7	*0*								
rxi2 shov	126	0.6737	**0.513**	**0.001**	0.122	0.000	0.700	0.711	0.224
bp1	*109*	---------	**0.574**	**0.026**	0.246	0.000	0.290	0.435	0.377
bp2	*18*	---------	**0.806**	**0.008**	0.197	0.000	0.461	0.842	0.264
bp3-bp7	*0*								
rxc shov	211	0.0510	**0.739**	**<0.001**	0.058	0.021	**0.006**	0.154	**0.038**
bp1	*160*	---------	**0.997**	**<0.001**	0.144	0.048	**0.017**	**0.019**	0.129
bp2	*21*	---------	0.348	0.184	0.370	0.000	0.234	0.777	0.355
bp3	*1*	---------	0.101	0.500	3.654	0.000	0.884	0.195	1.000
bp4-bp7	*0*								
rxi1 dshov*	118	5.9902	**0.749**	**<0.001**	0.081	0.000	0.554	0.274	0.195
bp1	*12*	---------	**0.922**	**0.001**	0.138	0.000	0.663	0.243	0.234
bp2	*1*	---------	0.000	0.500	-------	0.000	0.130	0.797	0.961
bp3-bp6	*0*								
rxc dshov	224	-0.3075	**0.558**	**<0.001**	0.099	0.000	0.662	0.108	0.263
bp1	*201*	---------	**0.782**	**0.001**	0.172	0.000	0.811	0.501	0.750
bp2	*146*	---------	**0.494**	**0.006**	0.167	0.011	0.353	**0.093**	0.416
bp3	*47*	---------	**0.692**	**<0.001**	0.154	0.000	0.526	0.369	0.491
bp4	*12*	---------	0.355	0.220	0.072	0.000	0.566	0.229	0.312
bp5-bp6	*0*								
rxi2 td	132	-0.8923	**0.556**	**0.002**	0.143	0.069	**0.022**	0.264	**0.010**
bp1	*64*	---------	**0.555**	**0.019**	0.228	0.010	0.113	0.548	**0.040**
bp2	*20*	---------	**0.708**	**0.042**	0.288	0.048	**0.040**	0.753	**0.029**
bp3	*4*	---------	**1.000**	**0.009**	-------	0.260	**0.040**	0.520	**0.010**
bp4	*2*	---------	1.000	0.295	-------	0.117	**0.039**	0.335	0.771
bp5-	*1*	---------	1.000	0.375	-------	0.101	**0.084**	0.476	0.907
bp5	*1*	---------	1.000	0.375	-------	0.101	**0.084**	0.476	0.907

bp6	*0*								
rxc td	226	-0.4054	**0.649**	**<0.001**	0.080	0.046	**0.038**	0.940	0.834
bp1	*193*	---------	**0.481**	**0.026**	0.216	0.000	0.599	0.591	0.615
bp2	*107*	---------	**0.758**	**<0.001**	0.121	0.033	**0.030**	0.613	0.940
bp3	*46*	---------	**0.447**	**0.046**	0.059	0.000	0.226	0.740	0.469
bp4	*13*	---------	1.000	0.063	-------	0.210	**0.013**	**0.035**	<**0.001**
bp5-	*8*	---------	**1.000**	**0.013**	-------	0.171	0.120	**0.001**	**0.002**
bp5	*5*	---------	**1.000**	**0.001**	-------	0.045	0.837	**0.079**	0.168
bp6	*0*								
rxc dar*	126	1.5861	**0.467**	**0.009**	0.169	0.000	0.472	0.773	0.339
bp1	*24*	---------	**0.695**	**0.021**	0.255	0.000	0.480	0.573	0.256
bp2	*3*	---------	0.000	0.500	-------	0.000	0.837	0.927	0.819
bp3-bp5	*0*								
rxm2 meta	270	-0.0603	**0.599**	**<0.001**	0.077	0.007	**0.093**	0.154	0.119
bp1	*269*	---------	0.000	0.500	-------	0.000	0.602	0.128	0.997
bp2	*269*	---------	0.000	0.500	-------	0.000	0.602	0.128	0.997
bp3	*263*	---------	0.000	0.500	-------	0.000	0.200	0.480	0.256
bp3.5	*186*	---------	**0.680**	**<0.001**	0.127	0.000	0.268	0.667	0.151
bp4	*38*	---------	**0.798**	**<0.001**	0.118	0.025	0.287	**0.041**	0.730
bp5	*1*	---------	0.000	0.500	-------	0.388	**0.017**	0.305	0.963
rxm1 hypo	237	-0.4746	**0.573**	**<0.001**	0.081	0.000	0.891	0.390	0.799
bp1	*96*	---------	**0.797**	**<0.001**	0.083	0.000	0.883	0.244	0.886
bp2	*36*	---------	**0.788**	**<0.001**	0.139	0.000	0.462	0.619	0.338
bp3	*6*	---------	**0.788**	**<0.001**	0.139	0.000	0.462	0.619	0.338
bp3.5	*1*	---------	0.000	0.500	-------	0.000	1.000	0.308	0.891
bp4-bp5	*0*								
rxm2 hypo	270	0.5145	**0.644**	**<0.001**	0.071	0.000	0.214	0.986	0.675
bp1	*270*								
bp2	*264*	---------	**0.818**	**0.016**	0.250	0.000	0.534	0.642	0.897
bp3	*255*	---------	**0.941**	**<0.001**	0.097	0.000	0.527	0.976	0.910
bp3.5	*191*	---------	**0.779**	**<0.001**	0.100	0.000	0.426	0.624	0.573

bp4	*25*	---------	**0.564**	**0.008**	0.203	0.006	**0.067**	0.576	0.111
bp5	*2*	---------	1.000	0.262	-------	0.152	0.556	**0.076**	0.997
rxm2 c5*	238	3.7617	**0.627**	**<0.001**	0.078	0.000	0.929	0.470	0.759
bp1	*33*	---------	**0.842**	**<0.001**	0.116	0.000	0.880	0.317	0.838
bp2	*9*	---------	**0.926**	**<0.001**	0.121	0.000	0.873	0.459	0.840
bp3	*7*	---------	**0.757**	**0.004**	0.157	0.000	0.886	0.183	0.780
bp4	*6*	---------	**0.858**	**0.002**	0.188	0.076	0.983	**0.052**	0.641
bp5	*0*								
rxm2 Carab	256	-0.5115	**0.739**	**<0.001**	0.058	0.000	0.667	0.675	0.439
bp1	*256*								
bp2	*247*	---------	0.480	0.134	0.351	0.021	0.261	0.952	**0.086**
bp3	*205*	---------	**0.813**	**<0.001**	0.116	0.000	0.908	0.922	0.390
bp4	*165*	---------	**0.940**	**<0.001**	0.070	0.000	0.837	0.325	0.673
bp5	*100*	---------	**0.780**	**<0.001**	0.110	0.000	0.868	0.441	0.699
bp6	*57*	---------	**0.815**	**<0.001**	0.124	0.000	0.957	0.671	0.804
bp7	*28*	---------	**0.698**	**0.002**	0.103	0.000	0.980	0.685	0.794
rxm2 para[j]	278	---------	-------	-------	-------	-------	-------	-------	-------
	0								
rni1 shov	82	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*20*	---------	**0.809**	**0.002**	0.169	0.000	0.507	0.245	0.973
bp2-bp7	*0*								
rni2 shov	143	-0.9165	**0.484**	**0.002**	0.140	0.055	**0.024**	0.127	**0.061**
bp1	*77*	---------	**0.720**	**0.001**	0.167	0.019	0.140	**0.075**	0.169
bp2	*6*	---------	0.000	0.500	-------	0.179	**0.003**	**0.091**	**0.020**
bp3-bp7	*0*								
rnc dar	128	0.9756	**0.443**	**0.006**	0.153	0.000	0.605	0.414	0.719
bp1	*28*	---------	**0.580**	**0.023**	0.299	0.000	0.636	0.603	0.792
bp2	*3*	---------	0.000	0.500	-------	0.000	0.579	0.214	0.349
bp3	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp4-bp5	*0*								
rnm2 ant fovea	238	-0.1814	**0.390**	**<0.001**	0.109	0.000	0.711	0.379	0.695

bp1	*236*	---------	0.000	0.500	-------	0.000	0.470	0.832	0.535
bp2	*225*	---------	0.421	0.213	0.336	0.000	0.781	0.359	0.699
bp3	*61*	---------	**0.761**	**<0.001**	0.277	0.000	0.733	0.166	0.616
bp4	*4*	---------	-------	-------	-------	-------	-------	-------	-------
rnm1 cno	219	-0.6271	**0.470**	**<0.001**	0.114	0.032	0.457	**0.049**	0.162
bp5	*96*	---------	**0.781**	**<0.001**	0.128	0.011	0.627	**0.087**	0.142
bp6	*2*	---------	0.799	0.427	2.406	0.115	0.997	**0.061**	1.000
rnm2 cno*	270	11.3756	**0.886**	**<0.001**	0.029	0.000	0.471	0.905	0.378
bp5	*270*								
bp6	*18*	---------	**0.906**	**0.002**	0.149	0.000	0.458	0.696	0.426
bp7	*2*	---------	0.936	0.393	1.908	0.141	0.881	**0.074**	1.000
rnm2 groove[i]	127	---------	-------	-------	-------	-------	-------	-------	-------
y	*105*	---------	**0.773**	**0.023**	0.271	0.000	0.634	0.525	0.339
x	*19*	---------	**1.000**	**0.038**	-------	0.000	0.737	0.812	0.135
+	*3*	---------	0.000	0.500	-------	0.000	0.901	0.464	0.827
rnm2 dwrink	240	-1.0146	**0.638**	**<0.001**	0.084	0.000	0.425	0.471	0.524
bp1	*158*	---------	**0.854**	**<0.001**	0.108	0.000	0.350	0.154	0.522
bp2	*64*	---------	**0.685**	**<0.001**	0.141	0.000	0.642	0.971	0.986
bp3	*2*	---------	0.000	0.500	-------	0.000	1.000	0.569	0.987
rnm1 c5	219	-0.7081	**0.669**	**<0.001**	0.084	0.000	0.743	0.799	0.213
bp1	*96*	---------	**0.812**	**<0.001**	0.117	0.000	0.668	0.117	0.183
bp2	*75*	---------	**0.772**	**<0.001**	0.097	0.000	0.521	0.635	0.580
bp3	*26*	---------	**0.878**	**<0.001**	0.137	0.000	0.469	0.130	0.230
bp4	*2*	---------	0.000	0.500	-------	0.000	0.397	0.513	0.975
bp5	*0*								
rnm2 c5*	271	2.0694	**0.466**	**<0.001**	0.115	0.000	0.159	0.275	0.678
bp1	*270*	---------	0.000	0.500	-------	0.000	0.870	0.451	0.988
bp2	*269*	---------	0.000	0.500	-------	0.000	1.000	0.139	1.000
bp3	*267*	---------	0.000	0.500	-------	0.000	0.876	0.716	0.662
bp4	*227*	---------	**0.732**	**<0.001**	0.143	0.000	0.370	0.760	0.958
bp5	*16*	---------	0.329	0.192	0.323	0.000	0.269	0.167	0.377

rnm1 c6	229	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*2*	---------	0.846	0.417	2.107	0.155	0.945	**0.060**	1.000
bp2	*2*	---------	0.846	0.417	2.107	0.155	0.945	**0.060**	1.000
bp3	*1*	---------	0.114	0.497	3.552	0.000	0.339	0.373	0.997
bp4	*1*	---------	0.114	0.497	3.552	0.000	0.340	0.373	0.997
bp5	*0*								
rnm2 c6*	269	10.8591	**0.809**	**<0.001**	0.052	0.000	0.400	0.955	0.326
bp1	*19*	---------	**0.797**	**0.006**	0.146	0.000	0.461	0.580	0.409
bp2	*13*	---------	**1.000**	**<0.001**	-------	0.000	0.198	0.604	0.190
bp3	*2*	---------	0.000	0.500	-------	0.000	0.659	0.809	0.633
bp4	*1*	---------	0.000	0.500	-------	0.000	0.757	0.214	1.000
bp5	*0*								
rnm2 c7	273	-0.8085	**0.765**	**<0.001**	0.051	0.000	0.321	0.866	0.553
bp1	*157*	---------	**0.914**	**<0.001**	0.078	0.000	0.359	0.775	0.749
bp1a	*123*	---------	**0.923**	**<0.001**	0.083	0.000	0.442	0.936	0.348
bp2	*14*	---------	**0.950**	**<0.001**	0.098	0.000	0.460	0.889	0.643
bp3	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*0*								
rnm2 dtcrest	232	---------	**0.907**	**<0.001**	0.111	0.000	0.654	0.116	0.460
	20								
xi1 shov max*	100	1.6881	**0.467**	**0.022**	0.177	0.019	0.970	**0.074**	0.348
bp1	*86*	---------	0.596	0.068	0.298	0.000	0.825	0.526	0.357
bp2	*7*	---------	0.552	0.307	0.707	0.061	0.990	**0.058**	0.475
bp3-bp7	*0*								
xi2 shov max*	143	0.8315	**0.545**	**<0.001**	0.144	0.000	0.508	0.767	0.761
bp1	*129*	---------	0.367	0.195	0.355	0.000	0.159	0.452	0.533
bp2	*24*	---------	**0.840**	**0.001**	0.141	0.000	0.479	0.994	0.638
bp3-bp7	*0*								
xc shov max	235	-0.1409	**0.792**	**<0.001**	0.046	0.068	**0.005**	**0.020**	**0.028**
bp1	*184*	---------	**1.000**	**<0.001**	-------	0.052	**0.034**	**0.004**	0.125
bp2	*36*	---------	**0.741**	**<0.001**	0.164	0.007	**0.069**	0.365	0.149

bp3	*2*	---------	0.000	0.500	-------	0.153	0.644	**0.073**	0.999
bp4-bp7	*0*								
xi1 dshov max*	129	5.2321	**0.589**	**<0.001**	0.115	0.000	0.443	0.520	0.148
bp1	*14*	---------	**0.806**	**0.005**	0.192	0.000	0.510	0.625	0.279
bp2	*1*	---------	0.000	0.500	-------	0.173	**<0.001**	0.271	0.985
bp3-bp6	*0*								
xc dshov max	239	-0.1687	**0.751**	**<0.001**	0.058	0.030	0.178	**0.042**	0.078
bp1	*225*	---------	**1.000**	**<0.001**	-------	0.000	0.357	0.771	0.350
bp2	*184*	---------	**0.570**	**0.004**	0.185	0.023	0.282	**0.022**	0.307
bp3	*73*	---------	**0.849**	**<0.001**	0.097	0.000	0.302	0.531	0.102
bp4	*17*	---------	**0.894**	**<0.001**	0.119	0.028	0.296	**0.069**	0.356
bp5	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*0*								
xi2 td max	149	-0.7430	**0.698**	**<0.001**	0.087	0.000	0.901	0.906	0.949
bp1	*84*	---------	**0.623**	**0.004**	0.195	0.000	0.576	0.898	0.516
bp2	*29*	---------	**0.882**	**<0.001**	0.115	0.000	0.405	0.491	0.161
bp3	*5*	---------	**1.000**	**0.011**	-------	0.048	0.278	0.446	**0.020**
bp4	*2*	---------	1.000	0.249	-------	0.194	0.268	**0.060**	0.995
bp5-	*1*	---------	1.000	0.357	-------	0.000	0.432	0.199	0.995
bp5	*1*	---------	1.000	0.357	-------	0.000	0.432	0.199	0.995
bp6	*0*								
xc td max	245	-0.4595	**0.606**	**<0.001**	0.080	0.043	**0.031**	0.640	0.578
bp1	*221*	---------	0.155	0.284	0.623	0.000	0.135	0.824	0.455
bp2	*137*	---------	**0.703**	**<0.001**	0.127	0.000	0.255	0.149	0.792
bp3	*54*	---------	**0.646**	**0.002**	0.737	0.000	0.177	0.611	0.489
bp4	*20*	---------	**1.000**	**0.001**	-------	0.259	**0.037**	**<0.001**	**<0.001**
bp5-	*13*	---------	**1.000**	**0.012**	-------	0.221	**0.067**	0.133	**<0.001**
bp5	*9*	---------	**0.889**	**0.003**	0.164	0.000	0.192	0.191	0.156
bp6	*0*								
xc dar max	165	0.9579	**0.516**	**<0.001**	0.104	0.000	0.988	0.769	0.547
bp1	*36*	---------	**0.744**	**<0.001**	0.148	0.000	0.931	1.000	0.498

bp2	*4*	---------	0.000	0.500	-------	0.000	0.966	0.642	0.937
bp3-bp5	*0*								
xm2 meta max	278	0.4024	**0.664**	**<0.001**	0.064	0.010	0.450	**0.080**	0.390
bp1-bp2	*278*								
bp3	*277*	---------	0.369	0.479	4.374	0.000	0.901	0.203	1.000
bp3.5	*235*	---------	**0.716**	**<0.001**	0.337	0.000	0.906	0.459	0.863
bp4	*52*	---------	**0.851**	**<0.001**	0.090	0.039	0.411	**0.004**	0.519
bp5	*2*	---------	0.000	0.500	-------	0.000	0.177	0.181	0.994
xm1 hypo max	251	-0.6429	**0.534**	**<0.001**	0.085	0.000	0.997	0.179	0.962
bp1	*119*	---------	**0.684**	**<0.001**	0.122	0.000	0.977	0.130	0.942
bp2	*51*	---------	**0.728**	**<0.001**	0.138	0.000	0.673	0.315	0.455
bp3	*13*	---------	**0.952**	**<0.001**	0.097	0.000	0.994	0.294	0.794
bp3.5	*2*	---------	**1.000**	**0.002**	-------	0.648	1.000	**<0.001**	0.915
bp4-bp5	*0*								
xm2 hypo max	279	0.6936	**0.722**	**<0.001**	0.055	0.000	0.313	0.694	0.645
bp1-bp2	*279*								
bp3	*271*	---------	**0.922**	**<0.001**	0.121	0.000	0.284	0.205	0.940
bp3.5	*230*	---------	**0.910**	**<0.001**	0.078	0.000	0.900	0.970	0.869
bp4	*44*	---------	**0.744**	**<0.001**	0.126	0.011	**0.077**	0.485	0.361
bp5	*2*	---------	1.000	0.264	-------	0.154	0.581	**0.071**	0.998
xm2 c5 max*	272	2.6874	**0.546**	**<0.001**	0.099	0.015	0.937	**0.030**	0.606
bp1	*47*	---------	**0.714**	**<0.001**	0.161	0.027	0.976	**0.012**	0.643
bp2	*12*	---------	**0.907**	**<0.001**	0.145	0.000	0.710	0.896	0.455
bp3	*8*	---------	**0.749**	**0.004**	0.207	0.000	0.998	0.435	0.665
bp4	*6*	---------	**0.865**	**0.002**	0.200	0.071	0.809	**0.058**	0.620
bp5	*0*								
xm2 Carab max	276	-0.5180	**0.857**	**<0.001**	0.034	0.000	0.952	0.118	0.636
bp1	*275*	---------	1.000	0.351	-------	0.271	**0.043**	0.981	0.789
bp2	*273*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*246*	---------	**0.783**	**<0.001**	0.150	0.057	0.313	**0.035**	**0.005**
bp4	*190*	---------	**0.998**	**<0.001**	0.055	0.000	0.994	0.588	0.882

bp5	*121*	---------	**0.890**	**<0.001**	0.085	0.009	0.833	**0.080**	0.906
bp6	*72*	---------	**0.916**	**<0.001**	0.081	0.000	0.974	0.331	0.757
bp7	*36*	---------	**0.862**	**<0.001**	0.125	0.000	0.870	0.849	0.943
xm2 para max[j]	278	---------	0.000	0.500	-------	0.000	0.913	0.198	1.000
	1								
ni1 shov max	92	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*23*	---------	**0.630**	**0.023**	0.227	0.000	0.587	0.218	0.931
bp2-bp7	*0*								
ni2 shov max	149	-0.6680	**0.509**	**0.001**	0.130	0.068	**0.085**	**0.066**	0.598
bp1	*89*	---------	**0.769**	**<0.001**	0.150	0.024	0.381	**0.033**	0.833
bp2	*6*	---------	0.109	0.463	1.097	0.109	**0.006**	0.119	**0.042**
bp3-bp7	*0*								
nc dar max	166	-0.4369	**0.468**	**0.002**	0.139	0.000	0.354	0.139	0.558
bp1	*62*	---------	**0.626**	**0.002**	1.665	0.000	0.363	**0.106**	0.702
bp2	*8*	---------	0.000	0.500	-------	0.000	0.770	0.983	0.773
bp3	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp4-bp5	*0*								
nm2 ant fovea max	268	0.4888	**0.400**	**<0.001**	0.111	0.032	**0.071**	0.529	0.685
bp1	*267*	---------	0.000	0.500	-------	0.000	0.999	0.322	0.998
bp2	*255*	---------	0.086	0.444	-------	0.109	**0.006**	**0.057**	0.268
bp3	*83*	---------	**0.710**	**<0.001**	0.139	0.000	0.181	0.182	0.879
bp4	*5*	---------	0.000	0.500	-------	0.000	0.444	0.200	0.335
nm1 cno max	239	-0.3197	**0.718**	**<0.001**	0.066	0.070	0.591	**0.001**	0.173
bp5	*128*	---------	**0.900**	**<0.001**	0.093	0.042	0.985	**0.001**	0.212
bp6	*5*	---------	**1.000**	**0.023**	<0.001	0.000	0.444	0.160	0.642
nm2 cno max	282	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*282*								
bp6	*23*	---------	**1.000**	**<0.001**	-------	0.000	0.165	0.217	0.258
bp7	*2*	---------	0.983	0.383	1.801	0.139	0.941	**0.073**	1.000
nm2 dwrink max	261	-0.8433	**0.775**	**<0.001**	0.059	0.000	0.390	0.368	0.794
bp1	*188*	---------	**0.816**	**<0.001**	0.112	0.013	0.703	**0.049**	0.776

bp2	*101*	---------	**0.934**	**<0.001**	**0.076**	0.000	0.701	0.350	0.656
bp3	*7*	---------	0.000	0.500	-------	0.000	0.443	0.603	0.643
nm1 c5 max	239	-0.6968	**0.688**	**<0.001**	0.061	0.031	0.764	**0.017**	0.286
bp1	*127*	---------	**0.931**	**<0.001**	0.089	0.040	0.964	**0.001**	0.256
bp2	*107*	---------	**0.876**	**<0.001**	0.090	0.018	0.147	**0.012**	0.646
bp3	*43*	---------	**0.662**	**<0.001**	0.105	0.000	0.650	0.890	0.151
bp4	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*0*								
nm2 c5 max*	281	4.0712	**0.290**	**0.006**	0.118	0.017	**0.012**	0.539	**0.070**
bp1	*281*								
bp2	*280*	---------	0.378	0.478	4.300	0.000	1.000	1.000	0.322
bp3	*278*	---------	0.000	0.500	-------	0.000	0.942	0.419	0.707
bp4	*267*	---------	0.000	0.500	-------	0.019	**0.084**	0.591	0.332
bp5	*27*	---------	**0.673**	**0.001**	0.174	0.022	**0.065**	0.584	**0.097**
nm1 c6 max	243	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*5*	---------	**1.000**	**0.023**	-------	0.000	0.507	0.155	0.660
bp2	*4*	---------	**1.000**	**0.018**	-------	0.001	0.499	**0.016**	0.999
bp3	*3*	---------	**1.000**	**0.017**	-------	0.172	0.645	**0.042**	1.000
bp4	*2*	---------	0.903	0.404	2.052	0.153	0.442	**0.088**	0.998
bp5	*0*								
nm2 c6 max	282	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*23*	---------	**1.000**	**<0.001**	-------	0.000	0.165	0.217	0.258
bp2	*16*	---------	**1.000**	**<0.001**	-------	0.000	0.262	0.689	0.288
bp3	*3*	---------	0.000	0.500	-------	0.000	0.637	0.289	0.946
bp4	*1*	---------	0.000	0.500	-------	0.000	0.799	0.207	1.000
bp5	*0*								
nm2 c7 max	283	-0.7121	**0.776**	**<0.001**	0.049	0.000	0.641	0.879	0.693
bp1	*184*	---------	**0.940**	**<0.001**	0.039	0.000	0.381	0.834	0.886
bp1a	*149*	---------	**0.887**	**<0.001**	0.083	0.000	0.380	0.931	0.187
bp2	*24*	---------	**0.768**	**<0.001**	0.178	0.000	0.539	0.918	0.763
bp3	*2*	---------	-------	-------	-------	-------	-------	-------	-------

bp4	*0*								
nm2 dtcrest max	256 *25*	---------	**0.876**	**<0.001**	0.108	0.000	0.431	0.178	0.210

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[a] l=left; r=right; x=maxillary; n=mandibular; max=maximum of the left and right antimeric expressions; bp breakpoint. All morphological trait abbreviations outlined in Appendix C. Ordinal traits were normalized and treated as continuous for the purpose for heritability estimation. Breakpoints indicate presence/absence dichotomization cutoffs for ordinal traits; each of these breakpoints was treated as an individual binary character for heritability estimation. Kurtosis is not estimated for binary character models. Certain breakpoints were omitted from the heritability analysis because expression was monomorphic across the sample. Traits marked with asterisks are associated with less stable heritability estimates because other model parameters could not be estimated, because sample size was too small, or because kurtosis values were too high after normalization. These results should be accepted with caution. Dashes are associated with incalculable parameter estimates. Traits marked with dashes for all parameters represent models that failed to converge. The traits xi1 labial convexity, xi2 double shovel, xm1 metacone, xm1 parastyle, nm2 protostylid, and nm1 cusp 7 were removed due to high levels of intra-observer error. [b] N=sample size for heritability estimation; Count=count for dichotomized trait expression (presence) at the denoted breakpoint (bp). Count values are italicized. If a trait is binary (i.e., its original scoring standards do not include ordinal scale scoring) this value is marked on a blank row beneath the sample size “N”. [c] K=model kurtosis value. [d] h2= maximum likelihood heritability estimate. [e] All significant heritability estimates (p-value<0.05) and associated probability value estimates are bolded. [f] SE= maximum likelihood standard error estimate; this parameter estimate is typically omitted when heritability estimated equal 0.000 or 1.000. [g] c2= maximum likelihood total covariate estimate. [h] All significant probability value estimates for the covariates of age, sex, and age/sex interaction are bolded. [i] As the winging and groove pattern data are categorical and not ordinal, each category was treated as a separate binary variable. [j] Parastyle for deciduous molars was scored only as a binary variable at the breakpoint of ASUDAS grade 3.

Table 3. University of Adelaide Twin Study sample heritability estimates: permanent crown morphology (ASUDAS standards).

			Heritability			Covariates			
Trait[a]	N[b] *Count*	K[c]	h2[d]	p-value[e]	SE[f]	c2[g]	age[h] p-value	sex[h] p-value	age*sex[h] p-value
LXI1 WING[i]	315	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*11*	---------	0.000	0.500	-------	0.000	0.765	0.288	0.786
bp2	*0*								
bp3	*193*	---------	**0.263**	**0.041**	0.158	0.000	0.378	0.821	0.972
bp4	*111*	---------	**0.299**	**0.025**	0.125	0.000	0.400	0.624	0.978
LXI1 SHOV*	283	-0.1414	**0.776**	**<0.001**	0.056	0.006	**0.090**	0.551	0.331
bp1	*246*	---------	**0.832**	**<0.001**	0.144	0.000	0.406	0.689	0.403
bp2	*107*	---------	**0.905**	**<0.001**	0.088	0.000	0.452	0.724	0.757
bp3	*28*	---------	**0.851**	**<0.001**	0.143	0.026	0.492	**0.004**	0.405
bp4	*5*	---------	0.635	0.095	0.415	0.000	0.180	0.141	0.908
bp5-bp7	*0*								
LXI2 SHOV*	214	-0.6172	**0.708**	**<0.001**	0.071	0.077	**0.038**	**0.006**	**0.067**
bp1	*180*	---------	**0.710**	**<0.001**	0.161	0.004	0.139	0.116	**0.094**
bp2	*85*	---------	**0.812**	**0.001**	0.118	0.028	0.215	**0.003**	0.410
bp3	*27*	---------	**0.850**	**0.001**	0.165	0.085	**0.096**	**0.006**	0.575
bp4	*7*	---------	**1.000**	**<0.001**	-------	0.000	0.249	0.155	0.107
bp5-bp7	*0*								
LXC SHOV	135	-0.6529	**0.654**	**<0.001**	0.139	0.000	0.223	0.773	0.294
bp1	*90*	---------	**0.898**	**0.002**	0.213	0.000	0.170	0.649	0.494
bp2	*27*	---------	**0.636**	**0.039**	0.311	0.000	0.783	0.792	0.536
bp3	*6*	---------	**0.795**	**0.011**	0.252	0.000	0.788	0.298	0.428
bp4-bp7	*0*								
LXI1 DSHOV	301	-0.3033	**0.501**	**<0.001**	0.111	0.000	0.611	0.709	0.561

bp1	*259*	---------	**0.625**	**0.007**	0.247	0.000	0.767	0.918	0.295
bp2	*128*	---------	**0.503**	**0.003**	0.179	0.007	0.324	0.706	**0.077**
bp3	*36*	---------	**0.676**	**<0.001**	0.167	0.000	0.510	0.292	0.291
bp4	*7*	---------	**0.712**	**0.003**	0.579	0.000	0.503	0.954	0.756
bp5-bp6	*0*								
LXI2 DSHOV	267	-0.7623	**0.607**	**<0.001**	0.081	0.002	0.104	0.289	**0.084**
bp1	*156*	---------	**0.645**	**<0.001**	0.154	0.011	0.195	**0.084**	0.129
bp2	*61*	---------	**0.679**	**<0.001**	0.132	0.000	0.282	0.490	0.300
bp3	*16*	---------	**0.464**	**0.043**	0.320	0.000	0.268	0.706	0.187
bp4	*2*	---------	0.000	0.500	-------	0.000	0.230	0.666	0.229
bp5-bp6	*0*								
LXC DSHOV	190	-0.3696	**0.784**	**<0.001**	0.080	0.026	0.334	**0.091**	0.772
bp1	*170*	---------	0.456	0.085	0.359	0.000	0.969	0.330	0.250
bp2	*122*	---------	**0.858**	**<0.001**	0.177	0.000	0.569	0.125	0.582
bp3	*65*	---------	**0.828**	**<0.001**	0.143	0.009	**0.035**	0.184	0.111
bp4	*20*	---------	**0.696**	**0.002**	0.203	0.000	0.416	0.202	0.691
bp5	*3*	---------	0.000	0.500	-------	0.000	0.173	0.992	0.250
bp6	*0*								
LXP1 DSHOV	223	-0.4225	**0.674**	**<0.001**	0.082	0.000	0.167	0.993	0.516
bp1	*195*	---------	**0.765**	**<0.001**	0.164	0.000	0.609	0.964	0.780
bp2	*150*	---------	**0.824**	**<0.001**	0.124	0.009	**0.097**	0.654	0.321
bp3	*65*	---------	**0.925**	**<0.001**	0.098	0.000	0.539	0.854	0.934
bp4	*16*	---------	0.302	0.209	0.390	0.000	0.239	0.766	0.542
bp5	*1*	---------	0.000	0.500	-------	0.000	0.930	0.172	1.000
bp6	*0*								
LXP2 DSHOV	185	-0.7008	**0.609**	**<0.001**	0.124	0.000	0.945	0.326	0.190
bp1	*105*	---------	**0.528**	**0.014**	0.269	0.000	0.617	0.193	0.397
bp2	*38*	---------	**0.554**	**0.003**	0.155	0.000	0.899	0.736	0.201
bp3	*12*	---------	**1.000**	**<0.001**	-------	0.000	0.230	0.375	0.201
bp4	*3*	---------	**1.000**	**0.002**	-------	0.000	0.179	0.113	0.991
bp5-bp6	*0*								

LXI1 TD	249	-0.4834	**0.682**	**<0.001**	0.085	0.000	0.650	0.580	0.757
bp1	*219*	---------	**0.506**	**0.044**	0.235	0.000	0.343	0.635	0.884
bp2	*171*	---------	**0.764**	**<0.001**	0.040	0.000	0.664	0.973	0.418
bp3	*91*	---------	0.271	0.066	0.185	0.000	0.295	0.505	0.685
bp4	*29*	---------	**0.794**	**0.004**	0.172	0.000	0.133	0.725	0.105
bp5-	*2*	---------	0.658	0.441	2.718	0.133	0.862	**0.086**	0.999
bp5	*2*	---------	0.658	0.441	2.718	0.133	0.862	**0.086**	0.999
bp6	*0*								
LXI2 TD	122	-0.8272	**0.800**	**<0.001**	0.085	0.000	0.266	0.619	0.743
bp1	*92*	---------	**0.507**	**0.046**	0.275	0.000	0.550	0.741	0.870
bp2	*80*	---------	**0.548**	**0.039**	0.215	0.000	0.595	0.512	0.663
bp3	*62*	---------	**0.934**	**<0.001**	0.139	0.000	0.166	0.893	0.757
bp4	*43*	---------	**0.799**	**0.002**	0.187	0.016	**0.042**	0.346	0.137
bp5-	*30*	---------	**0.975**	**<0.001**	0.117	0.000	0.316	0.296	0.128
bp5	*18*	---------	**1.000**	**0.002**	-------	0.000	0.218	0.846	0.231
bp6	*7*	---------	**1.000**	**0.002**	-------	0.000	0.636	0.875	0.940
LXC TD	102	-0.8997	**0.913**	**<0.001**	0.035	0.043	**0.060**	0.877	**0.076**
bp1	*96*	---------	**0.931**	**0.004**	0.177	0.043	**0.057**	0.730	**0.065**
bp2	*80*	---------	**1.000**	**<0.001**	-------	0.068	**0.008**	0.973	**0.023**
bp3	*60*	---------	**1.000**	**<0.001**	-------	0.060	**0.014**	0.181	**<0.001**
bp4	*42*	---------	**1.000**	**<0.001**	-------	0.000	0.157	0.931	0.146
bp5-	*30*	---------	**0.767**	**0.001**	0.167	0.000	0.425	0.539	0.775
bp5	*24*	---------	**0.850**	**0.001**	0.164	0.000	0.344	0.125	0.267
bp6	*9*	---------	**1.000**	**0.004**	-------	0.000	0.141	0.526	0.213
LXC MES RIDGE*	172	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	0.000	0.500	-------	0.000	1.000	0.309	1.000
bp2-bp3	*0*								
LXC DAR	170	-0.9141	**0.734**	**<0.001**	0.076	0.045	0.414	**0.003**	0.229
bp1	*133*	---------	**0.917**	**<0.001**	0.118	0.015	0.142	**0.060**	0.313
bp2	*117*	---------	0.808	<**0.001**	0.135	0.000	0.852	0.492	0.330
bp3	*81*	---------	**0.756**	**<0.001**	0.163	0.014	0.189	**0.055**	0.202

bp4	*21*	---------	**0.758**	**0.012**	0.238	0.098	0.458	**0.001**	0.367
bp5	*0*								
LXP1 UTO AZ	236	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LXP1 ODONT	235	---------	0.000	0.500	-------	0.000	0.805	0.296	0.997
	1								
LXP2 ODONT	183	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LXM2 META	148	-0.9157	**0.267**	**0.017**	0.130	0.000	0.183	0.402	0.483
bp1-bp3	*148*								
bp3.5	*125*	---------	0.357	0.095	0.573	0.000	0.311	0.889	0.626
bp4	*51*	---------	**0.594**	**0.004**	0.202	0.000	0.289	0.245	0.651
bp5	*0*								
LXM3 META	9	1.4117	0.342	0.396	1.240	0.000	0.592	0.444	0.180
bp1-bp2	*9*								
bp3	*8*	---------	0.000	0.500	-------	0.000	0.998	0.370	0.998
bp3.5	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*1*	---------	-------	-------	-------	-------	-------	-------	-------
LXM1 HYPO*	303	0.8302	**0.773**	**<0.001**	0.051	0.000	0.646	0.157	0.513
bp1	*303*								
bp2	*301*	---------	0.000	0.500	-------	0.000	1.000	0.411	1.000
bp3	*300*	---------	0.105	0.478	1.715	0.149	**0.035**	0.371	0.221
bp3.5	*295*	---------	**1.000**	**<0.001**	-------	0.000	0.110	0.312	0.251
bp4	*258*	---------	**0.840**	**<0.001**	0.093	0.013	0.609	**0.075**	0.840
bp5	*46*	---------	**0.925**	**<0.001**	0.084	0.000	0.898	0.162	0.359
LXM2 HYPO	88	-0.3884	**0.931**	**<0.001**	0.036	0.000	0.201	0.553	0.866
bp1	*84*	---------	1.000	0.317	-------	0.000	1.000	0.190	1.000
bp2	*52*	---------	**1.000**	**<0.001**	-------	0.000	0.794	0.928	0.918
bp3	*50*	---------	**1.000**	**<0.001**	-------	0.000	0.811	0.808	0.478
bp3.5	*35*	---------	**0.981**	**0.001**	0.157	0.063	**0.036**	0.787	0.329

bp4	*9*	---------	**0.859**	**0.002**	0.198	0.000	0.915	0.749	0.983
bp5	*2*	---------	1.000	0.258	-------	0.000	0.562	0.572	0.662
LXM3 HYPO	4	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*4*								
bp2	*2*	---------	0.000	0.500	-------	0.000	0.986	0.998	0.996
bp3-bp5	*0*								
LXM1 C5*	276	1.7594	**0.421**	**<0.001**	0.114	0.000	0.525	0.769	0.198
bp1	*55*	---------	**0.657**	**<0.001**	0.176	0.000	0.766	0.745	0.217
bp2	*23*	---------	**0.613**	**0.006**	0.226	0.000	0.470	0.536	0.276
bp3	*4*	---------	0.000	0.500	-------	0.000	0.204	0.900	0.183
bp4	*2*	---------	0.317	0.476	3.931	0.062	0.258	0.156	**0.069**
bp5	*1*	---------	0.000	0.500	-------	0.000	0.100	0.658	0.979
LXM2 C5	90	0.4333	**0.915**	**<0.001**	0.047	0.000	0.870	0.293	0.634
bp1	*22*	---------	**1.000**	**0.009**	-------	0.000	0.950	0.159	0.645
bp2	*13*	---------	**0.842**	**0.024**	0.243	0.000	0.569	0.878	0.968
bp3	*8*	---------	0.776	0.056	0.323	0.000	0.510	0.316	0.683
bp4-bp5	*0*								
LXM3 C5	8	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*2*	---------	1.000	0.326	-------	0.000	1.000	1.000	1.000
bp2	*1*	---------	1.000	0.392	-------	0.000	1.000	1.000	1.000
bp3	*1*	---------	1.000	0.392	-------	0.000	1.000	1.000	1.000
bp4	*1*	---------	1.000	0.392	-------	0.000	1.000	1.000	1.000
bp5	*0*								
LXM1 CARABELLI	283	-0.6401	**0.658**	**<0.001**	0.072	0.046	**0.004**	0.326	**0.001**
bp1	*265*	---------	**0.726**	**<0.001**	0.167	0.039	**0.072**	0.383	**0.009**
bp2	*244*	---------	**0.854**	**<0.001**	0.132	0.061	**0.002**	**0.029**	**<0.001**
bp3	*237*	---------	**0.877**	**<0.001**	0.129	0.069	**0.002**	**0.003**	**<0.001**
bp4	*201*	---------	**0.665**	**<0.001**	0.147	0.019	**0.026**	**0.011**	0.165
bp5	*152*	---------	**0.660**	**<0.001**	0.133	0.022	**0.005**	0.378	**0.012**
bp6	*75*	---------	**0.751**	**<0.001**	0.136	0.017	**0.044**	0.885	**0.030**
bp7	*32*	---------	**0.841**	**<0.001**	0.047	0.000	0.138	0.738	0.100

LXM2 CARABELLI	124	-0.8899	**0.893**	**<0.001**	0.047	0.000	0.178	0.100	0.428
bp1	*66*	---------	**0.901**	**<0.001**	0.174	0.011	0.817	**0.056**	0.773
bp2	*42*	---------	**0.886**	**0.008**	0.234	0.012	0.317	**0.058**	0.518
bp3	*31*	---------	**1.000**	**<0.001**	-------	0.019	0.163	**0.049**	0.557
bp4	*20*	---------	**1.000**	**0.003**	-------	0.035	**0.070**	0.606	0.392
bp5	*18*	---------	**1.000**	**0.002**	-------	0.047	**0.057**	0.728	0.255
bp6	*7*	---------	0.000	0.500	-------	0.085	**0.022**	0.450	0.170
bp7	*0*								
LXM3 CARABELLI*	7	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*3*	---------	0.100	0.500	0.707	0.000	1.000	1.000	0.989
bp2	*3*	---------	0.100	0.500	0.707	0.000	1.000	1.000	0.989
bp3	*3*	---------	0.100	0.500	0.707	0.000	1.000	1.000	0.989
bp4	*3*	---------	0.100	0.500	0.707	0.000	1.000	1.000	0.989
bp5	*3*	---------	0.100	0.500	0.707	0.000	1.000	1.000	0.989
bp6	*2*	---------	0.100	0.500	0.707	0.000	1.000	1.000	1.000
bp7	*2*	---------	0.100	0.500	0.707	0.000	1.000	1.000	1.000
LXM2 PARA*	133	23.5129	0.000	0.500	-------	0.000	0.236	0.322	0.927
bp1	*5*	---------	0.000	0.500	-------	0.000	0.177	0.150	0.634
bp2	*1*	---------	1.000	0.359	-------	0.000	1.000	0.316	0.999
bp3	*1*	---------	1.000	0.359	-------	0.000	1.000	0.316	0.999
bp4	*1*	---------	1.000	0.359	-------	0.000	1.000	0.316	0.999
bp5-bp6	*0*								
LXM3 PARA	6	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	0.100	0.500	0.707	0.000	1.000	1.000	1.000
bp2	*1*	---------	0.100	0.500	0.707	0.000	1.000	1.000	1.000
bp3	*1*	---------	0.100	0.500	0.707	0.000	1.000	1.000	1.000
bp4	*1*	---------	0.100	0.500	0.707	0.000	1.000	1.000	1.000
bp5	*1*	---------	0.100	0.500	0.707	0.000	1.000	1.000	1.000
bp6	*0*								
LXI2 PEG[j]	293 *3*	---------	0.000	0.500	-------	0.000	0.661	0.381	0.403

LXM3 PEG[j]	15	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LXI2 CONG ABS	286	---------	**0.928**	**0.001**	0.143	0.070	**0.053**	0.342	**0.020**
	9								
LXP2 CONG ABS	218	---------	**0.888**	**0.006**	0.174	0.000	0.905	0.242	0.978
	18								
LXM3 CONG ABS	14	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LNI1 SHOV	286	-0.5449	**0.537**	**<0.001**	0.081	0.000	0.643	0.647	0.183
bp1	*104*	---------	**0.735**	**<0.001**	0.058	0.000	0.638	0.368	0.120
bp2	*7*	---------	0.000	0.500	-------	0.035	0.732	**0.029**	0.552
bp3	*1*	---------	0.441	0.470	3.711	0.000	0.649	0.218	0.996
bp4-bp7	*0*								
LNI2 SHOV	286	-0.7720	**0.658**	**<0.001**	0.066	0.000	0.169	0.713	0.720
bp1	*118*	---------	**0.888**	**<0.001**	0.086	0.000	0.338	0.980	0.775
bp2	*8*	---------	0.648	0.052	0.264	0.031	0.266	**0.092**	0.555
bp3-bp7	*0*								
LNC DAR	204	-0.1702	**0.588**	**<0.001**	0.109	0.107	0.820	**<0.001**	0.282
bp1	*69*	---------	**0.692**	**<0.001**	0.148	0.053	0.338	**0.001**	0.491
bp2	*34*	---------	**0.668**	**0.001**	0.210	0.076	0.774	**0.001**	0.162
bp3	*11*	---------	**1.000**	**0.017**	-------	0.277	0.487	**0.001**	**0.077**
bp4	*2*	---------	0.000	0.500	-------	0.000	0.963	0.172	1.000
bp5	*0*								
LNP1 ODONT	231	---------	0.000	0.500	-------	0.000	0.581	0.235	0.994
	1								
LNP2 ODONT	193	---------	1.000	0.350	-------	0.000	1.000	0.356	0.993
	1								
LNM1 CNO*	262	2.4311	**0.216**	**0.028**	0.119	0.000	0.882	0.639	0.240
bp5	*253*	---------	**0.672**	**0.033**	0.280	0.016	**0.059**	0.214	0.124
bp6	*39*	---------	**0.565**	**0.012**	0.234	0.120	0.524	0.407	**0.091**
bp7-bp8	*0*								

LNM2 CNO	112	0.1150	**0.916**	**<0.001**	0.036	0.000	0.523	0.508	0.575
bp5	*29*	---------	**1.000**	**<0.001**	-------	0.000	0.633	0.267	0.507
bp6	*2*	---------	0.000	0.500	-------	0.000	0.961	0.130	0.998
bp7-bp8	*0*								
LNM3 CNO*	10	3.1977	0.100	0.500	-------	0.740	**0.011**	1.000	1.000
bp5	*6*	---------	0.100	0.500	0.707	0.500	**0.051**	1.000	0.991
bp6	*1*	---------	0.100	0.500	0.707	0.000	1.000	1.000	1.000
bp7-bp8	*0*								
LNM1 GROOVE	185	---------	-------	-------	-------	-------	-------	-------	-------
y	*162*	---------	**0.849**	**0.011**	0.247	0.034	**0.029**	0.303	**0.037**
x	*11*	---------	0.402	0.293	0.166	0.000	0.961	0.971	0.988
+	*12*	---------	**0.776**	**0.050**	0.342	0.070	**0.007**	0.135	**0.009**
LNM2 GROOVE	108	---------	-------	-------	-------	-------	-------	-------	-------
y	*33*	---------	**0.833**	**0.001**	0.158	0.023	**0.029**	0.998	0.135
x	*48*	---------	**0.602**	**0.026**	0.252	0.038	**0.016**	0.867	0.216
+	*27*	---------	0.479	0.063	0.270	0.000	0.532	0.769	0.994
LNM3 GROOVE	7	---------	-------	-------	-------	-------	-------	-------	-------
y	*1*	---------	0.100	0.500	0.707	0.000	0.306	1.000	1.000
x	*4*	---------	0.100	0.500	0.707	0.000	0.306	1.000	1.000
+	*2*	---------	0.100	0.500	0.707	1.000	**0.051**	1.000	1.000
LNM1 DWRINK	273	-0.5539	**0.658**	**<0.001**	0.066	0.000	0.773	0.812	0.544
bp1	*192*	---------	**0.597**	**<0.001**	0.012	0.000	0.887	0.885	0.653
bp2	*56*	---------	**0.931**	**<0.001**	0.073	0.000	0.991	**0.822**	0.944
bp3	*6*	---------	-------	-------	-------	-------	-------	-------	-------
LNM1 PSTYLID	254	-0.6600	**0.697**	**<0.001**	0.078	0.000	0.219	0.103	0.928
bp1	*176*	---------	**0.744**	**<0.001**	0.136	0.000	0.442	0.954	0.410
bp2	*103*	---------	**0.730**	**<0.001**	0.143	0.020	0.826	**0.024**	0.942
bp3	*25*	---------	**0.891**	**0.001**	0.161	0.048	0.613	**0.033**	0.522
bp4	*17*	---------	**0.914**	**<0.001**	0.125	0.073	0.120	**0.022**	0.486
bp5	*9*	---------	**0.871**	**0.007**	0.209	0.140	**0.041**	**0.049**	0.874
bp6	*3*	---------	0.000	0.500	-------	0.000	0.898	0.454	0.639

bp7	*0*								
LNM3 PSTYLID	7	---------	-------	-------	-------	-------	-------	-------	-------
bp1-bp7	*0*								
LNM1 C5	275	-0.2285	**0.910**	**<0.001**	0.022	0.033	**0.014**	0.109	**0.007**
bp1	*265*	---------	**0.649**	**0.039**	0.289	0.000	0.101	0.213	0.291
bp2	*252*	---------	**1.000**	**<0.001**	<0.001	0.021	0.815	**0.040**	0.728
bp3	*232*	---------	**0.942**	**<0.001**	0.087	0.000	0.271	0.149	0.109
bp4	*146*	---------	**0.991**	**<0.001**	0.085	0.000	0.459	0.338	0.217
bp5	*6*	---------	**1.000**	**0.021**	-------	0.176	**0.005**	0.792	**0.015**
LNM2 C5	117	0.2074	**0.939**	**<0.001**	0.025	0.031	0.830	**0.093**	0.269
bp1	*31*	---------	**1.000**	**<0.001**	-------	0.000	0.677	0.171	0.489
bp2	*28*	---------	**1.000**	**<0.001**	-------	0.059	0.473	**0.042**	**0.051**
bp3	*17*	---------	**1.000**	**<0.001**	-------	0.000	0.383	0.131	0.102
bp4	*6*	---------	0.257	0.338	0.575	0.196	0.432	**0.014**	**0.025**
bp5	*0*								
LNM3 C5	11	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*7*	---------	1.000	0.275	-------	0.000	1.000	1.000	1.000
bp2	*7*	---------	1.000	0.275	-------	0.000	1.000	1.000	1.000
bp3	*7*	---------	1.000	0.275	-------	0.000	1.000	1.000	1.000
bp4	*2*	---------	1.000	0.361	-------	0.000	1.000	1.000	1.000
bp5	*1*	---------	1.000	0.414	-------	0.000	1.000	1.000	1.000
LNM1 C6*	253	3.3193	**0.209**	**0.042**	0.127	0.023	0.390	0.258	**0.034**
bp1	*39*	---------	**0.541**	**0.016**	0.243	0.021	0.542	0.308	**0.087**
bp2	*12*	---------	0.000	0.500	-------	0.056	**0.016**	0.185	**0.012**
bp3	*6*	---------	0.000	0.500	-------	0.000	0.940	0.165	0.696
bp4	*1*	---------	0.000	0.500	-------	0.141	1.000	**<0.001**	0.998
bp5	*0*								
LNM2 C6*	120	58.2600	0.000	0.500	-------	0.000	1.000	0.200	0.740
bp1	*2*	---------	0.000	0.500	-------	0.000	0.773	0.129	1.000
bp2	*1*	---------	0.000	0.500	-------	0.000	1.000	0.208	0.994
bp3-bp5	*0*								

LNM3 C6	11	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	0.100	0.500	<0.001	0.000	1.000	1.000	1.000
bp2	*1*	---------	0.100	0.500	0.707	0.000	1.000	1.000	1.000
bp3-bp5	*0*								
LNM1 C7*	323	5.0997	**0.495**	**<0.001**	0.144	0.000	0.292	0.358	0.424
bp1	*39*	---------	**0.666**	**0.005**	0.235	0.000	0.215	0.208	0.279
bp1a	*21*	---------	**0.644**	**0.007**	0.236	0.000	0.729	0.872	0.943
bp2	*14*	---------	**0.813**	**0.002**	-------	0.000	0.903	0.867	0.278
bp3	*8*	---------	0.671	0.063	0.397	0.044	0.746	0.104	**0.038**
bp4	*4*	---------	**1.000**	**0.002**	-------	0.000	0.903	0.867	0.287
LNM3 C7	12	---------	-------	-------	-------	-------	-------	-------	-------
bp1-bp4	*0*								
LNM1 DTCREST	273	---------	**1.000**	**0.026**	-------	0.025	0.551	**0.044**	0.998
	4								
LNM2 DTCREST	165	---------	0.000	0.500	-------	0.000	0.626	0.247	0.996
	1								
LNM3 DTCREST	12	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LNI1 CONG ABS	315	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LNP2 CONG ABS	218	---------	0.602	0.092	0.350	0.000	0.285	0.586	0.357
	15								
LNM3 CONG ABS	16	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RXI1 WING	316	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*11*	---------	**0.676**	**0.047**	0.351	0.000	0.770	0.975	0.270
bp2	*4*	---------	**1.000**	**0.001**	-------	0.395	0.541	0.113	**<0.001**
bp3	*217*	---------	**0.416**	**0.002**	0.555	0.000	0.664	0.991	0.172
bp4	*84*	---------	**0.362**	**0.011**	0.172	0.000	0.504	0.926	0.873
RXI1 SHOV	291	-0.1749	**0.824**	**<0.001**	0.039	0.000	0.793	0.590	0.863
bp1	*247*	---------	**0.831**	**<0.001**	0.129	0.000	0.261	0.697	0.861

bp2	*101*	---------	**0.937**	**<0.001**	0.082	0.000	0.769	0.559	0.613
bp3	*18*	---------	**1.000**	**<0.001**	-------	0.000	0.277	0.439	0.855
bp4	*4*	---------	**1.000**	**<0.001**	-------	0.165	0.159	**0.072**	0.990
bp5	*1*	---------	0.000	0.500	-------	0.000	0.471	0.253	0.991
bp6-bp7	*0*								
RXI2 SHOV	230	-0.2692	**0.678**	**<0.001**	0.085	0.086	**0.048**	**0.001**	0.156
bp1	*191*	---------	**0.648**	**0.003**	0.199	0.007	0.129	**0.089**	0.164
bp2	*82*	---------	**0.864**	**<0.001**	0.148	0.034	0.250	**<0.001**	0.496
bp3	*30*	---------	**0.832**	**<0.001**	0.140	0.018	0.138	**0.021**	0.998
bp4	*6*	---------	**0.860**	**0.008**	0.203	0.043	0.247	**0.023**	0.995
bp5	*1*	---------	0.000	0.500	-------	0.000	0.998	0.211	1.000
bp6-bp7	*0*								
RXC SHOV	149	-0.5757	**0.643**	**<0.001**	0.108	0.000	0.619	0.653	0.939
bp1	*113*	---------	**0.658**	**0.002**	0.207	0.000	0.587	0.485	0.832
bp2	*39*	---------	**0.899**	**<0.001**	0.134	0.000	0.969	0.979	0.926
bp3	*3*	---------	0.000	0.500	-------	0.000	0.900	0.716	0.823
bp4-bp7	*0*								
RXI1 DSHOV	297	-0.1104	**0.406**	**<0.001**	0.089	0.000	0.760	0.268	0.963
bp1	*271*	---------	**0.533**	**0.010**	0.099	0.020	0.685	**0.071**	0.944
bp2	*131*	---------	**0.402**	**0.002**	0.235	0.014	0.496	**0.015**	0.998
bp3	*34*	---------	**0.811**	**<0.001**	0.126	0.000	0.994	0.535	0.568
bp4	*8*	---------	**0.838**	**0.003**	0.219	0.000	0.616	0.402	0.841
bp5-bp6	*0*								
RXI2 DSHOV	263	-0.7467	**0.454**	**<0.001**	0.092	0.000	0.274	0.862	0.603
bp1	*150*	---------	**0.531**	**<0.001**	0.154	0.000	0.166	0.814	0.241
bp2	*67*	---------	**0.686**	**<0.001**	0.139	0.000	0.576	0.624	0.535
bp3	*14*	---------	0.272	0.176	0.280	0.000	0.878	0.772	0.994
bp4	*4*	---------	0.000	0.500	-------	0.007	**0.007**	1.000	0.247
bp5-bp7	*0*								
RXC DSHOV	196	-0.3574	**0.487**	**<0.001**	0.124	0.014	**0.089**	0.248	0.411
bp1	*178*	---------	0.000	0.500	-------	0.000	0.716	0.104	0.990

bp2	*134*	---------	**0.486**	**0.024**	0.235	0.013	**0.054**	0.139	0.235
bp3	*73*	---------	**0.639**	**0.001**	0.147	0.016	**0.044**	0.453	0.228
bp4	*23*	---------	0.478	0.056	0.285	0.000	0.557	0.988	0.490
bp5	*6*	---------	**0.650**	**0.026**	0.076	0.000	0.754	0.167	0.813
bp6	*0*								
RXP1 DSHOV	229	-0.5182	**0.486**	**<0.001**	0.109	0.000	0.403	0.866	0.814
bp1	*201*	---------	**0.677**	**0.002**	0.190	0.014	**0.037**	0.764	0.112
bp2	*151*	---------	**0.641**	**<0.001**	0.117	0.000	0.479	0.636	0.933
bp3	*68*	---------	**0.501**	**0.002**	0.145	0.000	0.657	0.455	0.424
bp4	*17*	---------	**0.713**	**<0.001**	0.174	0.000	0.630	0.919	0.534
bp5-bp6	*0*								
RXP2 DSHOV	194	-0.1918	**0.419**	**0.001**	0.133	0.079	0.683	**0.004**	**0.069**
bp1	*98*	---------	**0.656**	**0.001**	0.197	0.053	0.914	**<0.001**	0.106
bp2	*39*	---------	**0.388**	**0.042**	0.261	0.000	0.951	0.431	0.384
bp3	*10*	---------	**0.830**	**0.001**	0.169	0.000	0.464	0.955	0.244
bp4	*3*	---------	**0.710**	**0.060**	0.339	0.000	0.225	0.548	0.344
bp5-bp6	*0*								
RXI1 TD	240	-0.2810	**0.681**	**<0.001**	0.086	0.012	0.234	**0.071**	0.336
bp1	*219*	---------	0.524	0.082	0.049	0.000	0.229	0.253	0.141
bp2	*161*	---------	**0.697**	**<0.001**	0.171	0.007	0.263	**0.049**	0.300
bp3	*90*	---------	**0.758**	**<0.001**	0.135	0.008	0.234	**0.025**	0.257
bp4	*23*	---------	0.333	0.208	0.027	0.000	0.846	0.516	0.466
bp5-	*8*	---------	**1.000**	**0.043**	-------	0.000	0.612	0.989	0.320
bp5	*5*	---------	**1.000**	**0.016**	-------	0.000	0.841	0.974	0.394
bp6	*0*								
RXI2 TD	115	-0.7431	**0.861**	**0.002**	0.093	0.024	0.858	**0.044**	0.842
bp1	*86*	---------	0.439	0.208	0.542	0.024	0.613	**0.080**	0.269
bp2	*75*	---------	**1.000**	**0.001**	-------	0.023	0.664	**0.040**	0.966
bp3	*53*	---------	0.316	0.155	0.001	0.000	0.492	0.249	0.333
bp4	*43*	---------	**0.660**	**0.023**	0.268	0.041	0.347	**0.080**	**0.085**
bp5-	*30*	---------	**0.881**	**0.004**	0.206	0.000	0.660	0.527	0.198

bp5	*18*	---------	**1.000**	**<0.001**	-------	0.000	0.383	0.346	0.996
bp6	*6*	---------	**1.000**	**0.014**	-------	0.000	0.915	0.853	0.528
RXC TD	138	-0.7477	**0.941**	**<0.001**	0.024	0.019	0.132	**0.062**	0.134
bp1	*118*	---------	**1.000**	**<0.001**	-------	0.050	**0.092**	0.634	**0.043**
bp2	*98*	---------	**0.995**	**<0.001**	0.099	0.000	0.423	0.784	0.280
bp3	*74*	---------	**0.877**	**<0.001**	0.124	0.000	0.249	0.380	0.585
bp4	*49*	---------	**1.000**	**<0.001**	-------	0.014	0.726	**0.041**	0.427
bp5-	*40*	---------	**0.877**	**<0.001**	0.134	0.028	0.927	**0.024**	0.615
bp5	*21*	---------	**0.870**	**0.007**	0.191	0.067	0.777	**0.004**	0.514
bp6	*7*	---------	1.000	0.063	-------	0.148	0.182	**0.010**	0.184
RXC MES RIDGE*	177	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*3*	---------	**1.000**	**0.002**	-------	0.000	0.996	0.130	1.000
bp2-bp3	*0*								
RXC DAR	173	-0.6307	**0.758**	**<0.001**	0.072	0.094	0.793	**<0.001**	0.246
bp1	*148*	---------	**0.801**	**0.001**	0.707	0.080	**0.020**	**0.022**	**0.077**
bp2	*129*	---------	**0.645**	**0.002**	0.183	0.070	**0.067**	**0.019**	0.448
bp3	*88*	---------	**0.809**	**<0.001**	0.149	0.036	0.923	**0.013**	0.998
bp4	*26*	---------	**1.000**	**0.002**	-------	0.104	0.146	**0.001**	**0.011**
bp5	*1*	---------	0.000	0.500	-------	0.000	0.842	0.157	0.998
RXP1 UTO AZ	235	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RXP1 ODONT	232	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RXP2 ODONT	193	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RXM2 META	152	-0.6812	**0.588**	**<0.001**	0.117	0.084	0.820	**0.076**	**0.052**
bp1-bp2	*152*								
bp3	*151*	---------	0.115	0.495	3.549	0.000	1.000	0.814	0.969
bp3.5	*130*	---------	**1.000**	**0.011**	-------	0.122	0.900	0.275	**0.064**
bp4	*68*	---------	**0.633**	**0.001**	0.215	0.000	0.899	0.236	0.266
bp5	*1*	---------	0.000	0.500	-------	0.085	0.991	**0.002**	1.000

RXM3 META	10	-0.9126	1.000	0.212	-------	0.000	0.774	0.499	0.742
bp1	*9*	---------	0.100	0.500	0.707	0.922	**0.036**	0.996	1.000
bp2	*9*	---------	0.100	0.500	0.707	0.922	**0.036**	0.996	1.000
bp3	*9*	---------	0.100	0.500	0.707	0.922	**0.036**	0.996	1.000
bp3.5	*4*	---------	1.000	0.260	-------	0.000	0.631	0.148	1.000
bp4-bp5	*0*								
RXM1 HYPO	303	0.5795	**0.629**	**<0.001**	0.074	0.020	0.399	**0.005**	0.398
bp1	*302*	---------	0.000	0.500	-------	0.000	1.000	0.335	0.993
bp2	*300*	---------	0.000	0.500	-------	0.000	1.000	0.335	0.993
bp3	*298*	---------	**1.000**	**<0.001**	-------	0.000	1.000	0.199	0.992
bp3.5	*292*	---------	**1.000**	**<0.001**	-------	0.000	1.000	0.573	1.000
bp4	*236*	---------	**0.818**	**<0.001**	0.114	0.042	0.769	**<0.001**	0.769
bp5	*40*	---------	**0.687**	**<0.001**	0.140	0.000	0.275	0.599	0.299
RXM2 HYPO	93	-0.4627	**0.940**	**<0.001**	0.036	0.000	0.432	0.483	0.562
bp1	*88*	---------	1.000	0.214	-------	0.000	1.000	0.179	0.991
bp2	*66*	---------	**1.000**	**0.009**	-------	0.000	0.737	0.844	0.640
bp3	*56*	---------	**1.000**	**0.021**	-------	0.000	0.309	0.641	0.937
bp3.5	*40*	---------	**1.000**	**0.002**	-------	0.000	0.926	0.493	0.268
bp4	*11*	---------	0.567	0.075	0.405	0.000	0.335	0.573	0.716
bp5	*1*	---------	0.000	0.500	-------	0.000	0.707	0.215	0.995
RXM3 HYPO	7	0.6330	0.100	0.500	-------	0.000	0.527	0.623	0.558
bp1	*6*	---------	0.100	0.500	<0.001	0.000	0.997	1.000	0.995
bp2	*5*	---------	0.100	0.500	<0.001	0.000	0.997	1.000	0.995
bp3	*1*	---------	0.100	0.500	0.707	0.000	0.603	0.543	1.000
bp3.5	*1*	---------	0.100	0.500	0.707	0.000	0.603	0.543	1.000
bp4	*1*	---------	0.100	0.500	0.707	0.000	0.603	0.543	1.000
bp5	*0*								
RXM1 C5*	264	1.4613	**0.873**	**<0.001**	0.036	0.033	**0.064**	0.660	**0.010**
bp1	*54*	---------	**0.997**	**<0.001**	0.073	0.013	0.172	0.848	**0.026**
bp2	*15*	---------	0.310	0.267	0.496	0.072	0.468	**0.018**	**0.041**
bp3	*5*	---------	0.000	0.500	-------	0.097	**0.099**	0.112	**0.037**

bp4	*2*	---------	0.000	0.500	-------	0.000	0.349	0.110	0.996
bp5	*0*								
RXM2 C5*	91	4.8756	0.190	0.267	0.308	0.000	0.794	0.382	0.768
bp1	*11*	---------	0.480	0.232	0.573	0.000	0.943	0.321	0.856
bp2	*5*	---------	0.000	0.500	-------	0.000	0.537	0.952	0.465
bp3	*1*	---------	0.000	0.500	-------	0.000	1.000	0.342	0.872
bp4-bp5	*0*								
RXM3 C5*	5	2.0000	0.100	0.500	-------	0.952	**<0.001**	**<0.001**	**<0.001**
bp1	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp3-bp5	*0*								
RXM1 CARABELLI	282	-0.5662	**0.767**	**<0.001**	0.056	0.048	**0.006**	0.432	**0.001**
bp1	*271*	---------	**0.798**	**0.001**	0.191	0.091	**0.046**	0.753	**0.001**
bp2	*251*	---------	**0.954**	**<0.001**	0.078	0.019	**0.094**	0.421	**0.045**
bp3	*239*	---------	**0.938**	**<0.001**	0.087	0.008	0.112	0.962	**0.035**
bp4	*218*	---------	**0.924**	**<0.001**	0.086	0.016	**0.042**	0.320	**0.030**
bp5	*172*	---------	**0.801**	**<0.001**	0.119	0.014	**0.031**	0.256	**0.029**
bp6	*68*	---------	**0.753**	**<0.001**	0.155	0.024	**0.013**	0.879	**0.019**
bp7	*37*	---------	**0.817**	**<0.001**	0.139	0.039	**0.040**	0.216	**0.006**
RXM2 CARABELLI	124	-0.8155	**0.722**	**<0.001**	0.099	0.057	**0.010**	0.202	**0.020**
bp1	*79*	---------	**0.724**	**0.003**	0.190	0.000	0.247	0.190	0.180
bp2	*44*	---------	**0.842**	**<0.001**	0.158	0.028	**0.061**	0.489	**0.071**
bp3	*36*	---------	**0.946**	**<0.001**	0.120	0.009	**0.067**	0.203	0.131
bp4	*30*	---------	**0.979**	**<0.001**	0.182	0.060	**0.015**	0.284	**0.053**
bp5	*27*	---------	**0.993**	**<0.001**	0.106	0.013	**0.073**	0.854	0.166
bp6	*8*	---------	0.000	0.500	-------	0.027	**0.013**	0.428	0.118
bp7	*0*								
RXM3 CARABELLI*	3	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	0.100	0.499	0.707	1.000	**0.096**	1.000	1.000
bp2	*1*	---------	0.100	0.499	0.707	1.000	**0.096**	1.000	1.000
bp3	*1*	---------	0.100	0.499	0.707	1.000	**0.096**	1.000	1.000

bp4-bp7	*0*								
RXM2 PARA	135	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	0.000	0.500	-------	0.000	0.991	0.345	0.604
bp2-bp6	*0*								
RXM3 PARA	12	---------	-------	-------	-------	-------	-------	-------	-------
bp1-bp6	*0*								
RXI2 PEG[j]	287	---------	-------	-------	-------	-------	-------	-------	-------
	3	---------	0.000	0.500	-------	0.000	0.846	0.692	0.985
RXM3 PEG[j]	15	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RXI2 CONG ABS	281	---------	**0.694**	**0.014**	0.238	0.034	**0.036**	0.198	**0.033**
	14								
RXP2 CONG ABS	217	---------	**0.823**	**0.022**	0.243	0.000	0.701	0.212	0.835
	16								
RXM3 CONG ABS	14	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RNI1 SHOV	294	-0.5819	**0.535**	**<0.001**	0.091	0.006	0.247	**0.057**	0.567
bp1	*105*	---------	**0.741**	**<0.001**	0.123	0.008	0.346	**0.057**	0.521
bp2	*5*	---------	0.000	0.500	-------	0.051	**0.045**	0.725	0.695
bp3	*1*	---------	0.422	0.471	3.849	0.000	0.695	0.218	0.998
bp4-bp7	*0*								
RNI2 SHOV	282	-0.8355	**0.572**	**<0.001**	0.071	0.031	**0.060**	0.944	0.887
bp1	*119*	---------	**0.774**	**<0.001**	0.094	0.016	**0.083**	0.848	0.761
bp2	*8*	---------	**0.735**	**0.016**	0.192	0.000	0.293	0.772	0.809
bp3-bp7	*0*								
RNC DAR	204	0.6418	**0.589**	**<0.001**	0.164	0.241	0.586	**<0.001**	0.373
bp1	*52*	---------	**0.892**	**<0.001**	0.203	0.156	0.350	<**0.001**	0.174
bp2	*32*	---------	**0.871**	**0.003**	0.197	0.199	0.888	**<0.001**	0.486
bp3	*8*	---------	0.247	0.349	0.814	0.111	0.483	**0.002**	0.997
bp4	*1*	---------	0.000	0.500	-------	0.000	0.471	0.304	0.988
bp5	*0*								

RNP1 ODONT	231	---------	-------	-------	-------	-------	-------	-------	-------
	1								
RNP2 ODONT	193	---------	0.000	0.500	-------	0.000	1.000	0.297	1.000
	1								
RNM1 CNO*	266	1.4074	**0.720**	**<0.001**	0.080	0.000	0.303	0.772	0.166
bp5	*245*	---------	**0.957**	**<0.001**	0.103	0.087	**0.004**	**0.011**	**0.010**
bp6	*40*	---------	**0.755**	**<0.001**	0.164	0.000	0.990	0.559	0.772
bp7-bp8	*0*								
RNM2 CNO*	114	1.9417	**0.554**	**<0.001**	0.137	0.000	0.712	0.903	0.255
bp5	*20*	---------	**0.778**	**0.004**	0.217	0.000	0.584	0.582	0.186
bp6	*2*	---------	0.000	0.500	-------	0.000	1.000	0.102	1.000
bp7-bp8	*0*								
RNM3 CNO*	5	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*5*	---------	1.000	0.245	-------	0.000	1.000	1.000	1.000
bp6	*1*	---------	1.000	0.382	-------	0.000	1.000	1.000	1.000
bp7-bp8	*0*								
RNM1 GROOVE	170	---------	-------	-------	-------	-------	-------	-------	-------
y	*139*	---------	0.375	0.158	0.373	0.000	0.115	0.102	0.278
x	*14*	---------	0.000	0.500	-------	0.000	1.000	0.910	0.819
+	*17*	---------	0.000	0.500	-------	0.027	**0.071**	**0.080**	0.133
RNM2 GROOVE	99	---------	-------	-------	-------	-------	-------	-------	-------
y	*26*	---------	0.452	0.120	2.293	0.000	0.253	0.172	0.701
x	*43*	---------	**0.835**	**0.002**	0.179	0.000	0.500	0.790	0.915
+	*30*	---------	0.124	0.362	0.812	0.000	0.940	0.123	0.856
RNM3 GROOVE	6	---------	-------	-------	-------	-------	-------	-------	-------
y	*1*	---------	0.100	0.500	0.707	0.384	**0.096**	1.000	1.000
x	*4*	---------	0.100	0.490	0.707	1.000	**0.069**	0.996	1.000
+	*1*	---------	-------	-------	-------	-------	-------	-------	-------
RNM1 DWRINK	272	-0.1349	**0.710**	**<0.001**	0.061	0.000	0.533	0.815	0.702
bp1	*214*	---------	**0.722**	**<0.001**	0.131	0.000	0.975	0.468	0.683

bp2	*55*	---------	**0.936**	**<0.001**	0.084	0.000	0.276	0.914	0.890
bp3	*8*	---------	**0.892**	**0.002**	0.214	0.000	0.635	0.726	0.721
RNM1 PSTYLID	260	-0.5878	**0.443**	**<0.001**	0.143	0.013	0.421	**0.030**	0.968
bp1	*189*	---------	**0.438**	**0.031**	0.223	0.000	0.623	0.195	0.228
bp2	*115*	---------	**0.624**	**<0.001**	0.176	0.012	0.832	**0.015**	0.790
bp3	*31*	---------	**0.471**	**0.048**	0.521	0.000	0.175	0.120	0.835
bp4	*16*	---------	**0.880**	**0.001**	0.182	0.000	0.108	0.494	0.557
bp5	*9*	---------	**0.911**	**<0.001**	0.133	0.083	**0.017**	0.395	0.416
bp6	*4*	---------	**1.000**	**0.001**	-------	0.173	**0.039**	0.606	0.924
bp7	*0*								
RNM3 PSTYLID*	9	1.6570	1.000	0.156	-------	0.000	0.412	1.000	1.000
bp1	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*1*	---------	1.000	0.360	-------	0.000	0.994	1.000	0.994
bp7	*0*								
RNM1 C5	265	-0.6042	**0.665**	**<0.001**	0.070	0.048	**0.013**	**0.053**	**0.030**
bp1	*254*	---------	**0.954**	**<0.001**	0.100	0.087	**0.004**	**0.012**	**0.009**
bp2	*243*	---------	**1.000**	**<0.001**	-------	0.023	**0.035**	**0.067**	0.295
bp3	*217*	---------	**0.831**	**<0.001**	0.119	0.011	0.241	0.400	**0.048**
bp4	*113*	---------	**0.651**	**<0.001**	0.125	0.007	**0.038**	0.162	0.124
bp5	*3*	---------	0.000	0.500	-------	0.147	0.291	**0.042**	0.995

RNM2 C5*	117	1.5803	**0.568**	**<0.001**	0.116	0.000	0.770	0.679	0.223
bp1	*24*	---------	**0.824**	**0.001**	0.178	0.000	0.684	0.906	0.241
bp2	*18*	---------	**0.798**	**0.001**	0.195	0.000	0.760	0.128	0.165
bp3	*12*	---------	**0.967**	**<0.001**	0.097	0.000	0.932	0.682	0.207
bp4	*4*	---------	0.000	0.500	-------	0.000	0.720	0.222	0.519
bp5	*1*	---------	1.000	0.344	-------	0.000	0.743	0.245	0.999
RNM3 C5*	8	2.8889	0.000	0.500	-------	0.950	**0.011**	**0.001**	**0.034**
bp1	*5*	---------	1.000	0.269	-------	0.000	1.000	0.997	0.998
bp2	*5*	---------	1.000	0.269	-------	0.000	1.000	0.997	0.998
bp3	*5*	---------	1.000	0.269	-------	0.000	1.000	0.997	0.998
bp4	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*0*								
RNM1 C6*	271	3.5976	**0.454**	**<0.001**	0.133	0.000	0.440	0.606	0.997
bp1	*39*	---------	**0.748**	**0.001**	0.168	0.000	0.571	0.428	0.894
bp2	*17*	---------	0.231	0.317	0.473	0.000	0.190	0.991	0.541
bp3	*6*	---------	0.000	0.500	-------	0.016	0.158	0.926	**0.083**
bp4-bp5	*0*								
RNM2 C6*	122	59.2725	0.000	0.500	-------	0.000	1.000	0.176	0.986
bp1	*2*	---------	0.000	0.500	-------	0.000	1.000	0.108	1.000
bp2	*1*	---------	1.000	0.349	-------	0.000	1.000	0.263	0.821
bp3	*1*	---------	1.000	0.349	-------	0.000	1.000	0.263	0.821
bp4	*1*	---------	1.000	0.349	-------	0.000	1.000	0.263	0.821
bp5	*0*								
RNM3 C6	7	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	1.000	0.382	-------	0.000	1.000	1.000	1.000
bp2-bp5	*0*								
RNM1 C7*	320	5.2535	**0.470**	**<0.001**	0.105	0.017	0.980	**0.038**	0.472
bp1	*38*	---------	**0.599**	**0.002**	0.163	0.024	0.744	**0.014**	0.216
bp1a	*25*	---------	**0.787**	**<0.001**	0.165	0.029	0.704	**0.035**	0.858
bp2	*16*	---------	**0.848**	**0.001**	0.158	0.030	0.717	**0.050**	0.220
bp3	*7*	---------	**1.000**	**0.008**	-------	0.014	0.110	0.968	**0.079**

bp4	*2*	---------	0.000	0.500	-------	0.000	0.845	0.728	0.528
RNM3 C7	12	---------	-------	-------	-------	-------	-------	-------	-------
bp1-bp4	*0*								
RNM1 DTCREST	268	---------	1.000	0.308	-------	0.150	0.443	**0.034**	0.995
	3								
RNM2 DTCREST	165	---------	0.000	0.500	-------	0.000	0.659	0.254	1.000
	1								
RNM3 DTCREST	12	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RNI1 CONG ABS	315	---------	0.000	0.500	-------	0.000	1.000	**0.267**	1.000
	1								
RNP2 CONG ABS	215	---------	**0.827**	**0.026**	0.257	0.000	0.272	0.928	0.358
	14								
RNM3 CONG ABS	16	---------	-------	-------	-------	-------	-------	-------	-------
	0								
XI1 SHOV	303	-0.0078	**0.811**	**<0.001**	0.042	0.002	**0.080**	0.368	0.197
bp1	*272*	---------	**0.925**	**<0.001**	0.080	0.000	0.550	0.694	0.871
bp2	*125*	---------	**0.925**	**<0.001**	0.080	0.000	0.550	0.694	0.871
bp3	*32*	---------	**0.826**	**<0.001**	0.157	0.020	0.508	**0.007**	0.405
bp4	*6*	---------	**1.000**	**0.001**	-------	0.000	0.167	0.259	0.743
bp5	*1*	---------	0.000	0.500	-------	0.000	0.469	0.250	0.991
bp6-bp7	*0*								
XI2 SHOV	254	-0.3066	**0.816**	**<0.001**	0.043	0.079	**0.041**	**0.002**	**0.053**
bp1	*223*	---------	**0.926**	**<0.001**	0.093	0.020	**0.076**	0.175	**0.054**
bp2	*112*	---------	**0.992**	**<0.001**	0.070	0.021	0.325	**0.003**	0.348
bp3	*37*	---------	**0.851**	**<0.001**	0.139	0.034	0.159	**0.002**	0.777
bp4	*8*	---------	**0.891**	**0.002**	0.165	0.022	0.265	**0.092**	0.204
bp5	*1*	---------	0.000	0.500	-------	0.000	1.000	0.216	1.000
bp6-bp7	*0*								
XC SHOV	165	-0.4466	**0.700**	**<0.001**	0.087	0.000	0.810	0.844	0.823
bp1	*130*	---------	**0.763**	**<0.001**	0.149	0.000	0.745	0.544	0.849

bp2	*47*	---------	**1.000**	**<0.001**	-------	0.000	0.747	0.635	0.668
bp3	*9*	---------	**0.718**	**0.010**	0.244	0.000	0.959	0.541	0.451
bp4-bp7	*0*								
XI1 DSHOV	311	-0.1300	**0.541**	**<0.001**	0.104	0.000	1.000	0.206	0.766
bp1	*296*	---------	**1.000**	**0.001**	-------	0.000	0.957	0.891	0.289
bp2	*181*	---------	**0.612**	**<0.001**	0.153	0.006	0.833	**0.082**	0.612
bp3	*49*	---------	**0.742**	**<0.001**	0.138	0.000	0.927	0.588	0.156
bp4	*11*	---------	**0.827**	**0.001**	0.167	0.000	0.454	0.397	0.787
bp5-bp6	*0*								
XI2 DSHOV	284	-0.6221	**0.595**	**<0.001**	0.080	0.001	**0.079**	0.395	0.213
bp1	*199*	---------	**0.433**	**0.004**	0.184	0.013	0.168	**0.093**	0.180
bp2	*96*	---------	**0.564**	**<0.001**	0.140	0.000	0.267	0.459	0.884
bp3	*24*	---------	**0.612**	**0.003**	0.145	0.000	0.494	0.770	0.349
bp4	*6*	---------	**0.755**	**0.027**	0.297	0.000	0.239	0.633	0.255
bp5-bp6	*0*								
XC DSHOV	210	-0.3186	**0.579**	**<0.001**	0.110	0.042	**0.091**	**0.082**	0.508
bp1	*199*	---------	0.567	0.194	0.552	0.077	0.874	**0.092**	0.487
bp2	*161*	---------	**0.460**	**0.013**	0.248	0.000	0.373	0.216	0.798
bp3	*94*	---------	**0.821**	**<0.001**	0.159	0.020	**0.020**	0.156	0.188
bp4	*34*	---------	**0.610**	**0.004**	0.211	0.000	0.271	0.239	0.261
bp5	*8*	---------	0.553	0.051	0.368	0.000	0.227	0.570	0.303
bp6	*0*								
XP1 DSHOV	234	-0.3837	**0.655**	**<0.001**	0.089	0.000	0.245	0.933	0.566
bp1	*216*	---------	**0.557**	**0.034**	0.265	0.000	0.510	0.267	0.673
bp2	*176*	---------	**0.793**	**<0.001**	0.133	0.000	0.488	0.731	0.560
bp3	*91*	---------	**0.799**	**<0.001**	0.123	0.000	0.312	0.886	0.795
bp4	*27*	---------	**0.579**	**0.002**	0.195	0.000	0.716	0.919	0.751
bp5	*1*	---------	0.000	0.500	-------	0.000	0.956	0.173	0.999
bp6	*0*								
XP2 DSHOV	197	-0.5225	**0.572**	**<0.001**	0.111	0.022	0.839	**0.036**	0.122
bp1	*129*	---------	**0.602**	**0.006**	0.037	0.027	0.522	**0.007**	0.177

bp2	*55*	---------	**0.531**	**0.002**	0.182	0.000	0.598	0.284	0.466
bp3	*17*	---------	**0.891**	**<0.001**	0.126	0.000	0.590	0.529	0.274
bp4	*4*	---------	**0.892**	**0.002**	0.149	0.000	0.244	0.480	0.362
bp5-bp6	*0*								
XI1 TD	274	-0.2925	**0.716**	**<0.001**	0.071	0.000	0.182	0.250	0.278
bp1	*255*	---------	0.341	0.244	0.502	0.052	**0.024**	**0.078**	**0.024**
bp2	*208*	---------	**0.683**	**<0.001**	0.161	0.016	**0.044**	0.575	**0.037**
bp3	*124*	---------	**0.615**	**<0.001**	0.118	0.000	0.210	0.367	0.164
bp4	*43*	---------	**0.981**	**<0.001**	0.094	0.000	0.460	0.246	0.352
bp5-	*8*	---------	**1.000**	**0.033**	<0.001	0.000	0.682	0.911	0.318
bp5	*5*	---------	**1.000**	**0.014**	-------	0.000	0.936	1.000	0.401
bp6	*0*								
XI2 TD	151	-0.7994	**0.907**	**<0.001**	0.036	0.000	0.101	0.737	0.264
bp1	*117*	---------	**0.859**	**0.001**	0.160	0.000	0.551	0.533	0.996
bp2	*103*	---------	**1.000**	**<0.001**	-------	0.000	0.285	0.612	0.966
bp3	*80*	---------	**1.000**	**<0.001**	-------	0.022	**0.098**	0.954	0.620
bp4	*62*	---------	**0.726**	**0.001**	0.183	0.023	**0.066**	0.579	**0.066**
bp5-	*41*	---------	**0.893**	**<0.001**	0.143	0.013	0.176	**0.056**	0.847
bp5	*24*	---------	**1.000**	**<0.001**	-------	0.000	0.296	0.764	0.170
bp6	*9*	---------	**1.000**	**0.004**	-------	0.000	0.668	0.722	0.953
XC TD	154	-0.6857	**0.932**	**<0.001**	0.023	0.000	0.199	0.254	0.217
bp1	*132*	---------	**1.000**	**<0.001**	-------	0.041	**<0.001**	0.773	**<0.001**
bp2	*113*	---------	**1.000**	**<0.001**	-------	0.000	0.396	0.517	0.489
bp3	*84*	---------	**0.953**	**<0.001**	0.068	0.000	0.189	0.327	0.397
bp4	*60*	---------	**0.981**	**<0.001**	0.093	0.000	0.585	0.299	0.557
bp5-	*49*	---------	**0.875**	**<0.001**	0.127	0.000	0.786	0.230	0.869
bp5	*29*	---------	**0.882**	**<0.001**	0.120	0.034	0.624	**0.024**	0.422
bp6	*12*	---------	**1.000**	**0.004**	-------	0.000	0.249	0.135	0.316
XC MES RIDGE	191	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*3*	---------	**1.000**	**0.002**	-------	0.000	0.951	0.137	0.954
bp2-bp3	*0*								

XC DAR	200	-0.6130	**0.874**	**<0.001**	0.037	0.106	0.352	**<0.001**	0.258
bp1	*173*	---------	**1.000**	**<0.001**	-------	0.051	**0.045**	**0.074**	**0.056**
bp2	*153*	---------	**0.944**	**<0.001**	0.088	0.052	**0.096**	**0.010**	0.272
bp3	*113*	---------	**0.944**	**<0.001**	0.088	0.052	**0.096**	**0.010**	0.272
bp4	*38*	---------	**0.991**	**<0.001**	0.080	0.037	0.818	**0.004**	0.952
bp5	*1*	---------	**0.921**	**<0.001**	0.126	0.122	**0.094**	**<0.001**	**0.038**
XP1 UTO AZ	242 *0*	---------	-------	-------	-------	-------	-------	-------	-------
XP1 ODONT	243 *1*	---------	0.000	0.500	-------	0.000	0.793	0.304	0.999
XP2 ODONT	199 *0*	---------	-------	-------	-------	-------	-------	-------	-------
XM2 META	170	-0.5820	**0.464**	**<0.001**	0.133	0.000	0.890	0.212	0.299
bp1-bp3	*170*								
bp3.5	*155*	---------	0.247	0.274	0.310	0.000	0.741	0.945	0.236
bp4	*79*	---------	**0.736**	**<0.001**	0.173	0.000	0.930	0.208	0.419
bp5	*1*	---------	0.000	0.500	-------	0.000	1.000	0.300	1.000
XM3 META	13	-0.2946	1.000	0.230	-------	0.000	0.517	0.764	0.313
bp1-bp3	*13*	---------	0.100	0.500	0.707	0.913	**0.034**	0.998	1.000
bp3.5	*6*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*1*	---------	-------	-------	-------	-------	-------	-------	-------
XM1 HYPO	319	0.4217	**0.721**	**<0.001**	0.055	0.013	**0.100**	0.274	0.613
bp1	*319*								
bp2	*317*	---------	0.000	0.500	-------	0.000	1.000	1.000	1.000
bp3	*315*	---------	0.107	0.478	1.595	0.140	**0.037**	0.355	0.213
bp3.5	*310*	---------	**1.000**	**<0.001**	-------	0.000	0.200	0.310	0.358
bp4	*282*	---------	**0.953**	**<0.001**	0.064	0.000	0.693	0.290	0.931
bp5	*62*	---------	**0.806**	**<0.001**	0.108	0.000	0.207	0.202	0.801
XM2 HYPO	112	-0.3669	**0.926**	**<0.001**	0.033	0.000	0.326	0.183	0.767
bp1	*107*	---------	1.000	0.181	-------	0.000	1.000	0.188	0.989

bp2	*78*	---------	**1.000**	**<0.001**	-------	0.000	0.975	0.553	0.628
bp3	*70*	---------	**1.000**	**<0.001**	-------	0.000	0.461	0.807	0.953
bp3.5	*49*	---------	**0.982**	**<0.001**	0.134	0.000	0.425	0.116	0.649
bp4	*14*	---------	**0.630**	**0.019**	0.286	0.000	0.417	0.970	0.872
bp5	*3*	---------	1.000	0.271	-------	0.037	0.992	**0.093**	0.426
XM3 HYPO	9	0.6460	0.000	0.500	-------	0.029	0.856	**0.090**	0.632
bp1	*8*	---------	1.000	0.401	-------	0.000	1.000	1.000	1.000
bp2	*6*	---------	0.000	0.500	-------	0.000	0.994	0.679	0.416
bp3	*1*	---------	1.000	0.401	-------	0.000	0.603	0.410	1.000
bp3.5	*1*	---------	1.000	0.401	-------	0.000	0.603	0.410	1.000
bp4	*1*	---------	1.000	0.401	-------	0.000	0.603	0.410	1.000
bp5	*0*								
XM1 C5	309	0.6472	**0.745**	**<0.001**	0.068	0.029	**0.056**	0.891	**0.004**
bp1	*78*	---------	**0.906**	**<0.001**	0.091	0.021	0.137	0.588	**0.005**
bp2	*34*	---------	**0.676**	**<0.001**	0.171	0.000	0.509	0.618	0.140
bp3	*8*	---------	0.000	0.500	-------	0.011	0.123	0.307	**0.066**
bp4	*4*	---------	0.000	0.500	-------	0.016	0.207	0.126	**0.062**
bp5	*1*	---------	0.000	0.500	-------	0.000	1.000	0.649	0.980
XM2 C5*	117	0.9169	**0.972**	**<0.001**	0.013	0.000	0.816	0.288	0.700
bp1	*26*	---------	**1.000**	**0.004**	-------	0.000	0.814	0.140	0.476
bp2	*15*	---------	**1.000**	**0.001**	-------	0.000	0.465	0.786	0.923
bp3	*8*	---------	0.768	0.052	0.244	0.000	0.533	0.392	0.636
bp4-bp5	*0*								
XM3 C5*	11	3.3279	1.000	0.311	-------	0.954	**<0.001**	**<0.001**	**<0.001**
bp1	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*1*	---------	1.000	0.414	-------	0.000	1.000	1.000	1.000
bp4	*1*	---------	1.000	0.414	-------	0.000	1.000	1.000	1.000
bp5	*0*								
XM1 CARABELLI	302	-0.5884	**0.650**	**<0.001**	0.066	0.043	**0.008**	0.449	**0.001**
bp1	*298*	---------	**0.757**	**0.003**	0.197	0.070	0.128	0.970	**0.004**

bp2	*275*	---------	**0.959**	**<0.001**	0.072	0.032	**0.030**	0.320	**0.007**
bp3	*267*	---------	**0.884**	**<0.001**	0.102	0.030	**0.009**	0.312	**0.004**
bp4	*244*	---------	**0.724**	**<0.001**	0.136	0.020	**0.018**	0.173	**0.011**
bp5	*202*	---------	**0.738**	**<0.001**	0.117	0.015	**0.019**	0.524	**0.040**
bp6	*93*	---------	**0.788**	**<0.001**	0.103	0.022	**0.026**	0.856	**0.008**
bp7	*46*	---------	**0.819**	**<0.001**	0.128	0.016	0.142	0.295	**0.012**
XM2 CARABELLI	153	-0.9306	**0.834**	**<0.001**	0.065	0.000	0.389	0.447	0.620
bp1	*104*	---------	**0.854**	**<0.001**	0.136	0.000	0.410	0.210	0.558
bp2	*65*	---------	**0.952**	**<0.001**	0.140	0.000	0.577	0.261	0.667
bp3	*53*	---------	**1.000**	**<0.001**	-------	0.000	0.412	0.199	0.767
bp4	*40*	---------	**0.983**	**<0.001**	0.125	0.020	**0.082**	0.473	0.389
bp5	*37*	---------	**0.961**	**<0.001**	0.118	0.000	0.218	0.924	0.615
bp6	*11*	---------	0.000	0.500	-------	0.028	**0.097**	0.856	0.291
bp7	*0*								
XM3 CARABELLI*	10	2.3139	1.000	0.296	-------	0.970	**<0.001**	**0.009**	**<0.001**
bp1	*4*	---------	0.000	0.500	-------	0.000	0.325	0.861	0.352
bp2	*4*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*4*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*2*	---------	1.000	0.351	-------	0.000	1.000	1.000	1.000
bp7	*2*	---------	1.000	0.351	-------	0.000	1.000	1.000	1.000
XM2 PARA*	154	27.7717	0.000	0.500	-------	0.000	0.195	0.280	0.929
bp1	*5*	---------	0.000	0.500	-------	0.073	0.134	**0.014**	0.605
bp2	*1*	---------	1.000	0.353	-------	0.000	1.000	0.291	1.000
bp3	*1*	---------	1.000	0.359	-------	0.091	0.968	**0.074**	1.000
bp4	*1*	---------	1.000	0.353	-------	0.000	1.000	0.291	1.000
bp5-bp6	*0*								
XM3 PARA	13	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	1.000	0.347	-------	0.000	1.000	1.000	1.000
bp2	*1*	---------	1.000	0.347	-------	0.000	1.000	1.000	1.000

bp3	*1*	---------	1.000	0.347	-------	0.000	1.000	1.000	1.000
bp4	*1*	---------	1.000	0.347	-------	0.000	1.000	1.000	1.000
bp5	*1*	---------	1.000	0.347	-------	0.000	1.000	1.000	1.000
bp6	*0*								
XI2 PEG[j]	290 *4*	---------	0.000	0.500	-------	0.000	0.873	0.819	0.900
XM3 PEG[j]	19 *0*	---------	-------	-------	-------	-------	-------	-------	-------
XI2 CONG ABS	286 *14*	---------	**0.686**	**0.014**	0.240	0.033	**0.040**	0.196	**0.035**
XP2 CONG ABS	222 *18*	---------	**0.875**	**0.007**	0.185	0.000	0.834	0.212	0.980
XM3 CONG ABS	17 *0*	---------	-------	-------	-------	-------	-------	-------	-------
NI1 SHOV	308	-0.6408	**0.599**	**<0.001**	0.085	0.000	0.407	0.313	0.223
bp1	*128*	---------	**0.717**	**<0.001**	0.126	0.034	0.447	0.170	**0.062**
bp2	*11*	---------	**1.000**	**0.018**	-------	0.000	0.417	0.298	0.888
bp3	*1*	---------	0.467	0.466	3.555	0.000	0.695	0.216	0.997
bp4-bp7	*0*								
NI2 SHOV	298	-0.8193	**0.725**	**<0.001**	0.057	0.000	0.228	0.338	0.235
bp1	*148*	---------	**0.984**	**<0.001**	0.068	0.000	0.290	0.206	0.221
bp2	*12*	---------	**0.755**	**0.003**	0.222	0.000	0.332	0.389	0.602
bp3-bp7	*0*								
NC DAR	226	-0.2386	**0.622**	**<0.001**	0.094	0.191	0.246	<**0.001**	0.143
bp1	*87*	---------	**0.808**	**<0.001**	0.122	0.102	0.129	<**0.001**	0.211
bp2	*46*	---------	**0.746**	**<0.001**	0.171	0.139	0.783	**<0.001**	0.160
bp3	*15*	---------	**0.857**	**0.003**	0.216	0.133	0.445	**<0.001**	0.107
bp4	*2*	---------	0.000	0.500	-------	0.153	0.692	**0.076**	1.000
bp5	*0*								
NP1 ODONT	239 *1*	---------	0.000	0.500	-------	0.000	0.571	0.232	0.997

NP2 ODONT	201	---------	0.000	0.500	<0.001	0.000	1.000	0.150	1.000
	2								
NM1 CNO*	293	0.8271	**0.499**	**<0.001**	0.100	0.000	0.658	0.591	0.679
bp5	*280*	---------	**0.713**	**0.007**	0.210	0.007	**0.090**	0.123	0.141
bp6	*63*	---------	**0.853**	**<0.001**	0.114	0.000	0.907	0.271	0.462
bp7-bp8	*0*								
NM2 CNO	140	0.3170	**0.697**	**<0.001**	0.090	0.000	0.584	0.784	0.591
bp5	*36*	---------	**0.937**	**<0.001**	0.103	0.000	0.631	0.369	0.531
bp6	*4*	---------	0.000	0.500	-------	0.130	1.000	**0.027**	1.000
bp7-bp8	*0*								
NM3 CNO*	12	-3.1048	0.000	0.500	-------	0.705	**0.014**	0.704	0.983
bp5	*7*	---------	0.100	0.500	0.707	0.393	**0.038**	0.976	0.990
bp6	*1*	---------	1.000	0.420	-------	0.000	1.000	1.000	1.000
bp7-bp8	*0*								
NM1 DWRINK	301	-0.1064	**0.923**	**<0.001**	0.017	0.000	0.404	0.375	0.681
bp1	*250*	---------	**1.000**	**<0.001**	-------	0.000	0.390	0.931	0.752
bp2	*77*	---------	**1.000**	**<0.001**	-------	0.000	0.390	0.930	0.635
bp3	*13*	---------	**1.000**	**<0.001**	-------	0.000	0.866	0.188	0.832
NM1 PSTYLID	293	-0.5446	**0.502**	**<0.001**	0.115	0.021	0.571	**0.007**	0.931
bp1	*227*	---------	**0.547**	**0.007**	0.218	0.000	0.722	0.105	0.363
bp2	*155*	---------	**0.745**	**<0.001**	0.148	0.011	0.855	**0.016**	0.932
bp3	*40*	---------	**0.688**	**0.001**	0.196	0.031	0.312	**0.035**	0.908
bp4	*26*	---------	**0.791**	**<0.001**	0.158	0.043	0.382	**0.033**	0.965
bp5	*13*	---------	**0.785**	**<0.001**	0.165	0.054	**0.034**	0.482	0.591
bp6	*7*	---------	**0.848**	**0.011**	0.231	0.078	**0.066**	0.345	0.953
bp7	*0*								
NM3 PSTYLID*	12	-3.3943	1.000	0.110	-------	0.000	0.323	0.282	0.445
bp1	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*2*	---------	-------	-------	-------	-------	-------	-------	-------

bp5	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*1*	---------	1.000	0.364	-------	0.000	1.000	1.000	1.000
bp7	*0*								
NM1 C5	292	0.1677	**0.846**	**<0.001**	0.034	0.009	0.131	0.136	**0.031**
bp1	*278*	---------	**0.715**	**0.007**	0.196	0.007	**0.098**	0.132	0.150
bp2	*267*	---------	**0.998**	**<0.001**	0.139	0.000	0.827	0.111	0.596
bp3	*244*	---------	**0.974**	**<0.001**	0.065	0.000	0.695	0.401	0.217
bp4	*172*	---------	**0.963**	**<0.001**	0.078	0.000	0.622	0.585	0.157
bp5	*6*	---------	**0.818**	**0.017**	0.232	0.137	**0.081**	**0.090**	0.626
NM2 C5	145	0.5514	**0.699**	**<0.001**	0.078	0.000	0.779	0.142	0.328
bp1	*38*	---------	**0.978**	**<0.001**	0.090	0.000	0.681	0.268	0.492
bp2	*33*	---------	**0.904**	**<0.001**	0.114	0.019	0.747	**0.074**	0.216
bp3	*19*	---------	**0.926**	**<0.001**	0.098	0.027	0.435	0.229	**0.098**
bp4	*9*	---------	0.488	0.084	0.329	0.133	0.676	**0.058**	**0.022**
bp5	*1*	---------	1.000	0.344	-------	0.000	0.674	0.240	0.998
NM3 C5*	13	3.6570	0.000	0.500	-------	0.933	**0.004**	**<0.001**	**0.017**
bp1	*9*	---------	1.000	0.156	-------	0.000	0.997	0.994	0.978
bp2	*9*	---------	1.000	0.156	-------	0.000	0.997	0.994	0.978
bp3	*9*	---------	1.000	0.156	-------	0.000	0.997	0.994	0.978
bp4	*4*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*1*	---------	1.000	0.355	-------	0.000	1.000	1.000	0.999
NM1 C6*	294	1.6555	**0.459**	**<0.001**	0.106	0.000	0.370	0.283	0.156
bp1	*60*	---------	**0.833**	**<0.001**	0.051	0.000	0.644	0.232	0.301
bp2	*23*	---------	0.467	0.077	0.278	0.009	**0.074**	0.681	0.171
bp3	*11*	---------	0.000	0.500	-------	0.034	0.165	0.142	**0.044**
bp4	*1*	---------	0.000	0.500	<0.001	0.000	0.962	0.287	0.998
bp5	*0*								
NM2 C6*	144	31.9549	0.000	0.500	-------	0.021	1.000	**0.068**	0.741
bp1	*4*	---------	0.000	0.500	-------	0.125	1.000	**<0.001**	0.999
bp2	*2*	---------	0.000	0.500	-------	0.000	0.125	1.000	0.995
bp3	*1*	---------	1.000	0.347	-------	0.000	1.000	0.291	0.997

bp4	*1*	---------	1.000	0.347	-------	0.000	1.000	0.291	0.997
bp5	*0*								
NM3 C6*	12	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	1.000	0.042	-------	0.000	1.000	1.000	1.000
bp2	*1*	---------	1.000	0.042	-------	0.000	1.000	1.000	1.000
bp3-bp5	*0*								
NM1 C7*	330	3.1016	**0.414**	**<0.001**	0.123	0.013	0.574	**0.095**	0.273
bp1	*53*	---------	**0.514**	**0.009**	0.225	0.023	0.364	**0.041**	**0.091**
bp1a	*30*	---------	**0.587**	**0.003**	0.214	0.000	0.671	0.177	0.955
bp2	*20*	---------	**0.804**	**<0.001**	0.162	0.015	0.908	**0.096**	0.190
bp3	*11*	---------	**0.806**	**0.014**	0.268	0.020	0.237	0.162	**0.034**
bp4	*4*	---------	**1.000**	**0.002**	-------	0.000	0.902	0.825	0.312
NM3 C7	12	---------	-------	-------	-------	-------	-------	-------	-------
	0								
NM1 DTCREST	301	---------	1.000	0.051	-------	0.057	0.278	**0.009**	0.996
	6								
NM2 DTCREST	182	---------	0.000	0.500	-------	0.000	0.666	0.240	0.997
	1								
NM3 DTCREST	12	---------	-------	-------	-------	-------	-------	-------	-------
	0								
NI1 CONG ABS	319	---------	0.000	0.500	-------	0.000	1.000	0.267	1.000
1									
NP2 CONG ABS	222	---------	0.579	0.103	0.332	0.000	0.224	0.875	0.312
	17								
NM3 CONG ABS	16	---------	-------	-------	-------	-------	-------	-------	-------
	0								

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[a] l=left; r=right; traits without a left or right designation represent the maximum of the left and right antimeric expressions; x=maxillary; n=mandibular; bp= breakpoint. All morphological trait abbreviations outlined in Appendix C. Ordinal traits were normalized and treated as continuous for the purpose for heritability estimation. Breakpoints indicate presence/absence dichotomization cutoffs for ordinal traits; each of these breakpoints was treated as an

individual binary character for heritability estimation. Kurtosis is not estimated for binary character models. Certain breakpoints were omitted from the heritability analysis because expression was monomorphic across the sample. Traits marked with asterisks are associated with less stable heritability estimates because other model parameters could not be estimated, because sample size was too small, or because kurtosis values were too high after normalization. These results should be accepted with caution. Dashes are associated with incalculable parameter estimates. Traits marked with dashes for all parameters represent models that failed to converge. The traits XI1 labial convexity, XM1 metacone, XM1 parastyle, NP1 lingual cusp variation, NP2 lingual cusp variation, NM1 anterior fovea, NM2 protostylid, NM2 cusp 7 were removed due to high levels of intra-observer error. [b]N=sample size for heritability estimation; Count=count for dichotomized trait expression (presence) at the denoted breakpoint (bp). Count values are italicized. If a trait is binary (i.e., its original scoring standards do not include ordinal scale scoring) this value is marked on a blank row beneath the sample size "N". [c]K=model kurtosis value. [d]h2= maximum likelihood heritability estimate. [e]All significant heritability estimates (p-value<0.05) and associated probability value estimates are bolded. [f]SE= maximum likelihood standard error estimate; this parameter estimate is typically omitted when heritability estimated equal 0.000 or 1.000. [g]c2= maximum likelihood total covariate estimate. [h]All significant probability value estimates for the covariates of age, sex, and age/sex interaction are bolded. [i]As the winging, premolar lingual cusp, and groove pattern data are categorical and not ordinal, each category was treated as a separate binary variable. [j]Peg-shaped incisor and peg-shaped molar were scored only as binary variables at the breakpoint of ASUDAS grade 2.

APPENDIX L

UNIVERSITY OF ADELAIDE YUENDUMU ABORIGINAL GROWTH STUDY SAMPLE HERITABILITY ESTIMATES

Table 1. University of Adelaide Yuendumu Growth Study sample heritability estimates: deciduous crown morphology (mixed deciduous standards).

			Heritability			Covariates			
Trait[a]	N[b] *Count*	K[c]	h2[d]	p-value[e]	SE[f]	c2[g]	age[h] p-value	sex[h] p-value	age*sex[h] p-value
lxi1 wing*	35	0.8994	0.520	0.325	1.561	0.179	0.144	0.423	**0.002**
bp1	*7*	---------	0.000	0.498	-------	0.245	0.165	1.000	**0.002**
bp2	*7*	---------	0.000	0.498	-------	0.245	0.165	1.000	**0.002**
lxi1 shov	30	-0.9754	0.000	0.500	-------	0.000	0.786	0.956	0.851
bp1	*29*	---------	1.000	0.367	-------	0.000	0.548	0.450	0.999
bp2	*12*	---------	0.000	0.500	-------	0.000	0.894	0.874	0.948
bp3	*0*								
lxi2 shov	40	-0.9973	0.000	0.500	-------	0.000	0.888	0.839	0.829
bp1	*38*	---------	0.000	0.500	-------	0.000	0.564	0.301	1.000
bp2	*19*	---------	0.000	0.500	-------	0.000	0.689	0.580	0.694
bp3	*0*								
lxc shov	72	-0.4831	**0.951**	**<0.001**	0.284	0.036	0.214	**0.039**	**0.093**
bp1	*33*	---------	**1.000**	**0.002**	-------	0.058	0.450	**0.026**	**0.091**
bp2	*3*	---------	0.694	0.242	0.945	0.000	0.204	0.652	0.686
bp3	*0*								
lxi1 dshov	33	---------	-------	-------	-------	-------	-------	-------	-------
bp1	2	1.9103	0.000	0.500	-------	0.000	0.419	0.333	0.991
bp2-bp3	*0*								
lxi2 dshov*	43	9.8241	0.000	0.500	-------	0.115	0.291	0.859	**0.016**
bp1	*3*	---------	0.000	0.500	-------	0.000	0.564	0.301	1.000
bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*0*								
lxc td*	83	0.9424	**0.469**	**0.034**	0.293	0.000	0.638	0.120	0.426

bp1	*83*								
bp2	*76*	---------	**1.000**	**0.036**	-------	0.125	**0.030**	0.361	0.606
bp3	*64*	---------	**0.000**	**0.500**	-------	0.055	**0.056**	0.316	0.873
bp4	*5*	---------	**1.000**	**0.023**	-------	0.140	**0.073**	0.204	1.000
lxm1 cno	70	-0.7632	**1.000**	**<0.001**	-------	0.115	**0.007**	**0.039**	0.683
bp3m	*43*	---------	**1.000**	**0.002**	-------	0.000	0.216	0.243	0.947
bp3h	*11*	---------	**1.000**	**<0.001**	-------	0.161	**0.057**	**0.092**	0.949
bp4-	*8*	---------	**1.000**	**0.007**	-------	0.336	**0.007**	**0.041**	0.378
bp4	*1*	---------	0.000	0.500	-------	0.263	1.000	**0.097**	1.000
lxm2 cno	99	-0.3206	0.047	0.411	0.216	0.000	0.112	0.844	0.651
bp3a	*99*								
bp3b	*96*	---------	1.000	0.381	-------	0.000	0.160	0.252	1.000
bp4-	*83*	---------	0.345	0.259	0.570	0.000	0.472	0.622	0.294
bp4	*65*	---------	0.017	0.480	0.334	0.000	0.128	0.846	0.436
lxm2 c5	70	---------	**1.000**	**0.014**	-------	0.000	0.121	0.268	0.353
	15								
lxm2 Carab	84	-0.4998	**0.741**	**0.001**	0.258	0.002	0.616	**0.100**	0.851
bp1	*80*	---------	0.000	0.500	-------	0.113	0.781	**0.032**	0.999
bp2	*48*	---------	**1.000**	**0.001**	-------	0.000	0.674	0.201	0.244
bp3	*26*	---------	**0.992**	**0.013**	0.492	0.000	0.469	0.280	0.123
bp4	*4*	---------	0.412	0.275	0.746	0.000	0.371	0.406	0.190
lni1 shov	11	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*10*	---------	0.000	0.500	-------	0.000	0.160	1.000	0.976
bp2-bp3	*0*								
lni2 shov	35	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*32*	---------	0.000	0.500	-------	0.049	**0.089**	0.248	0.141
bp2-bp3	*0*								
lnc shov	76	-0.1226	**0.587**	**0.003**	0.246	0.000	0.224	0.204	0.173
bp1	*20*	---------	**0.985**	**0.007**	0.405	0.000	0.326	0.159	0.221
bp2	*1*	---------	0.000	0.500	-------	0.000	0.366	0.535	1.000
bp3	*0*								

lni1 double	18	---------	-------	-------	-------	-------	-------	-------	-------
	0								
lni1 double	36	---------	-------	-------	-------	-------	-------	-------	-------
	0								
lnc double	78	---------	-------	-------	-------	-------	-------	-------	-------
	0								
lnc td	74	-0.9437	**0.842**	**<0.001**	0.253	0.000	0.515	0.537	0.399
bp1	*50*	---------	**0.970**	**<0.001**	-------	0.000	0.884	0.317	0.257
bp2	*29*	---------	**0.949**	**0.020**	0.386	0.000	0.318	0.322	0.786
bp3	*4*	---------	1.000	0.109	-------	0.105	0.629	**0.098**	1.000
bp4	*4*	---------	1.000	0.109	-------	0.105	0.629	**0.098**	1.000
lnm2 dwrink	83	---------	0.623	0.096	0.498	0.000	0.891	0.845	0.522
	61								
lnm2 pstylid	65	----------	-------	-------	-------	-------	-------	-------	-------
bp1	*64*	---------	1.000	0.384	-------	0.298	0.059	0.978	0.982
bp2	*0*								
lnm2 c7	94	-0.9346	0.090	0.344	0.238	0.000	0.831	0.292	0.134
bp1	*64*	---------	0.189	0.336	0.472	0.063	0.754	0.379	**0.013**
bp2	*37*	---------	**0.539**	**0.048**	0.369	0.000	0.314	0.807	0.701
bp3	*4*	---------	1.000	0.104	-------	0.092	0.880	**0.077**	1.000
bp4-bp5	*0*								
lnm1 delta	91	---------	0.000	0.500	-------	0.000	0.683	0.109	0.999
	3								
rxi1 wing	33	-0.4445	**0.611**	**0.243**	0.832	0.087	0.344	0.267	**0.036**
bp1	*9*	---------	**0.670**	**0.302**	1.241	0.000	0.472	0.266	0.172
bp2	*7*	---------	0.000	0.500	-------	0.247	0.160	0.957	**0.002**
rxi1 shov*	32	0.2688	0.000	0.500	-------	0.000	0.301	0.785	0.974
bp1	*30*	---------	1.000	0.273	-------	0.000	0.442	0.376	1.000
bp2	*8*	---------	0.000	0.500	-------	0.000	0.467	0.107	0.186
bp3	*0*								
rxi2 shov	40	-2.1081	0.507	0.147	0.521	0.000	0.488	0.297	0.816

bp1	*40*								
bp2	*20*	---------	0.739	0.152	0.750	0.000	0.484	0.260	0.705
bp3	*0*								
rxc shov	71	-0.9893	0.123	0.321	0.274	0.000	0.954	0.948	0.292
bp1	*40*	---------	0.138	0.376	1.766	0.000	0.925	0.687	0.265
bp2	*2*	---------	0.138	0.376	1.766	0.000	0.925	0.687	0.265
bp3	*0*								
rxi1 dshov*	32	1.7262	0.404	0.224	0.529	0.000	0.560	0.629	0.772
bp1	*6*	---------	0.959	0.170	0.927	0.000	0.550	0.205	0.265
bp2	*1*	---------	0.000	0.500	-------	0.000	0.794	0.456	0.999
bp3	*0*								
rxi2 dshov*	41	10.8381	0.000	0.500	-------	0.000	0.407	0.653	0.834
bp1	*3*	---------	0.000	0.500	-------	0.000	0.299	0.671	0.644
bp2	*1*	---------	0.000	0.500	-------	0.000	1.000	0.114	1.000
bp3	*0*								
rxc td*	84	-1.3269	0.000	0.500	-------	0.000	1.000	0.913	0.294
bp1	*83*	---------	0.000	0.500	-------	0.000	0.453	0.453	0.995
bp2	*74*	---------	0.293	0.332	1.661	0.000	0.227	0.410	0.412
bp3	*70*	---------	**1.000**	**0.024**	-------	0.066	0.685	0.827	**0.047**
bp4	*8*	---------	0.100	0.441	0.702	0.000	0.244	0.786	0.480
rxm1 cno	63	-1.1820	**0.991**	**0.001**	0.277	0.000	0.974	0.770	0.491
bp3m	*38*	---------	**1.000**	**0.017**	-------	0.000	0.276	0.950	0.217
bp3h	*14*	---------	**1.000**	**0.003**	-------	0.000	0.390	0.855	0.924
bp4-	*11*	---------	**1.000**	**0.011**	-------	0.062	**0.084**	0.782	0.728
bp4	*0*								
rxm2 cno	102	-1.0482	0.231	0.108	0.212	0.000	0.365	0.606	0.466
bp3a	*102*								
bp3b	*100*	---------	0.000	0.500	-------	0.000	0.253	0.270	1.000
bp4-	*75*	---------	0.000	0.500	-------	0.000	0.510	0.544	0.385
bp4	*46*	---------	0.431	0.069	0.330	0.000	0.452	0.783	0.783
rxm2 c5	78	---------	0.373	0.220	1.942	0.000	0.591	**0.015**	0.467

	27								
rxm2 Carab	86	-0.4235	**0.451**	**0.023**	0.270	0.022	0.260	**0.096**	0.502
bp1	*85*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*65*	---------	0.446	0.151	0.473	0.000	0.170	0.146	0.969
bp3	*30*	---------	**0.743**	**0.036**	0.469	0.000	0.850	0.122	0.400
bp4	*5*	---------	0.000	0.500	-------	0.052	**0.050**	0.262	0.182
rni1 shov*	15	1.6154	0.000	0.500	2.921	0.000	0.357	1.000	1.000
bp1	*13*	---------	0.000	0.500	-------	0.000	0.567	0.792	0.980
bp2	*2*	---------	0.000	0.500	-------	0.000	0.434	0.837	1.000
bp3	*0*								
rni2 shov	33	-1.3736	**1.000**	**0.003**	-------	0.124	0.668	**0.024**	0.265
bp1	*31*	---------	1.000	0.348	-------	0.504	0.875	**0.007**	0.994
bp2	*13*	---------	**1.000**	**0.020**	-------	0.000	0.575	0.591	0.547
bp3	*0*								
rnc shov	76	-0.9842	0.298	0.081	0.242	0.000	0.871	0.659	0.790
bp1	*27*	---------	0.304	0.196	0.370	0.000	0.935	0.730	0.818
bp2	*1*	---------	0.000	0.500	-------	0.000	0.474	0.476	0.995
bp3	*0*								
rni1 double	21	---------	-------	-------	-------	-------	-------	-------	-------
	0								
rni2 double	35	---------	-------	-------	-------	-------	-------	-------	-------
	0								
rnc double	78	---------	-------	-------	-------	-------	-------	-------	-------
	0								
rnc td*	74	-0.9415	**0.773**	**0.002**	0.282	0.000	0.626	0.903	0.605
bp1	*48*	---------	**0.983**	**0.009**	0.426	0.000	0.918	0.636	0.929
bp2	*31*	---------	**1.000**	**0.008**	-------	0.000	0.333	0.316	0.435
bp3	*5*	---------	**1.000**	**0.044**	-------	0.000	0.499	0.159	1.000
bp4	*4*	---------	**1.000**	**0.024**	-------	0.000	0.338	0.241	1.000
rnm2 dwrink	93	---------	0.333	0.245	0.522	0.035	**0.027**	0.584	0.212
	78								

rnm2 pstylid*	65	65.0000	0.000	0.500	-------	0.000	0.561	0.579	0.704
bp1	*65*								
bp2	*1*	---------	0.000	0.500	-------	0.000	0.580	0.426	1.000
rnm2 c7	98	-0.9545	0.120	0.307	0.256	0.000	0.898	0.729	0.707
bp1	*64*	---------	0.444	0.117	0.349	0.000	0.677	0.274	0.327
bp2	*31*	---------	0.029	0.476	0.494	0.000	0.905	0.597	0.997
bp3	*3*	---------	0.702	0.379	1.958	0.071	**0.100**	0.610	0.368
bp4-bp5	*0*								
rnm1 delta	92	---------	0.000	0.500	<0.001	0.000	0.595	0.135	1.000
	3								
xi1 wing max	35	0.3379	1.000	0.086	-------	0.179	0.324	0.456	**0.004**
bp1	*9*	---------	1.000	0.334	-------	0.209	0.434	0.975	**0.007**
bp2	*7*	---------	0.000	0.498	-------	0.245	0.166	1.000	**0.002**
xi1 shov max	33	-1.0811	0.000	0.500	-------	0.000	0.813	0.893	0.876
bp1	*32*	---------	1.000	0.356	-------	0.000	0.690	0.478	0.997
bp2	*14*	---------	0.000	0.500	-------	0.000	0.692	0.695	0.719
bp3	*0*								
xi2 shov max	48	-1.2737	0.000	0.500	-------	0.000	0.631	0.670	0.553
bp1	*47*	---------	0.000	0.500	-------	0.000	0.823	0.428	0.999
bp2	*24*	---------	0.000	0.500	-------	0.000	0.651	0.542	0.547
bp3	*0*								
xc shov max	81	-0.8301	0.380	0.052	0.258	0.000	0.884	0.367	0.524
bp1	*46*	---------	0.491	0.113	0.433	0.000	0.933	0.355	0.559
bp2	*4*	---------	0.299	0.362	0.862	0.000	0.949	0.727	0.737
bp3	*0*								
xi1 dshov max*	36	2.4064	0.300	0.284	0.524	0.000	0.487	0.557	0.898
bp1	*6*	---------	0.753	0.235	1.007	0.000	0.495	0.237	0.374
bp2	*1*	---------	0.000	0.500	-------	0.000	0.768	0.454	1.000
bp3	*0*								
xi2 dshov max*	47	5.4557	0.000	0.500	-------	0.050	0.430	0.602	**0.087**
bp1	*5*	---------	0.000	0.500	-------	0.000	0.289	0.778	0.122

bp2	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*0*								
xc td max	92	1.4191	**0.832**	**0.041**	0.259	0.000	0.547	0.539	0.234
bp1	*92*								
bp2	*86*	---------	0.000	0.500	-------	0.000	0.210	1.000	0.585
bp3	*79*	---------	**1.000**	**0.026**	-------	0.000	0.677	0.981	0.152
bp4	*10*	---------	**1.000**	**0.029**	-------	0.057	**0.064**	0.884	0.434
xm1 cno max	80	-0.6723	**0.879**	**<0.001**	0.252	0.000	0.530	0.887	0.184
bp3m	*54*	---------	**1.000**	**0.009**	-------	0.000	0.973	0.671	0.296
bp3h	*15*	---------	**1.000**	**0.005**	-------	0.000	0.201	0.606	0.366
bp4-	*12*	---------	**1.000**	**0.007**	-------	0.109	**0.017**	0.554	0.825
bp4	*1*	---------	0.000	0.500	-------	0.000	0.970	0.105	0.976
xm2 cno max	107	-0.2711	**0.355**	**0.041**	0.243	0.034	**0.072**	0.246	0.311
bp3a	*107*								
bp3b	*105*	---------	0.000	0.500	-------	0.000	0.238	0.270	0.994
bp4-	*93*	---------	0.823	0.055	0.535	0.000	0.776	0.217	0.369
bp4	*72*	---------	0.416	0.098	0.357	0.023	**0.035**	0.451	0.131
xm2 c5 max	89	---------	**0.860**	**0.016**	0.412	0.104	**0.039**	**0.034**	0.889
	37								
xm2 Carab max	98	-0.5732	**0.554**	**0.006**	0.261	0.000	0.740	0.422	0.901
bp1	97								
bp2	*72*	---------	0.479	0.116	1.022	0.000	0.618	0.232	0.391
bp3	*42*	---------	**1.000**	**0.002**	-------	0.000	0.761	0.610	0.628
bp4	*6*	---------	0.205	0.380	0.707	0.000	0.254	0.821	0.669

ni1 shov max*	16	1.8956	0.000	0.500	-------	0.000	0.351	1.000	1.000
bp1	*14*	---------	0.000	0.500	-------	0.000	0.526	1.000	1.000
bp2	*2*	---------	0.000	0.500	-------	0.000	0.465	0.904	0.988
bp3	*0*								
ni2 shov max	36	-1.0496	**1.000**	**0.001**	-------	0.107	0.772	**0.028**	0.281
bp1	*34*	---------	1.000	0.348	-------	0.515	0.875	**0.006**	0.996
bp2	*13*	---------	**1.000**	**0.012**	-------	0.000	0.668	0.818	0.603
bp3	*0*								
nc shov max	79	-0.9490	**0.606**	**0.003**	0.253	0.000	0.632	0.579	0.306
bp1	*32*	---------	**0.751**	**0.026**	0.448	0.000	0.540	0.465	0.390
bp2	*2*	---------	**1.000**	**0.044**	-------	0.000	0.819	0.431	1.000
bp3	*0*								
ni1 double max	22	---------	-------	-------	-------	-------	-------	-------	-------
	0								
ni2 double max	36	---------	-------	-------	-------	-------	-------	-------	-------
	0								
nc double max	78	---------	-------	-------	-------	-------	-------	-------	-------
	0								
nc td max	78	-0.8159	**0.842**	**<0.001**	0.234	0.000	0.949	0.566	0.290
bp1	*57*	---------	**1.000**	**0.001**	-------	0.000	0.621	0.624	0.255
bp2	*41*	---------	**1.000**	**0.001**	-------	0.000	0.595	0.944	0.427
bp3	*8*	---------	1.000	0.059	-------	0.100	0.787	**0.030**	1.000
bp4	*7*	---------	**1.000**	**0.044**	-------	0.099	0.617	**0.042**	1.000
nm2 dwrink max	100	---------	**0.956**	**0.035**	0.542	0.088	**0.011**	0.649	0.064
	87								
nm2 pstylid max	77	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*75*	---------	0.000	0.500	-------	0.000	0.495	0.470	1.000
bp2	*1*	---------	-------	-------	-------	-------	-------	-------	-------
nm2 c7 max	106	-0.7293	**0.575**	**0.011**	0.297	0.015	0.487	0.443	**0.084**
bp1	*79*	---------	**0.766**	**0.035**	0.511	0.047	0.236	0.309	**0.007**
bp2	*49*	---------	0.520	0.062	0.380	0.000	0.504	0.929	0.294

bp3	*6*	---------	1.000	0.088	-------	0.000	0.540	0.929	0.294
bp4-bp5	*0*								
nm1 delta max	93 *4*	---------	0.000	0.500	-------	0.097	0.443	**0.096**	0.999

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[a] l=left; r=right; x=maxillary; n=mandibular; max=maximum of the left and right antimeric expressions; bp= breakpoint. All morphological trait abbreviations outlined in Appendix C. Ordinal traits were normalized and treated as continuous for the purpose for heritability estimation. Breakpoints indicate presence/absence dichotomization cutoffs for ordinal traits; each of these breakpoints was treated as an individual binary character for heritability estimation. Kurtosis is not estimated for binary character models. Certain breakpoints were omitted from the heritability analysis because expression was monomorphic across the sample. Traits marked with asterisks are associated with less stable heritability estimates because other model parameters could not be estimated, because sample size was too small, or because kurtosis values were too high after normalization. These results should be accepted with caution. Dashes are associated with incalculable parameter estimates. Traits marked with dashes for all parameters represent models that failed to converge. The traits xc double shovel and xi2 tuberculum dentale were removed due to high levels of intra-observer error. [b] N=sample size for heritability estimation; Count=count for dichotomized trait expression (presence) at the denoted breakpoint (bp). Count values are italicized. If a trait is binary (i.e., its original scoring standards do not include ordinal scale scoring) this value is marked on a blank row beneath the sample size "N". [c] K=model kurtosis value. [d] h2= maximum likelihood heritability estimate. [e] All significant heritability estimates (p-value<0.05) and associated probability value estimates are bolded. [f] SE= maximum likelihood standard error estimate; this parameter estimate is typically omitted when heritability estimated equal 0.000 or 1.000. [g] c2= maximum likelihood total covariate estimate. [h] All significant probability value estimates for the covariates of age, sex, and age/sex interaction are bolded.

Table 2. University of Adelaide Yuendumu Growth Study sample heritability estimates: deciduous crown morphology (ASUDAS standards).

			Heritability			Covariates			
Trait[a]	N[b] *Count*	K[c]	h2[d]	p-value[e]	SE[f]	c2[g]	age[h] p-value	sex[h] p-value	age*sex[h] p-value
lxi1 wing[i]	35	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*7*	---------	0.000	0.500	-------	0.245	0.165	1.000	**0.002**
bp2	*0*								
bp3	*28*	---------	0.000	0.496	-------	0.245	0.165	0.423	**0.002**
bp4	*0*								
lxi1 lab cvx	32	0.0184	0.000	0.500	-------	0.000	0.496	0.793	0.409
bp1	*31*	---------	0.131	0.496	3.567	0.000	0.133	0.992	1.000
bp2	*26*	---------	0.000	0.500	-------	0.000	0.826	0.592	0.890
bp3	*8*	---------	0.696	0.291	1.183	0.026	0.230	0.269	**0.035**
bp4	*1*	---------	0.000	0.500	-------	0.000	0.131	0.992	1.000
lxi1 shov*	30	1.7483	0.000	0.500	-------	0.000	0.322	0.250	0.219
bp1	*27*	---------	1.000	0.403	-------	0.000	0.543	0.126	0.614
bp2	*4*	---------	0.413	0.377	1.337	0.049	0.193	0.370	**0.047**
bp3-bp7	*0*								
lxi2 shov	38	0.0117	**1.000**	**0.037**	-------	0.086	0.602	**0.069**	0.843
bp1	*27*	---------	0.000	0.500	-------	0.000	0.299	0.366	0.806
bp2	*11*	---------	**1.000**	**0.028**	-------	0.084	0.693	**0.037**	0.943
bp3-bp7	*0*								
lxc shov	73	-0.5781	**0.906**	**<0.001**	0.274	0.069	**0.090**	**0.063**	**0.032**
bp1	*27*	---------	**1.000**	**0.004**	-------	0.055	0.344	**0.057**	**0.068**
bp2	*6*	---------	1.000	0.079	-------	0.136	**0.018**	0.926	0.376
bp3-bp7	*0*								
lxi1 dshov	33	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*2*	---------	0.000	0.500	-------	0.000	0.419	0.367	0.992

bp2-bp6	*0*								
lxi2 dshov*	43	11.8289	0.000	0.500	-------	0.084	0.264	0.761	**0.026**
bp1	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*1*	---------	1.000	0.370	-------	0.224	**0.098**	0.985	0.985
bp3	*1*	---------	1.000	0.370	-------	0.224	**0.098**	0.985	0.985
bp4-bp6	*0*								
lxc dshov	75	-0.3947	0.000	0.500	-------	0.000	0.596	0.207	0.701
bp1	*69*	---------	0.952	0.098	0.705	0.108	0.169	**0.055**	0.998
bp2	*43*	---------	0.313	0.274	0.552	0.000	0.425	0.135	0.841
bp3	*9*	---------	0.000	0.500	-------	0.030	0.235	0.341	**0.082**
bp4-bp6	*0*								
lxi2 td	41	-0.4476	0.822	0.063	0.543	0.134	0.229	0.925	**0.003**
bp1	*24*	---------	**1.000**	**0.025**	-------	0.196	0.648	0.766	**0.007**
bp2	*10*	---------	0.000	0.500	-------	0.165	0.164	0.410	**0.002**
bp3	*2*	---------	1.000	0.348	-------	0.248	**0.020**	1.000	0.976
bp4	*1*	---------	0.143	0.490	-------	0.000	0.112	0.981	0.980
bp5--bp6	*0*								
lxc td	81	-0.3711	**1.000**	**<0.001**	-------	0.092	0.864	**0.033**	**0.055**
bp1	*81*								
bp2	*69*	---------	0.966	0.107	0.722	0.175	0.861	0.914	**0.008**
bp3	*37*	---------	**1.000**	**0.015**	-------	0.036	0.909	**0.020**	0.168
bp4	*21*	---------	**1.000**	**<0.001**	-------	0.000	0.795	0.993	0.856
bp5-	*5*	---------	**1.000**	**0.021**	-------	0.000	0.120	0.179	1.000
bp5	*4*	---------	1.000	0.071	-------	0.000	0.164	0.204	1.000
bp6	*2*	---------	1.000	0.071	-------	0.000	0.164	0.204	1.000
lxc dar	25	-0.2527	0.000	0.500	-------	0.260	**0.003**	0.134	**0.031**
bp1	*8*	---------	0.000	0.500	-------	0.037	**0.045**	0.215	0.165
bp2	*4*	---------	1.000	0.337	-------	0.483	**0.005**	**0.078**	0.709
bp3-bp5	*0*								
lxm2 meta	103	-0.6902	0.278	0.069	0.218	0.060	0.407	**0.008**	0.731
bp1-bp3	*103*								

bp3.5	*102*	---------	0.000	0.500	-------	0.000	0.573	0.718	0.929
bp4	*59*	---------	**0.711**	**0.020**	0.396	0.038	0.906	**0.033**	0.874
bp5	*2*	---------	0.000	0.500	-------	0.223	**0.017**	0.572	0.985
lxm1 hypo*	74	2.3377	**1.000**	**<0.001**	-------	0.124	**0.097**	**0.027**	0.146
bp1	*11*	---------	**1.000**	**0.001**	-------	0.101	**0.060**	0.109	0.958
bp2	*6*	---------	**1.000**	**0.023**	-------	0.119	0.253	**0.056**	0.845
bp3	*3*	---------	**0.681**	**0.239**	0.961	0.000	0.408	0.302	0.753
bp3.5-bp5	*0*								
lxm2 hypo	100	-0.3431	**0.577**	**0.005**	0.266	0.063	**0.064**	**0.050**	0.515
bp1-bp2	*100*								
bp3	*99*	---------	0.000	0.500	-------	0.000	0.414	0.538	0.995
bp3.5	*81*	---------	0.000	0.500	-------	0.000	0.154	0.354	0.991
bp4	*26*	---------	**1.000**	**0.001**	-------	0.048	0.196	**0.028**	0.261
bp5	*0*								
lxm2 c5	69	0.1845	**0.786**	**0.006**	0.325	0.000	0.173	0.744	0.735
bp1	*15*	---------	**1.000**	**0.017**	-------	0.000	0.192	0.306	0.344
bp2	*4*	---------	0.793	0.251	1.116	0.000	0.239	0.486	0.416
bp3-bp5	*0*								
lxm2 Carab	84	-0.4104	**0.603**	**0.002**	0.244	0.000	0.662	0.177	0.244
bp1	*80*	---------	0.000	0.500	-------	0.113	0.782	**0.059**	1.000
bp2	*76*	---------	0.682	0.110	0.568	0.000	0.304	0.630	0.967
bp3	*48*	---------	**1.000**	**0.001**	-------	0.000	0.694	0.201	0.317
bp4	*34*	---------	**0.716**	**0.036**	0.452	0.000	0.466	0.636	0.901
bp5	*26*	---------	**0.992**	**0.013**	0.492	0.000	0.504	0.354	0.229
bp6	*5*	---------	0.722	0.109	0.682	0.000	0.240	0.197	0.220
bp7	*4*	---------	0.413	0.275	0.743	0.000	0.371	0.406	0.190
lxm2 para[j]	86	---------	-------	-------	-------	-------	-------	-------	-------
	0								

lni1 shov	11	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*8*	---------	1.000	0.277	-------	0.000	0.218	0.686	0.980
bp2-bp7	*0*								
lni2 shov	35	0.3470	0.000	0.500	-------	0.248	**0.001**	0.181	**0.025**
bp1	*28*	---------	0.000	0.500	-------	0.104	**0.056**	0.281	**0.092**
bp2	*3*	---------	0.093	0.500	-------	0.358	**0.006**	0.347	0.994
bp3-bp7	*0*								
lnc dar	34	-0.5737	0.601	0.111	0.478	0.109	0.114	**0.021**	0.287
bp1	*10*	---------	1.000	0.114	-------	0.160	0.342	**0.010**	0.993
bp2	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp3-bp5	*0*								
lnm2 ant fovea*	85	2.8134	0.147	0.303	0.310	0.000	0.952	0.325	0.896
bp1	*84*	---------	0.000	0.500	-------	0.000	1.000	**<0.001**	0.998
bp2	*82*	---------	0.000	0.500	-------	0.000	0.397	0.911	0.532
bp3	*12*	---------	**1.000**	**0.050**	-------	0.041	0.614	**0.085**	0.474
bp4	*0*								
lnm1 cno	52	0.6112	**0.602**	**0.037**	0.361	0.000	0.459	0.334	0.928
bp5	*40*	---------	0.648	0.207	0.813	0.000	0.692	0.276	0.716
bp6	*2*	---------	**1.000**	**0.044**	-------	0.000	0.305	0.478	0.461
lnm2 cno	82	-0.6046	**0.710**	**0.010**	0.313	0.000	0.548	0.590	0.771
bp5	*82*								
bp6	*52*	---------	**0.806**	**0.050**	0.520	0.000	0.329	0.818	0.418
bp7	*5*	---------	1.000	0.138	-------	0.128	0.703	**0.038**	0.999
lnm2 groove[i]	80	---------	-------	-------	-------	-------	-------	-------	-------
y	*76*	---------	**1.000**	**0.013**	-------	0.113	0.899	**0.082**	0.998
x	*1*	---------	0.000	0.500	-------	0.000	0.101	0.734	0.834
+	*3*	---------	**1.000**	**0.013**	-------	0.114	0.899	**0.082**	1.000
lnm2 dwrink	80	-0.8358	0.139	0.281	0.255	0.000	0.875	0.164	0.369
bp1	*77*	---------	0.000	0.500	-------	0.273	1.000	**0.010**	0.952
bp2	*58*	---------	0.573	0.114	0.500	0.000	0.892	0.911	0.477
bp3	*26*	---------	0.000	0.500	-------	0.032	0.806	**0.059**	0.303

lnm2 pstylid	53	-0.6061	**1.000**	**0.050**	-------	0.052	0.174	**0.048**	**0.051**
bp1	*52*	---------	1.000	0.394	-------	0.273	**0.075**	0.985	0.982
bp2	*52*	---------	1.000	0.394	-------	0.273	**0.075**	0.985	0.982
bp3	*50*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*44*	---------	0.000	0.500	-------	0.000	0.235	0.311	0.299
bp5	*31*	---------	1.000	0.051	-------	0.000	0.304	0.394	0.125
bp6	*11*	---------	1.000	0.098	-------	0.024	**0.032**	0.103	0.306
bp7	*0*								
lnm1 c5	49	-0.6267	**0.722**	**0.025**	0.387	0.000	0.708	0.431	0.241
bp1	*37*	---------	1.000	0.073	-------	0.000	0.890	0.239	0.601
bp2	*31*	---------	**1.000**	**0.007**	-------	0.000	0.441	0.882	0.251
bp3	*8*	---------	0.000	0.500	-------	0.000	0.920	0.518	0.203
bp4	*1*	---------	0.000	0.500	-------	0.000	0.931	0.410	1.000
bp5	*0*								
lnm2 c5	91	0.2249	0.000	0.500	-------	0.077	0.135	**<0.001**	0.380
bp1-bp2	*91*								
bp3	*87*	---------	0.441	0.421	1.851	0.110	0.114	**0.060**	0.993
bp4	*73*	---------	0.247	0.314	0.568	0.042	0.310	**0.066**	0.283
bp5	*13*	---------	0.000	0.500	-------	0.231	0.403	**0.019**	**0.062**
lnm1 c6*	76	36.1034	**0.672**	**0.001**	0.218	0.000	0.439	0.423	0.770
bp1	*2*	---------	**1.000**	**0.030**	-------	0.000	0.411	0.447	0.639
bp2	*2*	---------	**1.000**	**0.030**	-------	0.000	0.411	0.447	0.639
bp3	*1*	---------	0.000	0.500	-------	0.000	1.000	0.111	0.999
bp4-bp5	*0*								
lnm2 c6	81	-0.9389	**0.652**	**0.016**	0.315	0.005	**0.073**	0.131	0.370
bp1	*52*	---------	**0.958**	**0.034**	0.534	0.000	0.411	0.924	0.464
bp2	29	---------	**0.810**	**0.045**	0.501	0.044	0.226	**0.014**	0.959
bp3	*5*	---------	0.000	0.500	-------	0.051	0.450	**0.058**	0.294
bp4	*2*	---------	0.000	0.500	-------	0.000	0.292	0.171	1.000
bp5	*0*								
lnm1 c7*	83	-1.0685	0.109	0.308	0.231	0.031	0.254	**0.084**	0.861

bp1	*54*	---------	0.043	0.454	0.372	0.000	0.258	0.352	0.857
bp1a	*40*	---------	0.000	0.500	-------	0.031	0.252	**0.037**	0.958
bp2	*2*	---------	0.000	0.500	-------	0.000	0.209	0.942	1.000
bp3-bp4	*0*								
lnm2 c7	98	-0.7617	0.000	0.500	-------	0.017	0.282	**0.060**	0.290
bp1	*67*	---------	0.256	0.291	0.548	0.060	0.928	0.288	**0.024**
bp1a	*58*	---------	0.087	0.409	0.847	0.000	0.785	0.149	0.233
bp2	*3*	---------	0.000	0.500	-------	0.013	**0.017**	0.267	0.994
bp3	*1*	---------	0.000	0.500	-------	0.000	0.278	0.488	1.000
bp4	*0*								
lnm2 dtcrest	58	---------	**1.000**	**0.050**	-------	0.000	0.527	0.556	0.663
	18								
rxi1 wing[i]	33	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*7*	---------	0.000	0.498	-------	0.247	0.160	1.000	**0.002**
bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*23*	---------	0.334	0.395	1.282	0.000	0.837	0.410	0.274
bp4	*1*	---------	0.126	0.493	3.559	0.000	0.148	0.960	0.999
rxi1 lab cvx	30	-0.3436	0.251	0.352	0.680	0.000	0.937	0.363	0.593
bp1	*28*	---------	1.000	0.301	-------	0.000	0.570	0.372	1.000
bp2	*27*	---------	1.000	0.224	-------	0.000	0.826	0.260	1.000
bp3	*13*	---------	0.143	0.441	0.964	0.122	0.481	**0.038**	**0.077**
bp4	*1*	---------	0.100	0.499	0.709	0.429	**0.034**	1.000	1.000
rxi1 shov	31	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*26*	---------	0.551	0.374	1.613	0.000	0.732	0.972	0.780
bp2-bp7	*0*								
rxi2 shov	39	0.0107	**1.000**	**0.026**	-------	0.070	0.489	**0.087**	0.349
bp1	*32*	---------	1.000	0.156	-------	0.000	0.291	0.166	0.354
bp2	*7*	---------	0.543	0.315	1.129	0.000	0.676	0.305	0.926
bp3-bp7	*0*								
rxc shov	71	-0.9092	0.211	0.226	0.299	0.000	0.704	0.483	0.290
bp1	*34*	---------	0.606	0.110	0.085	0.000	0.737	0.492	0.495

bp2	*4*	---------	0.000	0.500	-------	0.000	0.575	0.609	0.228
bp3-bp7	*0*								
rxi1 dshov	32	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*6*	---------	1.000	0.134	-------	0.015	0.550	**<0.001**	0.265
bp2-bp6	*0*								
rxi2 dshov*	41	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*2*	---------	0.000	0.500	-------	0.069	**0.096**	0.153	0.142
bp2-bp6	*0*								
rxc dshov	76	-0.1392	**0.179**	**0.298**	0.357	0.000	0.751	0.561	0.771
bp1	*68*	---------	1.000	0.092	-------	0.082	**0.069**	0.949	0.842
bp2	*29*	---------	0.000	0.500	-------	0.023	**0.062**	0.308	0.356
bp3	*5*	---------	0.000	0.500	-------	0.000	0.964	0.938	0.499
bp4	*1*	---------	0.000	0.500	-------	0.000	0.980	0.403	1.000
bp5-bp6	*0*								
rxi2 td	45	-0.7365	**1.000**	**0.011**	-------	0.039	0.417	0.205	**0.084**
bp1	*33*	---------	0.715	0.201	0.848	0.095	0.613	0.247	**0.093**
bp2	*13*	---------	**1.000**	**0.011**	-------	0.000	0.142	1.000	0.347
bp3	*1*	---------	1.000	0.430	-------	0.000	0.105	0.995	0.990
bp4-bp6	*0*								
rxc td	79	-0.4301	**0.241**	**0.199**	0.306	0.014	0.208	0.331	**0.081**
bp1	*78*	---------	0.000	0.500	-------	0.000	0.475	0.512	0.996
bp2	*67*	---------	0.174	0.399	0.650	0.000	0.843	0.692	0.226
bp3	*44*	---------	0.691	0.056	0.240	0.030	0.313	**0.064**	0.269
bp4	*16*	---------	0.247	0.372	0.262	0.104	**0.012**	0.822	**0.010**
bp5-	*7*	---------	0.000	0.500	-------	0.000	0.103	0.291	0.825
bp5	*6*	---------	0.000	0.500	-------	0.000	0.298	0.765	0.422
bp6	*0*								
rxc dar	28	-0.9810	0.383	0.265	0.683	0.000	0.421	0.276	0.355
bp1	*13*	---------	0.459	0.326	1.091	0.000	0.731	0.288	0.360
bp2	*6*	---------	0.254	0.382	0.880	0.000	0.316	0.321	0.598
bp3	*1*	---------	0.000	0.500	-------	0.000	0.553	0.374	0.996

bp4-bp5	*0*								
rxm2 meta	104	-0.1315	0.167	0.174	0.194	0.000	0.411	0.147	0.860
bp1-bp3	*104*								
bp3.5	*102*	---------	-------	-------	-------	-------	-------	-------	-------
bp4	*65*	---------	0.060	0.424	0.338	0.000	0.487	0.314	0.590
bp5	*7*	---------	0.149	0.398	0.609	0.000	0.979	0.137	0.617
rxm1 hypo*	67	1.2914	**1.000**	**<0.001**	-------	0.000	0.196	0.612	0.891
bp1	*14*	---------	**1.000**	**0.002**	<0.001	0.346	0.734	0.864	**0.001**
bp2	*7*	---------	**1.000**	**0.036**	<0.001	0.734	0.341	0.647	**0.001**
bp3	*1*	---------	0.000	0.500	-------	0.000	0.468	0.528	0.996
bp3.5-bp5	*0*								
rxm2 hypo	102	-0.4059	**0.529**	**0.003**	0.230	0.000	0.666	0.808	0.489
bp1-bp3	*102*								
bp3.5	*78*	---------	**0.369**	**0.139**	0.227	0.000	0.579	0.897	0.535
bp4	*20*	---------	**1.000**	**0.004**	-------	0.000	0.302	0.587	0.344
bp5	*1*	---------	0.000	0.500	-------	0.000	0.398	0.544	0.993
rxm2 c5	78	0.1845	0.215	0.175	0.254	0.063	0.793	**0.013**	0.270
bp1	*26*	---------	0.394	0.205	0.510	0.081	0.584	**0.002**	0.188
bp2	*11*	---------	0.739	0.078	0.573	0.000	0.825	0.118	0.235
bp3	*3*	---------	**0.507**	**0.273**	-------	0.000	0.642	0.970	0.921
bp4-bp5	*0*								
rxm2 Carab	86	-0.4112	**0.475**	**0.014**	0.262	0.000	0.515	0.164	0.636
bp1	*85*	---------	0.000	0.500	-------	0.000	0.301	0.546	0.994
bp2	*83*	---------	0.789	0.244	1.049	0.000	0.807	0.770	0.415
bp3	*66*	---------	0.772	0.069	0.557	0.021	0.173	**0.065**	0.889
bp4	*42*	---------	**0.769**	**0.013**	0.393	0.000	0.467	0.510	0.804
bp5	*29*	---------	**0.916**	**0.013**	0.437	0.032	0.850	**0.084**	0.389
bp6	*6*	---------	0.073	0.452	0.617	0.000	0.236	0.765	0.833
bp7	*4*	---------	**0.000**	**0.500**	-------	0.239	**0.050**	0.725	0.449
rxm2 para[j]	92	---------	0.100	0.499	-------	0.000	1.000	1.000	1.000
	0								

rni1 shov	15	-0.2192	1.000	0.206	-------	0.000	0.706	1.000	1.000
bp1	*13*	---------	0.000	0.500	-------	0.000	0.567	0.792	0.980
bp2	*4*	---------	1.000	0.316	-------	0.000	0.978	0.864	0.993
bp3-bp7	*0*								
rni2 shov	33	-0.7695	0.232	0.324	0.530	0.051	**0.091**	0.135	0.125
bp1	*30*	---------	1.000	0.153	-------	0.221	0.103	**0.008**	0.110
bp2	*14*	---------	0.000	0.500	-------	0.046	**0.071**	0.554	0.234
bp3-bp7	*0*								
rnc dar	25	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*11*	---------	0.000	0.500	-------	0.000	0.845	0.414	0.859
bp2-bp5	*0*								
rnm2 ant fovea*	86	2.8751	0.000	0.500	-------	0.000	0.884	0.181	0.226
bp1	*86*								
bp2	*81*	---------	0.000	0.500	-------	0.000	0.513	0.354	0.328
bp3	*11*	---------	0.187	0.362	0.553	0.039	0.869	**0.097**	0.639
bp4	*1*	---------	0.000	0.500	-------	0.000	0.541	0.418	1.000
rnm1 cno	49	0.6112	0.000	0.500	-------	0.000	0.249	0.848	0.508
bp5	*45*	---------	0.000	0.500	-------	0.000	0.207	0.394	0.187
bp6	*1*								
rnm2 cno	85	-0.4081	**0.624**	**0.021**	0.332	0.000	0.354	0.320	0.856
bp5	*85*								
bp6	*57*	---------	0.577	0.109	0.500	0.000	0.360	0.734	0.773
bp7	*5*	---------	1.000	0.070	-------	0.122	1.000	**0.037**	1.000
rnm2 groove[i]	94	---------	-------	-------	-------	-------	-------	-------	-------
y	*90*	---------	1.000	0.320	-------	0.164	0.235	0.555	**0.009**
x	*0*								
+	*4*	---------	1.000	0.320	-------	0.164	0.235	0.555	**0.009**
rnm2 dwrink	89	0.0214	**0.336**	**0.049**	0.231	0.000	0.103	0.705	0.860
bp1	*86*	---------	0.998	0.079	0.693	0.000	0.250	0.519	0.938
bp2	*74*	---------	0.361	0.235	0.541	0.039	**0.028**	0.605	0.247
bp3	*19*	---------	0.259	0.264	0.441	0.000	0.677	0.810	0.335

rnm2 pstylid	58	-0.6420	0.000	0.500	-------	0.126	**0.018**	**0.084**	**0.099**
bp1-bp2	*58*								
bp3	*56*	---------	0.000	0.500	-------	0.000	0.595	0.582	0.793
bp4	*45*	---------	0.000	0.500	-------	0.067	**0.036**	0.543	**0.004**
bp5	*32*	---------	0.000	0.500	-------	0.000	0.129	0.187	0.237
bp6	*12*	---------	0.000	0.500	-------	0.111	**0.034**	**0.061**	0.157
bp7	*0*								
rnm1 c5	44	-0.3577	0.000	0.500	-------	0.000	0.342	0.480	1.000
bp1	*39*	---------	0.000	0.500	-------	0.000	0.178	0.302	0.873
bp2	*33*	---------	0.085	0.465	0.984	0.000	0.809	0.934	0.863
bp3	*13*	---------	0.000	0.500	-------	0.000	0.627	0.622	0.945
bp4	*2*	---------	0.000	0.500	-------	0.000	0.156	0.368	1.000
bp5	*1*	---------	0.000	0.500	-------	0.000	0.505	0.470	1.000
rnm2 c5	93	0.7648	0.000	0.500	-------	0.064	0.144	**0.014**	0.232
bp1-bp2	*93*								
bp3	*88*	---------	0.000	0.500	-------	0.099	0.123	**0.071**	0.996
bp4	*70*	---------	0.000	0.500	-------	0.125	0.432	**<0.001**	0.455
bp5	*7*	---------	0.000	0.500	-------	0.000	0.752	0.380	0.276
rnm1 c6*	78	35.3647	0.081	0.433	0.472	0.049	0.522	0.929	**0.050**
bp1	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*1*	---------	0.000	0.500	-------	0.000	0.437	0.526	0.995
bp4	*1*	---------	0.000	0.500	-------	0.000	0.437	0.526	0.995
bp5	*1*	---------	0.000	0.500	-------	0.000	0.437	0.526	0.995
rnm2 c6	83	-0.8431	0.173	0.294	0.333	0.000	0.130	0.423	0.585
bp1	*56*	---------	0.333	0.261	0.540	0.000	0.257	0.622	0.629
bp2	*37*	---------	0.000	0.500	-------	0.000	0.228	0.983	0.818
bp3	*8*	---------	0.590	0.267	0.733	0.042	0.142	**0.089**	0.916
bp4	*4*	---------	0.000	0.500	-------	0.139	**0.039**	0.581	0.997
bp5	*0*								
rnm1 c7	85	-0.6655	**0.914**	**<0.001**	0.256	0.020	**0.093**	0.328	0.982

bp1	*61*	---------	0.896	0.064	0.718	0.000	0.155	0.877	0.666
bp1a	*37*	---------	**1.000**	**0.002**	-------	0.000	0.117	0.332	0.432
bp2	*7*	---------	0.000	0.500	-------	0.122	0.753	**0.017**	0.999
bp3-bp4	*0*								
rnm2 c7	101	-0.7106	0.292	0.072	0.232	0.000	0.473	0.708	0.335
bp1	*67*	---------	**1.000**	**0.001**	-------	0.000	0.204	0.892	0.345
bp1a	*58*	---------	**1.000**	**0.001**	-------	0.000	0.204	0.892	0.345
bp2	*4*	---------	0.000	0.500	-------	0.000	0.773	0.611	0.515
bp3	*1*	---------	0.000	0.500	-------	0.000	0.308	0.499	1.000
bp4	*0*								
rnm2 dtcrest	77	---------	0.266	0.313	0.574	0.042	0.418	**0.046**	0.347
	22								
xi1 lab cvx	34	-0.2588	0.855	0.076	0.506	0.000	0.740	0.664	0.596
bp1	*33*	---------	1.000	0.423	-------	0.000	0.142	0.961	1.000
bp2	*30*	---------	1.000	0.227	-------	0.000	0.962	0.131	1.000
bp3	*15*	---------	1.000	0.097	-------	0.000	0.542	0.298	0.575
bp4	*2*	---------	0.000	0.500	-------	0.000	0.632	0.297	0.997
xi1 shov max*	34	1.6550	0.094	0.413	0.440	0.000	0.228	0.375	0.179
bp1	*30*	---------	0.129	0.470	1.703	0.000	0.573	0.198	0.663
bp2	*4*	---------	0.675	0.314	1.231	0.095	0.121	**0.011**	**0.032**
bp3-bp7	*0*								
xi2 shov max	45	-0.07712	**1.000**	**0.026**	0.431	0.085	0.279	**0.029**	0.384
bp1	*34*	---------	0.784	0.272	1.247	0.052	0.270	**0.071**	0.830
bp2	*11*	---------	1.000	0.134	-------	0.067	0.370	**0.076**	0.764
bp3-bp7	*0*								
xc shov max	82	-0.9551	**0.423**	**0.030**	0.252	0.000	0.759	0.515	0.569
bp1	*42*	---------	0.546	0.086	0.422	0.000	0.514	0.250	0.856
bp2	*8*	---------	0.568	0.215	0.754	0.080	**0.026**	0.294	**0.068**
bp3-bp7	*0*								
xi1 dshov max	35	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*6*	---------	0.670	0.264	1.029	0.000	0.495	0.304	0.407

bp2-bp6	*0*								
xi2 dshov max*	47	8.7995	0.000	0.500	-------	0.045	0.293	0.560	**0.087**
bp1	*4*	---------	0.000	0.500	-------	0.070	0.244	0.485	**0.056**
bp2	*1*	---------	1.000	0.370	-------	0.235	**0.087**	0.987	0.983
bp3	*1*	---------	1.000	0.370	-------	0.235	**0.087**	0.987	0.983
bp4-bp6	*0*								
xc dshov max	86	-0.2355	0.000	0.500	-------	0.000	0.569	0.398	0.675
bp1	*80*	---------	0.538	0.296	1.010	0.144	**0.018**	0.169	0.437
bp2	*52*	---------	0.197	0.333	0.489	0.000	0.171	0.378	0.939
bp3	*12*	---------	0.415	0.217	0.559	0.000	0.205	0.992	0.222
bp4	*1*	---------	0.000	0.500	-------	0.000	0.972	0.373	1.000
bp5-bp6	*0*								
xi2 td max	46	-0.2998	0.705	0.054	0.450	0.090	0.276	0.464	**0.008**
bp1	*37*	---------	0.000	0.500	-------	0.217	0.326	0.785	**0.047**
bp2	*16*	---------	**1.000**	**0.013**	-------	0.088	**0.050**	0.701	**0.035**
bp3	*2*	---------	1.000	0.400	-------	0.262	**0.017**	0.968	0.985
bp4	*1*	---------	1.000	0.422	-------	0.000	0.105	0.990	0.985
bp5--bp6	*0*								
xc td max	87	-0.4350	**0.562**	**0.020**	0.304	0.002	0.208	0.270	**0.082**
bp1	*87*								
bp2	*77*	---------	0.000	0.500	-------	0.000	0.971	0.581	0.158
bp3	*49*	---------	0.392	0.153	0.416	0.000	0.365	0.110	0.143
bp4	*27*	---------	**1.000**	**0.002**	-------	0.000	0.134	0.423	0.305
bp5-	*9*	---------	0.599	0.208	0.821	0.073	**0.024**	0.726	0.246
bp5	*7*	---------	0.282	0.379	0.950	0.042	**0.099**	0.699	0.400
bp6	*2*	---------	0.000	0.500	-------	0.000	0.585	0.258	1.000
xc dar max	39	-0.9594	0.116	0.397	0.469	0.000	0.366	0.136	0.519
bp1	*17*	---------	0.000	0.500	-------	0.000	0.387	0.183	0.557
bp2	*9*	---------	0.244	0.368	0.754	0.000	0.343	0.177	0.495
bp3	*1*	---------	0.000	0.500	-------	0.000	0.649	0.418	0.997
bp4-bp5	*0*								

xm2 meta max	109	-0.2232	0.233	0.078	0.189	0.040	0.417	**0.028**	0.771
bp1-bp3.5	*109*								
bp4	*79*	---------	0.324	0.162	0.271	0.000	0.996	0.135	0.994
bp5	*9*	---------	0.301	0.298	0.589	0.059	0.207	**0.044**	0.949
xm1 hypo max*	80	1.8584	**0.744**	**0.001**	0.253	0.000	0.212	0.204	0.192
bp1	*15*	---------	**1.000**	**0.016**	-------	0.000	0.502	0.409	0.313
bp2	*9*	---------	**1.000**	**0.016**	-------	0.000	0.539	0.409	0.313
bp3	*3*	---------	0.625	0.257	0.513	0.000	0.384	0.254	0.725
bp3.5-bp5	*0*								
xm2 hypo max	107	-0.5049	**0.626**	**0.001**	0.232	0.000	0.394	0.985	0.362
bp1-bp3	*107*								
bp3.5	*93*	---------	0.310	0.262	0.394	0.000	0.334	0.463	0.393
bp4	*34*	---------	**1.000**	**<0.001**	-------	0.000	0.429	0.603	0.339
bp5	*1*	---------	0.000	0.500	-------	0.000	0.362	0.458	0.993
xm2 c5 max	88	-0.2215	**0.459**	**0.011**	0.233	0.065	0.121	**0.033**	0.539
bp1	*36*	---------	**0.827**	**0.018**	0.410	0.110	**0.054**	**0.011**	0.685
bp2	*14*	---------	**0.876**	**0.018**	1.266	0.000	0.690	0.302	0.760
bp3	*3*	---------	0.577	0.242	0.805	0.000	0.798	0.963	0.955
bp4-bp5	*0*								
xm2 Carab max	98	-0.5843	**0.523**	**0.005**	0.246	0.000	0.715	0.420	0.826
bp1	*97*	---------	0.000	0.500	-------	0.000	0.328	0.524	0.995
bp2	*97*	---------	0.000	0.500	-------	0.000	0.446	0.529	0.995
bp3	*73*	---------	0.660	0.059	0.456	0.000	0.666	0.124	0.333
bp4	*52*	---------	**0.903**	**0.005**	0.411	0.000	0.663	0.972	0.981
bp5	*41*	---------	**1.000**	**0.001**	-------	0.000	0.820	0.512	0.624
bp6	*7*	---------	0.468	0.181	0.566	0.000	0.160	0.819	0.828
bp7	*5*	---------	0.314	0.318	0.654	0.000	0.231	0.237	0.197
xm2 para max[j]	102	---------	0.100	0.500	0.707	0.000	1.000	1.000	1.000
	0								
ni1 shov max	16	-0.0203	1.000	0.189	-------	0.000	0.730	1.000	1.000
bp1	*14*	---------	0.000	0.500	-------	0.000	0.526	1.000	1.000

bp2	*4*	---------	1.000	0.285	-------	0.000	0.950	0.740	0.953
bp3-bp7	*0*								
ni2 shov max	36	-0.6764	0.210	0.338	0.522	0.045	**0.100**	0.154	0.124
bp1	*33*	---------	1.000	0.165	-------	0.301	0.105	**0.013**	**0.099**
bp2	*14*	---------	0.000	0.500	-------	0.038	**0.044**	0.254	0.795
bp3-bp7	*0*								
nc dar max*	42	-1.4242	0.393	0.220	0.511	0.112	**0.032**	0.909	**0.066**
bp1	*20*	---------	0.267	0.356	0.698	0.000	0.107	0.967	0.124
bp2	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp3-bp5	*0*								
nm2 ant fovea max	94	1.5513	0.000	0.500	-------	0.000	0.817	0.887	0.509
bp1	*94*								
bp2	*91*	---------	0.000	0.500	-------	0.000	0.453	0.992	0.665
bp3	*19*	---------	0.670	0.114	0.047	0.000	0.655	0.647	0.510
bp4	*1*	---------	0.000	0.500	-------	0.000	0.563	0.387	1.000
nm1 cno max*	71	2.4074	0.474	0.057	0.319	0.000	0.991	0.839	0.794
bp5	*60*	---------	0.249	0.368	0.771	0.000	0.669	0.778	0.599
bp6	*2*	---------	**1.000**	**0.032**	-------	0.000	0.412	0.479	0.631
nm2 cno max	102	-0.5269	**0.868**	**<0.001**	0.265	0.000	0.426	0.374	0.732
bp5	*102*								
bp6	*66*	---------	**1.000**	**0.002**	-------	0.000	0.162	0.877	0.417
bp7	*6*	---------	1.000	0.110	-------	0.129	0.491	**0.024**	1.000
nm2 dwrink max	97	-0.5451	**0.512**	**0.004**	0.229	0.000	0.198	0.257	0.903
bp1	*93*	---------	0.843	0.122	0.748	0.000	0.275	0.104	0.424
bp2	*84*	---------	**1.000**	**0.024**	-------	0.056	**0.013**	0.683	0.170
bp3	*34*	---------	0.442	0.103	0.449	0.035	0.986	**0.063**	0.525
nm2 pstylid max	69	-0.9393	0.000	0.500	-------	0.071	**0.045**	**0.075**	0.175
bp1-bp2	*69*								
bp3	*68*	---------	0.000	0.500	-------	0.000	1.000	0.206	0.988
bp4	*61*	---------	0.000	0.500	-------	0.028	**0.055**	0.215	0.220
bp5	*43*	---------	0.000	0.500	-------	0.000	0.462	0.553	0.343

bp6	*18*	---------	0.000	0.500	-------	0.115	**0.031**	**0.049**	**0.061**
bp7	*0*								
nm1 c5 max	68	-0.4314	0.128	0.316	0.282	0.000	0.256	0.363	0.243
bp1	*56*	---------	1.000	0.119	-------	0.000	0.462	0.349	0.522
bp2	*51*	---------	**1.000**	**0.037**	-------	0.000	0.594	0.640	0.427
bp3	*19*	---------	0.000	0.500	-------	0.000	0.437	0.592	0.323
bp4	*3*	---------	0.000	0.500	-------	0.000	0.152	0.173	0.993
bp5	*1*	---------	0.000	0.500	-------	0.000	0.417	0.441	1.000
nm2 c5 max	106	0.5543	0.164	0.232	0.246	0.125	**0.064**	**0.002**	0.463
bp1-bp2	*106*								
bp3	*102*	---------	0.009	0.498	2.056	0.107	0.170	**0.059**	0.994
bp4	*92*	---------	0.686	0.120	0.645	0.089	0.265	**0.008**	0.281
bp5	*18*	---------	0.299	0.300	0.606	0.118	0.156	0.212	**0.086**
nm1 c6 max*	86	40.6263	**0.573**	**0.002**	0.214	0.000	0.682	0.420	0.212
bp1	*3*	---------	**1.000**	**0.044**	-------	0.000	0.296	0.143	0.144
bp2	*3*	---------	**1.000**	**0.044**	-------	0.000	0.392	0.400	0.142
bp3	*2*	---------	**1.000**	**0.027**	-------	0.000	0.390	0.396	0.671
bp4	*1*	---------	0.000	0.500	-------	0.000	0.448	0.499	0.996
bp5	*1*	---------	0.000	0.500	-------	0.000	0.448	0.499	0.996
nm2 c6 max	100	-0.8217	0.420	0.051	0.282	0.000	0.138	0.246	0.357
bp1	*66*	---------	**1.000**	**0.001**	-------	0.000	0.335	0.769	0.451
bp2	*46*	---------	0.336	0.231	3.179	0.000	0.298	0.329	0.486
bp3	*10*	---------	0.000	0.500	-------	0.000	0.172	0.211	0.775
bp4	*4*	---------	0.000	0.500	-------	0.147	0.640	**0.032**	0.998
bp5	*0*								
nm1 c7 max	91	-0.7230	**0.507**	**0.029**	0.291	0.039	0.365	**0.094**	0.918
bp1	*69*	---------	0.072	0.439	0.121	0.000	0.370	0.348	0.518
bp1a	*54*	---------	0.351	0.160	0.378	0.000	0.299	0.151	0.621
bp2	*8*	---------	0.770	0.179	0.827	0.122	0.810	**0.012**	0.998
bp3-bp4	*0*								
nm2 c7 max	108	-0.0713	0.323	0.052	0.232	0.000	0.538	0.509	0.138

bp1	*82*	---------	**0.789**	**0.029**	0.430	0.034	0.304	0.543	**0.024**
bp1a	*74*	---------	**1.000**	**0.005**	-------	0.032	**0.038**	0.620	**0.057**
bp2	*6*	---------	0.000	0.500	-------	0.000	0.204	0.848	0.815
bp3	*1*	---------	0.000	0.500	-------	0.000	0.313	0.460	1.000
bp4	*0*								
nm2 dtcrest max	84	---------	0.270	0.223	0.076	0.042	**0.093**	0.198	0.943
	29								

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[a] l=left; r=right; x=maxillary; n=mandibular; max=maximum of the left and right antimeric expressions; bp= breakpoint. All morphological trait abbreviations outlined in Appendix C. Ordinal traits were normalized and treated as continuous for the purpose for heritability estimation. Breakpoints indicate presence/absence dichotomization cutoffs for ordinal traits; each of these breakpoints was treated as an individual binary character for heritability estimation. Kurtosis is not estimated for binary character models. Certain breakpoints were omitted from the heritability analysis because expression was monomorphic across the sample. Traits marked with asterisks are associated with less stable heritability estimates because other model parameters could not be estimated, because sample size was too small, or because kurtosis values were too high after normalization. These results should be accepted with caution. Dashes are associated with incalculable parameter estimates. Traits marked with dashes for all parameters represent models that failed to converge. The traits xm1 metacone and xm1 parastyle were removed due to high levels of intra-observer error. [b] N=sample size for heritability estimation; Count=count for dichotomized trait expression (presence) at the denoted breakpoint (bp). Count values are italicized. If a trait is binary (i.e., its original scoring standards do not include ordinal scale scoring) this value is marked on a blank row beneath the sample size “N”. [c] K=model kurtosis value. [d] h2= maximum likelihood heritability estimate. [e] All significant heritability estimates (p-value<0.05) and associated probability value estimates are bolded. [f] SE= maximum likelihood standard error estimate; this parameter estimate is typically omitted when heritability estimated equal 0.000 or 1.000. [g] c2= maximum likelihood total covariate estimate. [h] All significant probability value estimates for the covariates of age, sex, and age/sex interaction are bolded. [i] As the winging and groove pattern data are categorical and not ordinal, each category was treated as a separate binary variable. [j] Parastyle for deciduous molars was scored only as a binary variable at the breakpoint of ASUDAS grade 3.

Table 3. University of Adelaide Yuendumu Growth Study sample heritability estimates: permanent crown morphology (ASUDAS standards).

			Heritability			Covariates			
Trait[a]	N[b] *Count*	K[c]	h2[d]	p-value[e]	SE[f]	c2[g]	age[h] p-value	sex[h] p-value	age*sex[h] p-value
LXI1 WING[i]	143	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*8*	---------	0.697	0.054	0.515	0.000	0.842	0.483	0.248
bp2	*4*	---------	0.000	0.500	-------	0.000	0.133	0.303	0.154
bp3	*104*	---------	0.000	0.500	-------	0.000	0.429	0.952	0.607
bp4	*27*	---------	0.000	0.500	-------	0.000	0.153	0.433	0.504
LXI1 SHOV	138	0.0007	0.066	0.346	0.175	0.000	0.368	0.337	0.869
bp1	*138*								
bp2	*125*	---------	0.341	0.259	0.545	0.000	0.892	0.826	0.954
bp3	*46*	---------	0.111	0.331	0.194	0.000	0.184	0.118	0.998
bp4	*9*	---------	0.260	0.321	0.565	0.000	0.915	0.902	0.810
bp5-bp7	*0*								
LXI2 SHOV*	136	-0.2030	**0.438**	**0.006**	0.204	0.033	0.566	**0.079**	0.957
bp1	*132*	---------	0.000	0.500	-------	0.157	1.000	**0.032**	1.000
bp2	*92*	---------	0.249	0.206	0.336	0.036	0.857	**0.009**	0.591
bp3	*31*	---------	**0.914**	**0.003**	0.372	0.000	0.904	0.753	0.898
bp4	*5*	---------	**0.388**	**0.308**	1.854	0.000	0.113	0.778	0.381
bp5	*1*	---------	0.000	0.500	-------	0.000	0.390	0.261	0.977
bp6-bp7	*0*								
LXC SHOV	120	-0.0970	**0.445**	**0.002**	0.183	0.072	**0.012**	**0.093**	0.345
bp1	*100*	---------	0.504	0.083	0.413	0.044	**0.046**	**0.094**	**0.076**
bp2	*38*	---------	**0.683**	**0.005**	0.280	0.075	**0.013**	0.108	0.645
bp3	*7*	---------	0.469	0.203	0.591	0.000	0.405	0.867	0.913
bp4-bp7	*0*								

LXI1 DSHOV	136	-0.2906	0.000	0.500	-------	0.074	0.230	**0.025**	**0.024**
bp1	*125*	---------	**0.000**	**0.500**	-------	0.195	**<0.001**	**0.007**	0.644
bp2	*63*	---------	**0.442**	**0.041**	0.302	0.030	**0.043**	0.129	**0.014**
bp3	*6*	---------	0.754	0.135	0.683	0.000	0.875	0.885	0.663
bp4	*1*	---------	**0.000**	**0.500**	-------	0.000	0.900	0.280	1.000
bp5-bp6	*0*								
LXI2 DSHOV	138	-0.3880	**0.251**	**0.022**	0.153	0.016	**0.066**	0.145	**0.053**
bp1	*113*	---------	0.262	0.198	0.338	0.036	**0.014**	0.154	**0.016**
bp2	*63*	---------	**0.558**	**0.008**	0.282	0.028	**0.092**	**0.073**	**0.098**
bp3	*10*	---------	0.449	0.158	0.459	0.000	0.479	0.579	0.765
bp4	*2*	---------	**1.000**	**0.024**	-------	0.000	0.502	0.962	0.796
bp5-bp6	*0*								
LXC DSHOV	126	-0.2792	**0.293**	**0.034**	0.191	0.000	0.262	0.733	0.899
bp1	*120*	---------	1.000	0.079	-------	0.266	**0.036**	**0.074**	0.995
bp2	*76*	---------	0.034	0.445	0.248	0.000	0.728	0.995	0.436
bp3	*26*	---------	0.419	0.081	0.363	0.000	0.730	0.843	0.870
bp4	*3*	---------	0.000	0.500	-------	0.000	0.396	0.671	0.218
bp5	*1*	---------	0.000	0.500	-------	0.000	1.000	0.425	0.998
bp6	*0*								
LXP1 DSHOV	132	-0.2816	**0.488**	**0.003**	0.225	0.000	0.237	0.620	0.236
bp1	*124*	---------	0.940	0.074	0.651	0.121	**0.070**	0.939	**0.010**
bp2	*94*	---------	**0.484**	**0.044**	0.368	0.000	0.170	0.402	0.660
bp3	*32*	---------	0.343	0.149	0.371	0.000	0.735	0.951	0.999
bp4	*2*	---------	**1.000**	**0.037**	-------	0.000	0.998	0.169	1.000
bp5-bp6	*0*								
LXI1 TD	135	-0.2700	**0.270**	**0.037**	0.176	0.059	0.143	**0.003**	0.124
bp1	*131*	---------	0.000	0.500	-------	0.589	1.000	**0.040**	0.998
bp2	*110*	---------	**0.245**	**0.275**	0.438	0.101	**0.005**	**0.005**	**0.003**
bp3	*71*	---------	0.324	0.096	0.280	0.017	0.488	**0.065**	0.525
bp4	*23*	---------	0.547	0.088	0.178	0.060	0.314	**0.006**	0.402
bp5-	*3*	---------	0.000	0.500	-------	0.000	0.856	0.582	0.628

bp5	*2*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*1*	---------	0.000	0.500	-------	0.124	1.000	**<0.001**	0.994
LXI2 TD	111	-0.4389	**0.677**	**<0.001**	0.224	0.000	0.454	0.212	0.405
bp1	*98*	---------	**0.936**	**0.016**	0.568	0.000	0.546	0.252	0.242
bp2	*77*	---------	**0.802**	**0.007**	0.377	0.000	0.696	0.283	0.446
bp3	*41*	---------	**0.796**	**0.003**	0.197	0.000	0.135	0.472	0.328
bp4	*21*	---------	**0.840**	**0.015**	0.450	0.000	0.682	0.641	0.851
bp5-	*9*	---------	**0.487**	**0.202**	0.623	0.000	0.841	0.302	0.771
bp5	*2*	---------	**1.000**	**0.035**	-------	0.000	0.590	0.616	0.286
bp6	*1*	---------	0.000	0.500	-------	0.000	0.583	0.265	1.000
LXC TD	120	-0.4661	**0.665**	**<0.001**	0.216	0.087	**0.014**	**<0.001**	0.266
bp1	*119*	---------	0.000	0.500	-------	0.000	1.000	0.333	0.995
bp2	*104*	---------	**0.689**	**0.044**	0.446	0.055	**0.043**	**0.073**	**0.068**
bp3	*71*	---------	**0.527**	**0.032**	0.321	0.071	**0.025**	**0.001**	0.158
bp4	*42*	---------	**0.527**	**0.032**	0.321	0.071	**0.025**	**0.001**	0.158
bp5-	*21*	---------	**0.900**	**0.013**	0.422	0.081	0.847	**0.002**	0.245
bp5	*12*	---------	0.500	0.202	**0.015**	0.065	0.648	**0.006**	0.346
bp6	*2*	---------	0.000	0.500	-------	0.000	0.582	0.106	0.995
LXC MES RIDGE	131	---------	-------	-------	-------	-------	-------	-------	-------
bp1-bp3	*0*								
LXC DAR	120	0.1199	**0.408**	**0.003**	0.188	0.154	0.506	**<0.001**	0.663
bp1	*115*	---------	**0.611**	**0.187**	0.721	0.073	0.181	**0.028**	0.269
bp2	*105*	---------	1.000	**0.001**	-------	0.000	0.821	0.181	0.913
bp3	*48*	---------	0.326	0.116	0.314	0.138	0.786	**<0.001**	0.883
bp4	*7*	---------	0.000	0.500	-------	0.000	0.529	**0.003**	0.997
bp5	*1*	---------	0.000	0.500	-------	0.000	0.947	0.277	0.999
LXP1 UTO AZ	141	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LXP1 ODONT	140	---------	0.000	0.500	-------	0.000	0.960	0.896	0.558
	2								
LXP2 ODONT	135	---------	0.000	0.500	-------	0.000	1.000	0.422	0.893

	1								
LXM1 META*	144	3.1863	0.203	0.102	0.190	0.063	0.190	**0.003**	**0.086**
bp1-bp3.5	*144*								
bp4	*136*	---------	**1.000**	**0.004**	-------	0.000	0.399	0.464	0.733
bp5	*14*	---------	0.197	0.412	0.895	0.253	**0.059**	**<0.001**	0.996
LXM2 META	125	-0.3433	0.092	0.264	0.162	0.037	0.257	**0.013**	0.500
bp1-bp3	*125*								
bp3.5	*109*	---------	0.347	0.188	0.433	0.000	0.642	0.371	0.488
bp4	*59*	---------	**0.226**	**0.187**	0.285	0.033	0.581	**0.008**	0.869
bp5	*2*	---------	0.000	0.500	-------	0.000	0.412	0.316	0.427
LXM3 META	62	---------	-------	-------	-------	-------	-------	-------	-------
bp1-bp2	*62*								
bp3	59	---------	-------	-------	-------	-------	-------	-------	-------
bp3.5	*26*	---------	0.000	0.500	-------	0.000	0.655	0.206	0.937
bp4	*5*	---------	1.000	0.131	-------	0.073	**0.001**	0.393	0.350
bp5	*0*								
LXM1 HYPO*	140	0.6065	**0.444**	**0.008**	0.217	0.000	0.159	0.227	0.819
bp1-bp2	*140*								
bp3	*139*	---------	1.000	0.379	-------	0.000	0.181	0.312	0.998
bp3.5	*136*	---------	0.000	0.500	-------	0.082	**<0.001**	0.162	0.550
bp4	*100*	---------	**0.515**	**0.032**	0.308	0.000	0.354	0.427	0.599
bp5	*7*	---------	0.415	0.315	0.892	0.000	0.179	0.665	0.321
LXM3 HYPO	60	-0.2089	0.000	0.500	-------	0.108	**0.009**	0.657	**0.039**
bp1	*60*								
bp2	*53*	---------	0.000	0.500	-------	0.000	0.455	0.988	0.984
bp3	*34*	---------	0.490	0.214	0.662	0.047	**0.062**	0.770	**0.086**
bp3.5	*7*	----------	0.000	0.500	-------	0.377	**0.001**	**0.030**	**<0.001**
bp4	*1*	----------	0.000	0.500	-------	0.000	1.000	0.353	0.979
bp5	*0*								
LXM1 C5	135	-0.7101	0.000	0.500	-------	0.028	**0.048**	0.514	0.317
bp1	*82*	---------	0.187	0.237	0.297	0.000	0.152	0.987	0.662

bp2	*51*	---------	**0.000**	**0.500**	-------	0.019	**0.025**	0.460	0.161
bp3	*26*	---------	0.000	0.500	-------	0.021	**0.074**	0.108	**0.070**
bp4	*4*	---------	0.881	0.092	0.623	0.000	0.856	0.895	0.618
bp5	*1*	---------	0.000	0.500	-------	0.000	0.447	0.387	0.998
LXM2 C5	116	-0.7442	**0.420**	**0.007**	0.203	0.035	**0.078**	0.720	0.413
bp1	*75*	---------	**0.660**	**0.014**	0.336	0.040	**0.049**	0.798	0.291
bp2	*51*	---------	**0.816**	**0.004**	0.348	0.000	0.255	0.838	0.910
bp3	*36*	---------	0.093	0.381	0.458	0.000	0.247	0.475	0.926
bp4	*19*	---------	0.052	0.450	0.415	0.025	0.105	**0.038**	**0.060**
bp5	*8*	---------	0.000	0.500	-------	0.000	0.828	0.494	0.719
LXM3 C5	57	-0.8849	**0.787**	**0.021**	0.364	0.064	**0.011**	**0.008**	**0.015**
bp1	*47*	---------	0.000	0.500	-------	0.000	0.605	0.152	0.884
bp2	*42*	---------	0.259	0.425	1.458	0.041	0.298	**0.076**	0.223
bp3	*36*	---------	0.000	0.500	-------	0.019	0.105	**0.086**	**0.081**
bp4	*29*	---------	**1.000**	**0.029**	-------	0.140	**0.003**	**0.004**	**0.002**
bp5	*16*	---------	**1.000**	**0.009**	-------	0.364	**0.005**	**0.031**	**0.011**
LXM1 CARAB	121	-0.5209	**0.644**	**<0.001**	0.218	0.000	0.126	0.103	0.527
bp1	*104*	---------	**0.954**	**0.002**	0.370	0.025	**0.065**	0.232	0.203
bp2	*93*	---------	**0.722**	**0.014**	0.393	0.048	**0.035**	**0.075**	**0.052**
bp3	*89*	---------	**0.547**	**0.034**	0.345	0.000	0.657	0.124	0.436
bp4	*67*	---------	**0.561**	**0.026**	0.260	0.000	0.844	0.237	0.896
bp5	*60*	---------	**0.643**	**0.010**	0.325	0.000	0.674	0.215	0.997
bp6	*7*	---------	0.789	0.183	0.935	0.083	**0.016**	0.991	0.190
bp7	*6*	---------	0.631	0.207	0.840	0.000	0.165	0.903	0.609
LXM2 CARAB	88	-0.9447	**0.550**	**0.013**	0.275	0.000	0.510	0.130	0.187
bp1	*40*	---------	**0.619**	**0.038**	0.394	0.000	0.931	0.145	0.485
bp2	*23*	---------	0.491	0.107	0.420	0.016	0.219	0.456	**0.093**
bp3	*20*	---------	**0.817**	**0.028**	0.425	0.033	0.146	0.462	**0.031**
bp4	*10*	---------	0.000	0.500	-------	0.000	0.733	0.152	0.114
bp5	*9*	---------	0.000	0.500	-------	0.048	0.732	**0.075**	0.169
bp6-bp7	*0*								

LXM3 CARAB*	37	-0.2373	**0.932**	**0.032**	0.491	0.088	0.554	**0.056**	0.860
bp1	*12*	---------	**1.000**	**0.043**	-------	0.000	0.344	0.196	0.624
bp2	*9*	---------	1.000	0.080	-------	0.000	0.656	0.770	0.860
bp3	*7*	---------	0.000	0.500	-------	0.000	0.558	0.317	0.948
bp4	*5*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*4*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp7	*1*	---------	0.000	0.500	-------	0.000	0.674	0.169	0.998
LXM1 PARA*	137	-1.0062	**0.283**	**0.039**	0.191	0.019	0.182	**0.069**	0.887
bp1	*46*	---------	**0.444**	**0.044**	0.326	0.007	0.121	**0.071**	0.817
bp2	*1*	---------	1.000	0.375	-------	0.000	0.140	0.704	0.998
bp3	*1*	---------	1.000	0.375	-------	0.000	0.140	0.704	0.998
bp4-bp6	*0*								
LXM2 PARA*	116	25.8037	0.000	0.500	-------	0.011	**0.082**	0.400	0.195
bp1	*4*	---------	0.000	0.500	-------	0.000	0.136	0.804	0.338
bp2	*3*	---------	0.000	0.500	-------	0.000	0.135	0.532	0.218
bp3	*1*	---------	0.000	0.500	-------	0.000	0.363	0.231	0.977
bp4-bp6	*0*								
LXM3 PARA*	54	25.0000	0.000	0.500	-------	0.000	0.474	0.397	0.618
bp1	*2*	---------	0.106	0.485	2.660	0.000	0.562	0.400	0.802
bp2	*2*	---------	0.106	0.485	2.660	0.000	0.562	0.400	0.802
bp3	*1*	---------	0.000	0.500	-------	0.000	0.998	0.481	0.814
bp4-bp6	*0*								
LXI2 PEG[j]	144 *2*	---------	0.000	0.500	-------	0.000	0.718	0.135	0.996
LXM3 PEG[j]	68 *0*	---------	-------	-------	-------	-------	-------	-------	-------
LXI2 CONG ABS	147 *3*	---------	0.000	0.500	-------	0.000	0.221	0.877	0.307
LXP2 CONG ABS	141 *3*	---------	-------	-------	-------	-------	-------	-------	-------

LXM3 CONG ABS	71	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LNI1 SHOV	125	0.0983	**0.620**	**0.020**	0.243	0.000	0.137	0.202	0.919
bp1	*99*	---------	**1.000**	**0.002**	-------	0.063	**0.037**	0.486	0.681
bp2	*18*	---------	**0.823**	**0.027**	0.452	0.000	0.866	0.159	0.496
bp3	*1*	---------	1.000	0.410	-------	0.000	0.848	0.229	0.999
bp4-bp7	*0*								
LNI2 SHOV	140	0.2371	**0.542**	**0.001**	0.229	0.045	**0.057**	0.987	0.425
bp1	*110*	---------	**1.000**	**0.001**	-------	0.056	**0.006**	0.316	**0.093**
bp2	*15*	---------	0.216	0.300	0.437	0.000	0.790	0.603	0.813
bp3-bp7	*0*								
LNC DAR	129	-0.7829	**0.427**	**0.003**	0.196	0.151	0.223	**<0.001**	0.428
bp1	*76*	---------	**0.657**	**0.009**	0.331	0.078	0.778	**<0.001**	0.968
bp2	*43*	---------	**0.512**	**0.030**	0.339	0.099	0.531	**<0.001**	0.983
bp3	*8*	---------	0.819	0.164	0.786	0.228	**0.089**	**0.001**	1.000
bp4	*1*	---------	0.000	0.500	-------	0.000	0.729	0.257	0.997
bp5	*0*								
LNP1 ODONT	134	---------	0.000	0.500	-------	0.000	0.989	0.417	0.976
	2								
LNP2 ODONT	131	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LNM1 ANT FOVEA	129	-0.4180	**0.596**	**<0.001**	0.217	0.000	0.316	0.136	0.294
bp1	*126*	---------	0.000	0.500	-------	0.000	0.727	0.333	0.253
bp2	*94*	---------	**0.767**	**0.002**	0.306	0.026	0.616	**0.053**	0.688
bp3	*46*	---------	**0.727**	**0.004**	0.328	0.000	0.176	0.999	0.278
bp4	*9*	---------	0.919	0.095	0.546	0.000	0.517	0.144	0.464
LNM1 CNO	130	-0.0192	**0.485**	**<0.001**	0.173	0.057	**0.011**	0.614	0.575
bp5	*130*								
bp6	*96*	---------	**0.994**	**<0.001**	0.303	0.081	**0.004**	0.625	0.341
bp7	*1*	---------	0.000	0.500	-------	0.000	0.678	0.223	0.996
bp8	*0*								

LNM2 CNO	99	-0.3790	**0.250**	**0.098**	0.215	0.054	0.149	**0.088**	**0.078**
bp5	*93*	---------	0.829	0.117	0.671	0.147	1.000	**0.015**	1.000
bp6	*39*	---------	0.399	0.095	0.344	0.000	0.155	0.246	0.116
bp7	*2*	---------	1.000	0.106	-------	0.059	0.147	0.647	**0.076**
bp8	*0*								
LNM3 CNO	51	0.6581	0.000	0.500	-------	0.091	0.563	**0.019**	0.940
bp5	*49*	---------	0.000	0.500	-------	0.000	0.232	0.536	0.631
bp6	*33*	---------	0.000	0.500	-------	0.096	0.253	**0.007**	0.447
bp7	*3*	---------	1.000	0.225	-------	0.000	0.698	0.340	0.313
bp8	*0*								
LNM1 GROOVE	132	---------	-------	-------	-------	-------	-------	-------	-------
y	*111*	---------	**1.000**	**0.001**	-------	0.000	0.530	0.279	0.985
x	*2*	---------	0.000	0.500	-------	0.000	0.714	0.435	0.653
+	*19*	---------	**1.000**	**0.001**	-------	0.000	0.626	0.190	0.440
LNM2 GROOVE	100	---------	-------	-------	-------	-------	-------	-------	-------
y	*5*	---------	0.113	0.439	0.612	0.000	0.258	0.285	0.290
x	*47*	---------	0.095	0.381	0.339	0.024	0.470	**0.082**	0.325
+	*48*	---------	0.199	0.274	0.357	0.000	0.745	0.167	0.580
LNM3 GROOVE	52	---------	-------	-------	-------	-------	-------	-------	-------
y	*4*	---------	0.617	0.224	0.879	0.000	0.968	0.528	0.320
x	*38*	---------	0.299	0.264	0.499	0.000	0.991	0.798	0.613
+	*10*	---------	0.188	0.365	0.508	0.000	0.905	0.559	0.462
LNM1 DWRINK	134	-0.7450	0.149	0.159	0.168	0.000	0.272	0.487	0.457
bp1	*132*	---------	**1.000**	**0.029**	-------	0.000	0.206	0.347	0.342
bp2	*96*	---------	**0.489**	**0.039**	0.322	0.018	**0.090**	0.329	0.465
bp3	*34*	---------	0.055	0.417	0.270	0.000	0.782	0.834	0.668
LNM1 C5	133	0.0817	**0.613**	**<0.001**	0.227	0.000	0.526	0.220	0.214
bp1	*133*								
bp2	*129*	---------	0.000	0.500	-------	0.157	0.201	0.130	**0.003**
bp3	*116*	---------	**0.628**	**0.046**	0.429	0.044	0.695	0.921	**0.092**
bp4	*89*	---------	**0.543**	**0.022**	0.262	0.000	0.520	0.584	0.333

bp5	*13*	---------	**1.000**	**0.001**	-------	0.000	0.956	0.429	0.863
LNM2 C5	104	-0.6553	0.051	0.383	0.175	0.130	**0.067**	**0.001**	**0.068**
bp1	*98*	---------	0.812	0.126	0.611	0.160	1.000	**0.010**	1.000
bp2	*79*	---------	0.108	0.397	0.431	0.073	**0.069**	**0.013**	**0.059**
bp3	*46*	---------	0.065	0.412	0.306	0.048	0.538	**0.010**	0.420
bp4	*6*	---------	**1.000**	**0.047**	-------	0.144	**0.022**	0.121	**0.033**
bp5	*0*								
LNM3 C5	57	-0.9656	0.000	0.500	-------	0.000	0.472	0.754	0.810
bp1	*55*	---------	0.000	0.500	-------	0.000	0.329	0.392	0.597
bp2	*55*	---------	0.000	0.500	-------	0.000	0.330	0.393	0.801
bp3	*46*	---------	0.000	0.500	-------	0.000	0.880	0.742	0.244
bp4	*35*	---------	0.000	0.500	-------	0.000	0.920	0.493	0.471
bp5	*21*	---------	0.000	0.500	-------	0.000	0.267	0.859	0.106
LNM1 C6	131	-0.5182	**0.760**	**<0.001**	0.183	0.029	**0.062**	0.994	0.690
bp1	*96*	---------	**1.000**	**<0.001**	-------	0.083	**0.004**	0.554	0.337
bp2	*46*	---------	**1.000**	**<0.001**	-------	0.000	0.480	0.822	0.853
bp3	*15*	---------	**0.795**	**0.024**	0.433	0.000	0.915	0.722	0.951
bp4	*4*	---------	**1.000**	**0.014**	-------	0.000	0.264	0.555	0.187
bp5	*2*	---------	0.000	0.500	-------	0.034	0.266	0.846	**0.042**
LNM3 C6	53	-0.4301	0.204	0.309	0.428	0.156	0.405	**0.003**	0.427
bp1	*33*	---------	0.000	0.500	-------	0.109	0.329	**0.006**	0.310
bp2	*25*	---------	0.416	0.266	0.726	0.146	0.224	**0.001**	0.201
bp3	*16*	---------	0.699	0.176	0.375	0.093	0.871	**0.025**	0.755
bp4	*8*	---------	0.025	0.488	0.890	0.000	0.176	0.192	0.404
bp5	*1*	---------	0.094	0.500	3.637	0.000	0.221	0.819	0.996
LNM1 C7*	142	4.7415	0.093	0.203	0.127	0.047	**0.057**	**0.089**	0.612
bp1	*17*	---------	0.160	0.301	0.343	0.000	0.231	0.166	0.789
bp1a	*9*	---------	0.268	0.225	0.406	0.000	0.217	0.141	0.467
bp2	*8*	---------	0.651	0.093	0.615	0.039	0.356	**0.058**	0.372
bp3	*5*	---------	0.651	0.093	0.615	0.039	0.356	**0.058**	0.372
bp4	*1*	---------	0.000	0.500	-------	0.000	0.277	0.554	0.999

LNM2 C7*	127	8.2481	0.000	0.500	-------	0.000	0.841	0.405	0.649
bp1	*11*	---------	0.000	0.500	-------	0.000	0.843	0.179	0.503
bp1a	*4*	---------	0.000	0.500	-------	0.000	0.699	0.280	0.360
bp2	*1*	---------	0.000	0.500	-------	0.129	0.988	**<0.001**	0.998
bp3-bp4	*0*								
LNM3 C7*	59	2.5291	0.049	0.428	0.278	0.000	0.443	0.462	0.256
bp1	*9*	---------	0.093	0.452	0.784	0.000	0.288	0.421	0.177
bp1a	*8*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*8*	---------	-------	-------	-------	-------	-------	-------	-------
bp3	*6*	---------	0.241	0.382	0.839	0.000	0.420	0.188	0.341
bp4	*6*	---------	0.241	0.382	0.843	0.000	0.424	0.190	0.344
LNM1 DTCREST	139	---------	**0.563**	**0.038**	0.356	0.000	0.112	0.535	0.492
	16								
LNM2 DTCREST	129	---------	0.000	0.500	-------	0.000	0.132	0.899	1.000
	1								
LNM3 DTCREST	60	---------	0.791	0.193	1.105	0.000	0.645	0.337	0.794
	4								
LNI1 CONG ABS	152	---------	-------	-------	-------	-------	-------	-------	-------
	0								
LNP2 CONG ABS	136	---------	-------	-------	-------	-------	-------	-------	-------
	4								
LNM3 CONG ABS	75	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RXI1 WING	144	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*8*	---------	**1.000**	**0.015**	-------	0.120	0.906	0.552	**0.096**
bp2	*11*	---------	0.000	0.500	-------	0.000	0.180	0.796	0.442
bp3	*110*	---------	0.008	0.486	0.208	0.000	0.825	0.704	0.468
bp4	*15*	---------	**1.000**	**0.013**	-------	0.000	0.117	0.781	0.165
RXI1 SHOV	140	0.0716	**0.312**	**0.029**	0.187	0.000	0.127	0.415	0.123
bp1	*138*	---------	0.000	0.500	-------	0.000	0.249	0.816	0.252
bp2	*116*	---------	**0.175**	**0.325**	0.391	0.000	0.408	0.794	0.306

bp3	*37*	---------	**0.472**	**0.036**	0.283	0.002	**0.086**	0.450	0.125
bp4	*4*	---------	**1.000**	**0.044**	-------	0.000	0.613	0.231	0.496
bp5-bp7	*0*								
RXI2 SHOV	136	-0.3618	**0.397**	**0.024**	0.239	0.070	0.621	**0.006**	0.604
bp1	*126*	---------	0.000	0.500	-------	0.214	0.427	<**0.001**	1.000
bp2	*72*	---------	0.358	0.080	0.193	0.016	0.931	**0.068**	0.603
bp3	*19*	---------	0.056	0.454	0.501	0.000	0.441	0.110	0.746
bp4	*4*	---------	**1.000**	**0.044**	-------	0.000	0.204	0.208	0.697
bp5	*2*	---------	0.000	0.500	-------	0.129	0.721	**0.098**	0.995
bp6	*2*	---------	0.000	0.500	-------	0.129	0.721	**0.098**	0.995
bp7	*1*	---------	0.000	0.500	-------	0.000	0.656	0.346	0.997
RXC SHOV	127	-0.2392	**0.485**	**0.001**	0.181	0.060	**0.003**	0.654	**0.029**
bp1	*105*	---------	0.471	0.124	0.445	0.066	**0.010**	0.812	**0.014**
bp2	*39*	---------	**0.726**	**0.004**	0.227	0.017	**0.039**	0.347	0.196
bp3	*11*	---------	0.628	0.060	0.454	0.000	0.140	0.292	0.771
bp4	*1*	---------	0.000	0.500	-------	0.000	1.000	0.426	0.807
bp5-bp7	*0*								
RXI1 DSHOV	138	-0.2251	**0.280**	**0.019**	0.164	0.000	0.887	0.299	0.438
bp1	*129*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*74*	---------	**0.628**	**0.002**	0.063	0.000	0.824	0.673	0.700
bp3	*3*	---------	0.000	0.500	-------	0.000	0.313	0.288	0.572
bp4-bp6	*0*								
RXI2 DSHOV	137	-0.2465	**0.348**	**0.007**	0.181	0.014	**0.040**	**0.090**	0.119
bp1	*125*	---------	0.000	0.500	-------	0.057	**0.067**	0.318	**0.023**
bp2	*63*	---------	**0.450**	**0.019**	0.252	0.000	0.169	0.205	0.578
bp3	*13*	---------	0.448	0.103	0.395	0.000	0.366	0.208	0.523
bp4-bp7	*0*								
RXC DSHOV	122	-0.1567	0.112	0.240	0.173	0.000	0.397	0.225	0.364
bp1	*116*	---------	0.000	0.500	-------	0.123	**0.073**	0.179	**0.074**
bp2	*71*	---------	0.190	0.235	0.829	0.000	0.559	0.592	0.416
bp3	*17*	---------	0.482	0.144	0.483	0.000	0.811	0.390	0.796

bp4	*3*	---------	0.000	0.500	-------	0.411	0.986	**0.052**	1.000
bp5-bp6	*0*								
RXP1 DSHOV	133	-0.3924	0.228	0.055	0.171	0.000	0.308	0.253	0.218
bp1	*117*	---------	0.184	0.316	0.410	0.013	0.228	0.819	**0.089**
bp2	*79*	---------	0.207	0.185	0.253	0.000	0.503	0.266	0.528
bp3	*24*	---------	0.503	0.069	0.816	0.000	0.320	0.164	0.313
bp4	*3*	---------	0.878	0.092	0.702	0.000	0.607	0.807	0.797
bp5-bp6	*0*								
RXI1 TD	137	-0.0127	**0.225**	**0.095**	0.197	0.090	**0.010**	**0.011**	**0.027**
bp1	*136*	---------	0.000	0.500	-------	0.000	1.000	0.351	1.000
bp2	*112*	---------	0.560	0.100	0.473	0.086	**0.005**	**0.006**	**0.012**
bp3	*68*	---------	0.000	0.500	-------	0.066	**0.003**	**0.009**	**0.011**
bp4	*19*	---------	0.160	0.319	0.353	0.000	0.176	0.120	0.233
bp5-	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*2*	---------	**1.000**	**0.050**	-------	0.150	1.000	**<0.001**	0.971
RXI2 TD	112	-0.4310	**0.337**	**0.019**	0.196	0.000	0.796	0.129	0.827
bp1	*98*	---------	**0.989**	**0.002**	0.375	0.000	0.687	0.401	0.778
bp2	*80*	---------	**0.528**	**0.035**	0.340	0.054	0.722	**0.005**	0.773
bp3	*38*	---------	0.403	0.096	0.352	0.000	0.757	0.605	0.580
bp4	*22*	---------	0.188	0.287	0.741	0.000	0.729	0.897	0.675
bp5-	*11*	---------	0.166	0.360	0.464	0.000	0.432	0.576	0.573
bp5	*4*	---------	0.000	0.500	-------	0.146	**0.029**	0.370	**0.014**
bp6	*0*								
RXC TD	121	0.0694	**0.532**	**0.001**	0.204	0.120	**0.006**	**0.001**	**0.061**
bp1	*121*								
bp2	*114*	---------	**0.876**	**0.026**	0.502	0.000	0.258	0.287	0.377
bp3	*75*	---------	0.322	0.168	0.492	0.073	**0.003**	**0.007**	0.127
bp4	*49*	---------	0.223	0.190	0.276	0.121	**0.001**	**<0.001**	**0.020**
bp5-	*19*	---------	**1.000**	**0.001**	-------	0.046	0.166	**0.029**	0.145
bp5	*16*	---------	**0.995**	**0.026**	0.502	0.075	0.112	**0.001**	0.145

bp6	*2*	---------	0.000	0.500	-------	0.169	**0.081**	0.556	1.000
RXC MES RIDGE	129	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp2-bp3	*0*								
RXC DAR	126	-0.0942	**0.414**	**0.003**	0.193	0.116	0.735	**<0.001**	0.193
bp1	*121*	---------	0.000	0.500	-------	0.000	0.570	0.262	0.984
bp2	*112*	---------	0.430	0.135	0.409	0.000	0.875	0.231	0.762
bp3	*66*	---------	**0.662**	**0.006**	0.323	0.079	0.602	<**0.001**	0.539
bp4	*10*	---------	0.806	0.091	0.611	0.114	0.231	**0.036**	0.466
bp5	*0*								
RXP1 UTO AZ	141	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RXP1 ODONT	136	---------	0.000	0.500	-------	0.000	0.543	0.926	1.000
	2								
RXP2 ODONT	130	---------	0.000	0.500	-------	0.000	1.000	0.457	0.699
	1								
RXM1 META	145	0.7566	0.166	0.151	0.182	0.000	0.782	0.323	0.594
bp1-bp3.5	*145*								
bp4	*139*	---------	0.000	0.500	-------	0.046	**0.056**	0.328	0.213
bp5	*32*	---------	0.406	0.098	0.348	0.000	0.183	0.489	0.178
RXM2 META	126	-0.4288	**0.340**	**0.013**	0.193	0.000	0.110	0.225	0.543
bp1-bp3	*126*								
bp3.5	*111*	---------	0.000	0.500	-------	0.078	**0.008**	0.781	**0.061**
bp4	*58*	---------	**0.718**	**0.003**	0.307	0.000	0.448	0.164	0.878
bp5	*3*	---------	0.000	0.500	-------	0.000	0.409	0.517	0.195
RXM3 META	60	-0.2809	0.000	0.500	-------	0.000	0.869	0.602	0.480
bp1-bp2	*60*								
bp3	*54*	---------	0.000	0.500	-------	0.000	0.341	0.817	0.425
bp3.5	*23*	---------	0.717	0.186	0.665	0.000	0.646	0.523	0.374
bp4	*6*	---------	0.611	0.217	0.778	0.000	0.538	0.958	0.664
bp5	*0*								

RXM1 HYPO	144	0.3754	**0.780**	**<0.001**	0.213	0.000	0.944	0.134	0.319
bp1	*144*								
bp2	*143*	---------	0.000	0.500	-------	0.000	0.999	0.468	0.989
bp3	*143*	---------	0.000	0.500	-------	0.000	0.999	0.468	0.989
bp3.5	*138*	---------	0.000	0.500	-------	0.000	0.557	0.527	0.659
bp4	*101*	---------	**1.000**	**<0.001**	-------	0.019	0.511	**0.053**	0.784
bp5	*11*	---------	0.616	0.130	0.586	0.000	0.910	0.951	0.800
RXM3 HYPO	50	-0.1005	0.000	0.500	-------	0.041	**0.043**	0.245	0.201
bp1	*49*	---------	1.000	0.418	-------	0.282	1.000	0.799	**0.074**
bp2	*43*	---------	0.000	0.500	-------	0.003	**0.036**	0.972	0.244
bp3	*34*	---------	0.000	0.500	-------	0.000	0.267	0.768	0.752
bp3.5	*10*	---------	0.000	0.500	-------	0.000	0.102	0.109	0.178
bp4	*2*	---------	0.000	0.499	-------	0.471	**0.089**	**0.039**	0.982
bp5	*0*								
RXM1 C5	137	-0.6941	**0.355**	**0.034**	0.215	0.102	**0.014**	0.486	0.630
bp1	*94*	---------	0.086	0.392	0.522	0.038	0.237	**0.041**	0.957
bp2	*53*	---------	0.413	0.122	0.431	0.084	**0.006**	0.791	0.497
bp3	*23*	---------	0.337	0.164	0.379	0.000	0.118	0.362	0.548
bp4	*7*	---------	0.010	0.494	0.554	0.044	**0.029**	0.511	0.101
bp5	*0*								
RXM2 C5	113	-0.9005	**0.612**	**0.002**	0.258	0.075	**0.003**	**0.097**	**0.053**
bp1	*79*	---------	0.521	0.067	0.416	0.041	**0.035**	**0.056**	0.210
bp2	*58*	---------	**0.795**	**0.006**	0.381	0.031	**0.011**	0.165	**0.023**
bp3	*38*	---------	**0.581**	**0.024**	0.348	0.019	**0.062**	0.906	0.193
bp4	*19*	---------	0.584	0.070	0.435	0.000	0.162	0.307	0.859
bp5	*7*	---------	1.000	0.062	-------	0.173	**0.003**	0.326	**0.030**
RXM3 C5	50	-1.0542	0.057	0.441	0.401	0.000	0.994	0.288	0.362
bp1	*43*	---------	0.000	0.500	-------	0.170	1.000	**0.013**	0.993
bp2	*43*	---------	0.000	0.500	-------	0.170	1.000	**0.013**	0.993
bp3	*38*	---------	0.000	0.500	-------	0.000	0.509	0.313	0.534
bp4	*31*	---------	0.000	0.500	-------	0.000	0.321	0.169	0.105

bp5	*15*	---------	0.606	0.185	0.900	0.000	0.687	0.811	0.434
RXM1 CARAB	113	-0.6051	**0.715**	**0.001**	0.260	0.000	0.667	0.130	0.678
bp1	*97*	---------	**1.000**	**0.024**	-------	0.000	0.297	0.358	0.846
bp2	*90*	---------	**1.000**	**0.008**	-------	0.001	0.481	**0.023**	0.950
bp3	*85*	---------	**0.539**	**0.071**	0.408	0.031	0.627	**0.057**	0.679
bp4	*61*	---------	**0.886**	**0.003**	0.357	0.032	0.495	**0.032**	0.331
bp5	*51*	---------	**0.942**	**0.002**	0.004	0.000	0.787	0.252	0.642
bp6	*7*	---------	0.277	0.334	0.678	0.000	0.219	0.514	0.454
bp7	*7*	---------	0.277	0.334	0.678	0.000	0.219	0.514	0.454
RXM2 CARAB	91	-0.8670	**0.585**	**0.009**	0.279	0.016	0.284	0.365	**0.081**
bp1	*35*	---------	0.502	0.061	0.368	0.000	0.265	0.300	0.175
bp2	*19*	---------	0.745	0.051	0.444	0.041	0.363	0.427	**0.066**
bp3	*18*	---------	0.635	0.109	0.137	0.000	0.589	0.628	0.115
bp4	*8*	---------	0.000	0.500	-------	0.123	0.594	0.577	**0.036**
bp5	*8*	---------	0.000	0.500	-------	0.001	0.611	0.577	**0.036**
bp6-bp7	*0*								
RXM3 CARAB	29	-1.0833	0.438	0.278	0.740	0.000	0.644	0.604	0.873
bp1	*14*	---------	0.000	0.500	-------	0.000	0.434	0.483	0.809
bp2	*13*	---------	0.000	0.500	-------	0.000	0.312	0.659	0.523
bp3	*12*	---------	0.000	0.500	-------	0.000	0.434	0.849	0.333
bp4	*9*	---------	0.547	0.381	1.721	0.000	0.666	0.854	0.390
bp5	*6*	---------	1.000	0.200	-------	0.000	0.937	0.854	0.972
bp6	*3*	---------	1.000	0.069	-------	0.000	0.765	0.849	0.452
bp7	*3*	---------	1.000	0.069	-------	0.000	0.765	0.849	0.452
RXM1 PARA	126	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*35*	---------	**0.350**	**0.076**	0.288	0.033	**0.034**	**0.083**	0.185
bp2-bp6	*0*								
RXM2 PARA*	110	15.3217	0.166	0.216	0.238	0.000	0.971	0.132	0.939
bp1	*6*	---------	0.629	0.228	0.905	0.000	0.995	0.132	0.886
bp2	*5*	---------	0.000	0.500	-------	0.000	0.676	0.249	0.891
bp3	*2*	---------	0.000	0.500	-------	0.000	0.730	0.139	1.000

bp4	*1*	---------	0.000	0.500	-------	0.000	0.374	0.242	0.973
bp5	*1*	---------	0.000	0.500	-------	0.000	0.374	0.242	0.973
bp6	*0*								
RXM3 PARA	49	49.0000	**1.000**	**0.002**	-------	0.000	0.425	0.135	0.445
bp1	*1*	---------	1.000	0.324	-------	0.000	0.616	0.127	0.990
bp2	*1*	---------	1.000	0.324	-------	0.000	0.616	0.127	0.990
bp3-bp6	*0*								
RXI2 PEG[j]	143	---------	-------	-------	-------	-------	-------	-------	-------
	1	---------	0.000	0.500	-------	0.000	0.603	0.355	0.997
RXM3 PEG[j]	70	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RXI2 CONG ABS	148	---------	1.000	0.350	-------	0.000	0.920	0.990	0.880
	2								
RXP2 CONG ABS	135	---------	-------	-------	-------	-------	-------	-------	-------
	2								
RXM3 CONG ABS	70	---------	-------	-------	-------	-------	-------	-------	-------
	0								
RNI1 SHOV	129	-0.3747	**0.767**	**<0.001**	0.197	0.045	**0.049**	**0.044**	0.431
bp1	*97*	---------	**1.000**	**<0.001**	-------	0.046	**0.038**	**0.049**	0.278
bp2	*19*	---------	**1.000**	**0.001**	-------	0.000	0.327	0.171	0.882
bp3-bp7	*0*								
RNI2 SHOV	139	0.0689	**0.402**	**0.015**	0.227	0.000	0.176	0.708	0.306
bp1	*119*	---------	0.504	0.122	0.500	0.025	**0.081**	0.996	0.326
bp2	*26*	---------	**1.000**	**<0.001**	-------	0.000	0.685	0.578	0.693
bp3-bp7	*0*								
RNC DAR	120	-0.5867	0.163	0.163	0.187	0.198	**0.099**	**<0.001**	0.609
bp1	*55*	---------	0.008	0.488	0.254	0.093	0.742	<**0.001**	0.427
bp2	*32*	---------	0.517	0.066	0.373	0.182	0.123	**<0.001**	0.642
bp3	*6*	---------	0.000	0.500	-------	0.048	0.198	**0.034**	0.383
bp4	*2*	---------	0.000	0.500	-------	0.193	**0.018**	0.345	0.960
bp5	*0*								

RNP1 ODONT	137 *0*	---------	-------	-------	-------	-------	-------	-------	-------
RNP2 ODONT	130 *1*	---------	0.000	0.500	-------	0.000	1.000	0.622	0.529
RNM1 ANT FOV	130	-0.3965	**0.358**	**0.022**	0.210	0.000	0.157	0.526	0.357
bp1	*121*	---------	**0.917**	**0.044**	0.657	0.062	0.722	**0.034**	0.377
bp2	*96*	---------	0.073	0.398	0.240	0.007	0.018	0.898	0.107
bp3	*51*	---------	**0.658**	**0.014**	0.340	0.000	0.371	0.784	0.667
bp4	*8*	---------	0.704	0.079	0.530	0.000	0.302	0.991	0.256
RNM1 CNO	137	0.1181	**0.374**	**0.005**	0.176	0.000	0.964	0.759	0.122
bp5	*135*	---------	**1.000**	**0.036**	-------	0.000	1.000	0.248	0.994
bp6	*102*	---------	**0.635**	**0.014**	0.341	0.000	0.923	0.924	0.198
bp7-bp8	*0*								
RNM2 CNO	97	-0.3364	0.000	0.500	-------	0.000	0.976	0.391	0.820
bp5	*88*	---------	0.116	0.415	0.495	0.000	0.336	0.824	0.148
bp6	*35*	---------	0.000	0.500	-------	0.000	0.410	0.281	0.489
bp7	*1*	---------	0.000	0.500	-------	0.000	0.218	0.679	0.997
bp8	*0*								
RNM3 CNO	54	-0.3251	0.474	0.095	0.387	0.027	0.341	**0.091**	0.583
bp5	*53*	---------	0.000	0.500	-------	0.000	0.890	0.492	0.983
bp6	*39*	---------	0.616	0.160	0.645	0.000	0.371	0.127	0.474
bp7-bp8	*0*								
RNM1 GROOVE	129	---------	-------	-------	-------	-------	-------	-------	-------
y	*104*	---------	**0.849**	**0.003**	0.352	0.020	0.449	**0.064**	0.950
x	*6*	---------	**1.000**	**0.028**	-------	0.192	0.869	**0.004**	0.999
+	*19*	---------	**1.000**	**<0.001**	-------	0.000	0.435	0.627	0.941
RNM2 GROOVE	108	---------	-------	-------	-------	-------	-------	-------	-------
y	*2*	---------	-------	-------	-------	-------	-------	-------	-------
x	*55*	---------	0.301	0.115	0.279	0.000	0.323	0.432	0.655
+	*51*	---------	0.328	0.097	0.280	0.000	0.297	0.348	0.294
RNM3 GROOVE	53	---------	-------	-------	-------	-------	-------	-------	-------

y	*3*	---------	0.841	0.176	0.866	0.134	1.000	**0.045**	0.993
x	*40*	---------	**1.000**	**0.016**	-------	0.109	0.914	**0.017**	0.565
+	*10*	---------	**1.000**	**0.041**	-------	0.000	0.794	0.132	0.414
RNM1 DWRINK	129	-0.4875	**0.355**	**0.017**	0.200	0.000	0.375	0.139	0.372
bp1	*128*	---------	0.000	0.500	-------	0.000	0.626	0.286	0.996
bp2	*95*	---------	**0.534**	**0.048**	0.362	0.000	0.413	0.549	0.262
bp3	*24*	---------	0.484	0.085	0.403	0.000	0.560	0.106	0.694
RNM1 C5	137	-0.0393	**0.547**	**<0.001**	0.203	0.000	0.519	0.362	0.884
bp1	*135*	---------	**1.000**	**0.029**	-------	0.000	0.998	0.325	0.993
bp2	*134*	---------	**1.000**	**0.079**	-------	0.098	0.223	0.921	**0.054**
bp3	*116*	---------	**1.000**	**0.001**	-------	0.000	0.516	0.637	0.583
bp4	*79*	---------	**0.663**	**0.004**	0.321	0.000	0.922	0.470	0.670
bp5	*4*	---------	1.000	0.052	-------	0.104	**0.053**	0.277	**0.019**
RNM2 C5	102	-0.6412	0.135	0.212	0.183	0.058	**0.028**	0.236	**0.068**
bp1	*92*	---------	0.000	0.500	-------	0.000	0.260	0.671	0.192
bp2	*75*	---------	0.000	0.500	-------	0.025	**0.001**	0.552	0.185
bp3	*28*	---------	0.143	0.318	0.267	0.000	0.284	0.217	0.314
bp4	*3*	---------	1.000	0.168	-------	0.307	**0.012**	0.751	1.000
bp5	*0*								
RNM3 C5	63	-0.5032	0.000	0.500	-------	0.000	0.148	0.313	0.175
bp1	*62*	---------	0.000	0.500	-------	0.110	0.999	**<0.001**	0.984
bp2	*59*	---------	0.000	0.500	-------	0.000	0.850	0.611	0.400
bp3	*50*	---------	0.000	0.500	-------	0.016	0.691	**0.065**	0.772
bp4	*23*	---------	0.000	0.500	-------	0.000	0.260	0.470	0.152
bp5	*12*	---------	0.000	0.500	-------	0.044	**0.028**	0.847	0.146
RNM1 C6	137	-0.5650	**0.600**	**<0.001**	0.179	0.000	0.279	0.849	0.566
bp1	*102*	---------	**0.635**	**0.014**	0.324	0.000	0.923	0.924	0.198
bp2	*46*	---------	**0.924**	**<0.001**	0.278	0.000	0.129	0.368	0.963
bp3	*19*	---------	**1.000**	**<0.001**	-------	0.013	**0.044**	0.351	0.187
bp4	*7*	---------	0.828	0.105	0.656	0.000	0.496	0.930	0.871
bp5	*2*	---------	0.000	0.500	-------	0.000	0.372	0.976	0.217

RNM3 C6	56	-0.8007	0.007	0.492	0.372	0.000	0.483	0.134	0.424
bp1	*42*	---------	1.000	0.073	-------	0.067	0.356	**0.025**	0.445
bp2	*36*	---------	0.133	0.428	0.151	0.048	0.738	**0.068**	0.930
bp3	*23*	---------	**1.000**	**0.035**	-------	0.117	0.262	**0.002**	**0.004**
bp4	*12*	---------	0.000	0.500	-------	0.000	0.818	0.595	0.261
bp5	*5*	---------	0.000	0.500	-------	0.000	1.000	0.316	0.846
RNM1 C7*	145	6.7961	**0.182**	**0.037**	0.128	0.031	**0.032**	0.656	0.287
bp1	*14*	---------	**0.491**	**0.039**	0.360	0.000	0.312	0.955	0.875
bp1a	*9*	---------	0.298	0.245	0.489	0.090	**0.063**	0.832	0.796
bp2	*9*	---------	0.298	0.245	0.488	0.090	**0.063**	0.832	0.796
bp3	*3*	---------	0.000	0.500	-------	0.220	**0.026**	0.869	**0.077**
bp4	*1*	---------	1.000	0.377	-------	0.000	0.977	0.223	1.000
RNM2 C7*	124	10.3317	**0.707**	**0.002**	0.237	0.000	0.596	0.172	0.862
bp1	*9*	---------	**1.000**	**0.030**	-------	0.000	0.342	0.159	0.895
bp1a	*2*	---------	1.000	0.379	-------	0.000	0.857	0.917	0.615
bp2	*2*	---------	1.000	0.379	-------	0.000	0.857	0.917	0.615
bp3-bp4	*0*								
RNM3 C7*	59	2.8693	0.000	0.500	-------	0.000	0.884	0.921	0.501
bp1	*8*	---------	0.000	0.500	-------	0.000	0.913	0.797	0.499
bp1a	*8*	---------	0.000	0.500	-------	0.000	0.916	0.885	0.367
bp2	*8*	---------	0.000	0.500	-------	0.000	0.916	0.885	0.367
bp3	*8*	---------	0.000	0.500	-------	0.000	0.916	0.885	0.367
bp4	*6*	---------	0.000	0.500	-------	0.000	0.916	0.885	0.367
RNM1 DTCREST	134	---------	0.364	0.091	0.303	0.000	0.487	0.172	0.821
	23								
RNM2 DTCREST	128	---------	0.000	0.500	-------	0.000	0.707	0.897	0.916
	2								
RNM3 DTCREST	62	---------	**1.000**	**0.013**	-------	0.000	0.365	0.880	0.818
	9								
RNI1 CONG ABS	151	---------	-------	-------	-------	-------	-------	-------	-------
	0								

RNP2 CONG ABS	137	---------	-------	-------	-------	-------	-------	-------	-------
	5								
RNM3 CONG ABS	73	---------	-------	-------	-------	-------	-------	-------	-------
	0								
XI1 SHOV	142	0.0825	**0.345**	**0.017**	0.188	0.000	0.434	0.353	0.586
bp1	*141*	---------	0.000	0.500	-------	0.000	1.000	0.215	0.997
bp2	*130*	---------	0.547	0.146	0.529	0.000	0.579	0.987	0.622
bp3	*51*	---------	**0.523**	**0.025**	0.312	0.000	0.149	0.181	0.395
bp4	*9*	---------	0.287	0.306	0.614	0.000	0.891	0.907	0.748
bp5-bp7	*0*								
XI2 SHOV	140	-0.2551	**0.533**	**0.001**	0.199	0.040	0.465	**0.052**	0.831
bp1	*136*	---------	0.000	0.500	-------	0.159	1.000	**0.030**	0.708
bp2	*97*	---------	0.402	0.076	0.326	0.034	0.951	**0.014**	0.539
bp3	*36*	---------	**1.000**	**<0.001**	-------	0.000	0.314	0.673	0.575
bp4	*6*	---------	**1.000**	**0.032**	-------	0.000	0.232	0.940	0.596
bp5	*2*	---------	0.000	0.500	-------	0.132	0.725	**0.086**	0.995
bp6	*2*	---------	0.000	0.500	-------	0.131	0.725	**0.086**	0.995
bp7	*1*	---------	0.000	0.500	-------	0.000	0.650	0.351	0.997
XC SHOV	128	0.1638	**0.601**	**<0.001**	0.171	0.077	**0.002**	0.248	0.104
bp1	*119*	---------	0.818	0.095	0.615	0.080	**0.012**	0.258	**0.022**
bp2	*48*	---------	**0.809**	**0.001**	0.312	0.064	**0.007**	0.312	0.169
bp3	*14*	---------	**0.861**	**0.006**	0.265	0.000	0.265	0.251	0.933
bp4	*1*	---------	0.000	0.500	-------	0.000	1.000	0.425	1.000
bp5-bp7	*0*								
XI1 DSHOV	140	0.1974	0.145	0.138	0.150	0.033	0.683	**0.072**	0.126
bp1	*133*	---------	0.000	0.500	-------	0.197	0.478	**0.003**	0.999
bp2	*91*	---------	**0.504**	**0.016**	0.426	0.000	0.575	0.142	0.170
bp3	*7*	---------	**0.940**	**0.048**	0.581	0.000	0.842	0.703	0.634
bp4	*1*	---------	0.000	0.500	-------	0.000	0.917	0.279	1.000
bp5-bp6	*0*								
XI2 DSHOV	141	-0.1958	**0.529**	**<0.001**	0.196	0.015	**0.020**	**0.056**	0.103

bp1	*133*	---------	-------	-------	-------	-------	-------	-------	-------
bp2	*83*	---------	**0.693**	**0.002**	0.301	0.015	**0.047**	0.151	0.261
bp3	*20*	---------	0.332	0.122	0.318	0.000	0.954	0.158	0.903
bp4	*2*	---------	**1.000**	**0.024**	-------	0.000	0.486	0.946	0.721
bp5-bp6	*0*								
XC DSHOV	130	-0.1864	0.172	0.100	0.156	0.000	0.218	0.932	0.575
bp1	*125*	---------	0.000	0.500	-------	0.182	**0.020**	0.939	**0.029**
bp2	*91*	---------	0.014	0.477	0.241	0.000	0.529	0.938	0.514
bp3	*33*	---------	0.292	0.124	0.298	0.000	0.484	0.899	0.772
bp4	*6*	---------	0.000	0.500	-------	0.015	0.405	0.329	**0.011**
bp5	*1*	---------	0.000	0.500	-------	0.000	1.000	0.434	1.000
bp6	*0*								
XP1 DSHOV	136	-0.2579	**0.423**	**0.004**	0.196	0.000	0.243	0.734	0.203
bp1	*127*	---------	0.000	0.500	-------	0.000	0.141	0.599	**0.024**
bp2	*104*	---------	**0.667**	**0.016**	0.339	0.000	0.127	0.413	0.250
bp3	*42*	---------	0.397	0.088	0.337	0.000	0.689	0.890	0.561
bp4	*4*	---------	**1.000**	**0.006**	-------	0.000	0.701	0.963	0.590
bp5-bp6	*0*								
XI1 TD	141	-0.0579	**0.366**	**0.014**	0.196	0.115	**0.011**	**0.001**	**0.008**
bp1	*139*	---------	0.000	0.500	-------	0.000	1.000	0.132	1.000
bp2	*123*	---------	0.094	0.415	0.464	0.120	**0.024**	**0.001**	**0.018**
bp3	*87*	---------	**0.414**	0.086	0.335	0.061	**0.004**	**0.010**	**0.013**
bp4	*34*	---------	0.423	0.102	0.383	0.075	**0.057**	**0.004**	**0.055**
bp5-	*4*	---------	0.861	0.106	2.107	0.000	0.761	0.611	0.363
bp5	*3*	---------	-------	-------	-------	-------	-------	-------	-------
bp6	*2*	---------	1.000	0.044	-------	0.145	1.000	**<0.001**	0.992
XI2 TD	129	-0.3759	**0.482**	**0.002**	0.209	0.000	0.732	0.194	0.655
bp1	*117*	---------	**0.938**	**0.009**	0.441	0.000	0.842	0.228	0.485
bp2	*99*	---------	**0.866**	**0.004**	-------	0.000	0.304	0.136	0.429
bp3	*58*	---------	0.266	0.156	0.297	0.000	0.701	0.113	0.953
bp4	*32*	---------	**0.629**	**0.023**	0.379	0.000	0.383	0.941	0.200

bp5-	*13*	---------	0.403	0.185	0.323	0.000	0.750	0.995	0.818
bp5	*5*	---------	0.619	0.196	0.777	0.076	**0.097**	0.686	**0.093**
bp6	*1*	---------	0.000	0.500	-------	0.000	0.566	0.993	0.242
XC TD	129	-0.3179	**0.686**	**<0.001**	0.215	0.129	**0.014**	**<0.001**	**0.065**
bp1	*129*								
bp2	*121*	---------	0.743	0.130	0.702	0.048	0.102	**0.040**	**0.077**
bp3	*88*	---------	**0.750**	**0.019**	0.410	0.089	**0.002**	**0.001**	**0.017**
bp4	*58*	---------	0.396	0.066	0.300	0.108	**0.003**	**<0.001**	**0.018**
bp5-	*25*	---------	**1.000**	**0.001**	-------	0.079	0.556	**0.002**	0.752
bp5	*19*	---------	**0.939**	**0.010**	0.444	0.081	0.266	**0.002**	0.472
bp6	*3*	---------	0.000	0.500	-------	0.147	0.716	**0.066**	0.999
XC MES RIDGE	133	---------	-------	-------	-------	-------	-------	-------	-------
bp1	*1*	---------	-------	-------	-------	-------	-------	-------	-------
bp2-bp3	*0*								
XC DAR	130	-0.0508	**0.419**	**0.002**	0.186	0.167	0.695	**<0.001**	0.305
bp1	*126*	---------	0.000	0.500	-------	0.607	1.000	**<0.001**	0.997
bp2	*121*	---------	**0.704**	**0.049**	0.484	0.000	0.458	0.299	0.780
bp3	*78*	---------	**0.474**	**0.031**	0.932	0.106	0.390	<**0.001**	0.384
bp4	*15*	---------	**0.340**	**0.241**	0.517	0.144	0.857	**0.001**	0.918
bp5	*1*	---------	0.000	0.500	-------	0.000	0.964	0.269	1.000
XP1 UTO AZ	143	---------	-------	-------	-------	-------	-------	-------	-------
	0								
XP1 ODONT	142	---------	0.000	0.500	-------	0.000	0.685	0.610	0.750
	3								
XP2 ODONT	136	---------	0.000	0.500	-------	0.000	1.000	0.414	0.989
	1								
XM1 META	146	0.4312	0.211	0.088	0.179	0.019	0.960	**0.056**	0.801
bp1-bp3.5	*146*								
bp4	*142*	---------	-------	-------	-------	-------	-------	-------	-------
bp5	*37*	---------	**0.470**	**0.076**	0.357	0.025	0.317	**0.087**	0.292
XM2 META	130	-0.0384	**0.363**	**0.008**	0.190	0.000	0.352	0.508	0.813

bp1-bp3	*130*								
bp3.5	*121*	---------	0.365	0.274	0.620	0.062	**0.041**	0.556	0.495
bp4	*78*	---------	0.681	0.003	0.305	0.000	0.742	0.182	0.777
bp5	*4*	---------	0.000	0.500	-------	0.000	0.399	0.951	0.254
XM3 META	68	-0.5476	0.186	0.316	0.399	0.000	0.430	0.252	0.262
bp1-bp2	*68*								
bp3	*67*	---------	0.000	0.500	-------	0.000	1.000	0.465	0.985
bp3.5	*36*	---------	**1.000**	**0.017**	-------	0.000	**0.075**	**0.055**	**0.091**
bp4	*7*	---------	0.757	0.167	0.769	0.000	0.429	0.728	0.826
bp5	*0*								
XM1 HYPO	146	0.7019	**0.628**	**<0.001**	0.209	0.000	0.710	0.175	0.276
bp1-bp3	*146*								
bp3.5	*143*	---------	0.000	0.500	-------	0.000	0.175	0.192	0.338
bp4	*119*	---------	**1.000**	**<0.001**	-------	0.000	1.000	0.113	0.170
bp5	*18*	---------	**0.823**	**0.017**	0.400	0.000	0.439	0.867	0.543
XM3 HYPO	64	0.1213	0.122	0.300	0.253	0.102	**0.009**	0.708	**0.084**
bp1	*64*								
bp2	*59*	---------	0.000	0.500	-------	0.000	0.530	0.518	0.771
bp3	*44*	---------	0.248	0.304	0.521	0.000	0.237	0.881	0.616
bp3.5	*12*	---------	0.000	0.500	-------	0.090	**0.007**	0.110	**<0.001**
bp4	*3*	---------	0.000	0.500	-------	0.113	**0.047**	0.330	0.367
bp5	*0*								
XM1 C5	143	-0.4807	**0.326**	**0.039**	0.212	0.048	**0.077**	0.601	0.737
bp1	*108*	---------	**0.729**	**0.006**	0.294	0.000	0.869	0.636	0.364
bp2	*70*	---------	**0.107**	**0.349**	0.199	0.046	**0.041**	0.959	0.536
bp3	*36*	---------	0.167	0.312	0.363	0.038	**0.047**	0.159	0.587
bp4	*10*	---------	0.676	0.074	0.480	0.025	**0.060**	0.886	0.177
bp5	*1*	---------	0.000	0.500	-------	0.000	0.477	0.388	0.999
XM2 C5	124	-0.7633	**0.440**	**0.006**	0.208	0.041	**0.013**	0.474	0.150
bp1	*94*	---------	0.474	0.065	0.353	0.035	**0.021**	0.505	0.133
bp2	*75*	---------	**0.892**	**0.004**	0.391	0.033	**0.031**	0.339	0.231

bp3	*49*	---------	0.334	0.116	0.271	0.000	0.162	0.617	0.783
bp4	*29*	---------	0.437	0.091	0.438	0.000	0.206	0.296	0.537
bp5	*12*	---------	0.573	0.184	0.663	0.082	**0.019**	0.944	**0.015**
XM3 C5*	65	-1.1303	0.060	0.420	0.313	0.000	0.561	0.315	0.810
bp1	*56*	---------	0.000	0.500	-------	0.000	0.767	0.205	0.591
bp2	*56*	---------	0.000	0.500	-------	0.000	0.767	0.164	0.266
bp3	*50*	---------	0.000	0.500	-------	0.000	0.291	0.275	0.903
bp4	*43*	---------	0.000	0.500	-------	0.006	0.112	0.120	**0.098**
bp5	*24*	---------	0.263	0.262	0.447	0.000	0.810	0.657	0.649
XM1 CARAB	137	-0.2069	**0.433**	**0.006**	0.206	0.008	0.268	**0.073**	0.916
bp1	*124*	---------	0.389	0.214	0.022	0.000	0.108	0.485	0.559
bp2	*113*	---------	0.524	0.063	0.395	0.012	0.209	**0.097**	0.643
bp3	*107*	---------	0.278	0.150	0.271	0.000	0.959	0.117	0.950
bp4	*82*	---------	**0.633**	**0.010**	0.368	0.000	0.982	0.104	0.816
bp5	*72*	---------	**0.511**	**0.022**	0.059	0.020	0.976	**0.041**	0.476
bp6	*8*	---------	0.309	0.318	0.691	0.094	**0.016**	0.595	**0.085**
bp7	*7*	---------	**0.354**	**0.291**	0.644	0.000	0.181	0.501	0.376
XM2 CARAB	109	-1.1185	**0.496**	**0.005**	0.229	0.000	0.386	0.115	0.113
bp1	*57*	---------	**0.475**	**0.035**	0.312	0.000	0.563	0.157	0.336
bp2	*33*	---------	**0.812**	**0.004**	0.330	0.020	0.227	0.254	**0.075**
bp3	*29*	---------	**0.972**	**0.002**	0.328	0.034	0.340	0.377	**0.058**
bp4	*15*	---------	0.000	0.500	-------	0.072	0.416	0.317	**0.035**
bp5	*14*	---------	0.000	0.500	-------	0.058	0.562	0.213	**0.051**
bp6-bp7	*0*								
XM3 CARAB	45	-0.7035	**0.923**	**0.028**	0.464	0.000	0.581	0.291	0.758
bp1	*18*	---------	1.000	0.065	-------	0.000	0.360	0.392	0.579
bp2	*16*	---------	0.633	0.209	0.836	0.000	0.360	0.881	0.646
bp3	*15*	---------	0.338	0.348	0.918	0.000	0.338	0.690	0.535
bp4	*11*	---------	0.276	0.374	0.897	0.000	0.533	0.412	0.485
bp5	*8*	---------	0.848	0.221	0.546	0.000	0.713	0.345	0.908
bp6	*4*	---------	**1.000**	**0.050**	-------	0.000	0.851	0.547	0.704

bp7	*3*	---------	**1.000**	**0.047**	-------	0.000	0.643	0.913	0.388
XM1 PARA	142	-1.3946	**0.233**	**0.050**	0.168	0.025	0.127	**0.023**	0.754
bp1	*60*	---------	**0.378**	**0.040**	0.256	0.046	**0.076**	**0.027**	0.646
bp2	*1*	---------	1.000	0.374	-------	0.000	0.170	0.790	1.000
bp3	*1*	---------	1.000	0.374	-------	0.000	0.170	0.790	1.000
bp4-bp6	*0*								
XM2 PARA*	123	14.5323	0.257	0.152	0.293	0.000	0.843	0.234	0.994
bp1	*7*	---------	0.885	0.167	0.893	0.000	0.921	0.287	0.808
bp2	*5*	---------	0.000	0.500	-------	0.000	0.801	0.219	0.952
bp3	*3*	---------	0.000	0.500	-------	0.000	0.857	0.126	1.000
bp4	*1*	---------	0.000	0.500	-------	0.000	0.339	0.243	0.969
bp5	*1*	---------	0.000	0.500	-------	0.000	0.339	0.243	0.969
bp6	*0*								
XM3 PARA*	58	27.0185	0.000	0.500	-------	0.000	0.437	0.426	0.528
bp1	*2*	---------	0.000	0.500	-------	0.000	0.515	0.458	0.592
bp2	*2*	---------	0.000	0.500	-------	0.000	0.515	0.458	0.662
bp3	*1*	---------	0.000	0.500	-------	0.000	0.998	0.450	0.935
bp4-bp6	*0*								
XI2 PEG[j]	146	---------	0.000	0.500	-------	0.000	0.726	0.149	0.997
	2								
XM3 PEG[j]	73	---------	-------	-------	-------	-------	-------	-------	-------
	0								
XI2 CONG ABS	148	---------	1.000	0.150	-------	0.000	0.344	0.718	0.417
	4								
XP2 CONG ABS	138	---------	-------	-------	-------	-------	-------	-------	-------
	3								
XM3 CONG ABS	73	---------	-------	-------	-------	-------	-------	-------	-------
	0								
NI1 SHOV	136	0.0047	**0.667**	**<0.001**	0.206	0.017	0.220	**0.068**	0.611
bp1	*112*	---------	**1.000**	**0.002**	-------	0.060	**0.012**	**0.074**	**0.053**
bp2	*25*	---------	**1.000**	**0.001**	-------	0.000	0.814	0.141	0.421

bp3	*1*	---------	1.000	0.398	-------	0.000	0.869	0.262	0.999
bp4-bp7	*0*								
NI2 SHOV	141	0.2598	**0.542**	**<0.001**	0.203	0.000	0.182	0.845	0.401
bp1	*125*	---------	**1.000**	**<0.001**	-------	0.000	0.787	0.922	0.890
bp2	*28*	---------	**1.000**	**<0.001**	-------	0.000	0.787	0.931	0.892
bp3-bp7	*0*								
NC DAR	131	-0.5160	**0.386**	**0.005**	0.192	0.180	0.148	<**0.001**	0.528
bp1	*83*	---------	0.274	0.149	0.301	0.064	0.903	**0.001**	0.408
bp2	*52*	---------	**0.566**	**0.012**	0.319	0.173	0.239	**<0.001**	0.624
bp3	*12*	---------	0.398	0.174	0.177	0.123	0.212	**<0.001**	0.524
bp4	*3*	---------	0.000	0.500	-------	0.090	**0.026**	0.113	0.972
bp5	*0*								
NP1 ODONT	139	---------	0.000	0.500	-------	0.000	0.829	0.415	0.918
	2								
NP2 ODONT	131	---------	0.000	0.500	-------	0.000	1.000	0.208	0.771
	1								
NM1 ANT FOVEA	136	-0.4820	**0.362**	**0.021**	0.213	0.000	0.156	0.300	0.240
bp1	*134*	---------	0.000	0.500	-------	0.000	0.339	0.143	1.000
bp2	*107*	---------	0.193	0.244	0.295	0.000	0.305	0.349	0.364
bp3	*61*	---------	0.367	0.078	0.299	0.000	0.361	0.956	0.405
bp4	*14*	---------	0.586	0.111	20.565	0.000	0.176	0.197	0.158
NM1 CNO*	138	2.2118	**0.299**	**0.012**	0.156	0.000	0.413	0.127	0.393
bp5	*137*	---------	0.000	0.500	-------	0.000	1.000	0.258	0.997
bp6	*114*	---------	**0.634**	**0.019**	0.735	0.000	0.347	0.334	0.602
bp7	*1*	---------	0.000	0.500	-------	0.000	0.678	0.265	0.996
bp8	*0*								
NM2 CNO	117	-0.2957	0.134	0.202	0.176	0.000	0.911	0.123	0.732
bp5	*108*	---------	0.693	0.088	0.505	0.000	0.579	0.488	0.470
bp6	*49*	---------	0.000	0.500	-------	0.000	0.546	0.102	0.819
bp7	*2*	---------	1.000	0.112	-------	0.062	0.133	0.280	**0.015**
bp8	*0*								

NM3 CNO	61	0.6552	0.433	0.151	0.451	0.000	0.692	0.117	0.901
bp5	*60*	---------	0.000	0.500	-------	0.000	1.000	0.502	0.982
bp6	*45*	---------	0.289	0.303	0.599	0.000	0.384	0.248	0.433
bp7	*3*	---------	1.000	0.378	-------	0.211	0.848	**0.092**	1.000
bp8	*0*								
NM1 DWRINK	139	-1.0794	0.151	0.152	0.166	0.000	0.210	0.269	0.414
bp1	*139*								
bp2	*111*	---------	**0.558**	**0.035**	0.356	0.000	0.106	0.540	0.661
bp3	*46*	---------	**0.137**	**0.272**	0.217	0.000	0.663	0.299	0.565
NM1 C5	143	-0.0309	**0.563**	**<0.001**	0.198	0.000	0.453	0.311	0.682
bp1	*142*	---------	0.000	0.499	-------	0.125	1.000	**<0.001**	1.000
bp2	*141*	---------	**1.000**	**0.034**	-------	0.000	0.824	0.302	0.993
bp3	*128*	---------	**1.000**	**0.034**	-------	0.000	0.900	0.303	0.629
bp4	*94*	---------	**0.604**	**0.006**	0.296	0.000	0.499	0.624	0.759
bp5	*16*	---------	**1.000**	**0.001**	-------	0.000	0.635	0.559	0.958
NM2 C5	118	-0.4169	0.039	0.377	0.130	0.077	0.520	**0.004**	0.369
bp1	*108*	---------	0.437	0.186	0.515	0.000	0.559	0.205	0.554
bp2	*95*	---------	0.000	0.500	-------	0.000	0.641	0.131	0.868
bp3	*55*	---------	0.000	0.500	-------	0.037	0.132	**0.011**	0.357
bp4	*9*	---------	**1.000**	**0.007**	-------	0.107	0.354	**0.014**	0.155
bp5	*0*								
NM3 C5	67	-0.8876	0.014	0.485	0.354	0.000	0.425	0.835	0.654
bp1	*66*	---------	0.000	0.500	-------	0.000	1.000	0.518	0.982
bp2	*65*	---------	0.879	0.401	2.256	0.000	0.996	0.155	0.992
bp3	*56*	---------	0.000	0.500	-------	0.000	0.752	0.565	0.718
bp4	*38*	---------	0.000	0.500	-------	0.000	0.667	0.822	0.950
bp5	*23*	---------	0.000	0.500	-------	0.000	0.273	0.916	0.151
NM1 C6	138	-0.4842	**0.637**	**<0.001**	0.168	0.000	0.203	0.468	0.614
bp1	*114*	---------	**0.634**	**0.019**	0.250	0.000	0.347	0.334	0.602
bp2	*63*	---------	**0.977**	**<0.001**	0.302	0.000	0.237	0.646	0.919
bp3	*26*	---------	**1.000**	**<0.001**	-------	0.000	0.728	0.838	0.779

bp4	*8*	---------	**0.872**	**0.045**	0.539	0.000	0.459	0.680	0.823
bp5	*3*	---------	0.000	0.500	-------	0.022	0.146	0.695	**0.023**
NM3 C6	63	-0.7890	0.000	0.500	-------	0.000	0.278	0.138	0.242
bp1	*48*	---------	0.485	0.248	0.780	0.029	0.315	**0.086**	0.357
bp2	*43*	---------	0.089	0.438	0.594	0.043	0.435	**0.043**	0.599
bp3	*30*	---------	0.917	0.080	0.700	0.078	0.152	**0.005**	0.134
bp4	*16*	---------	0.000	0.500	-------	0.037	**0.023**	0.737	**<0.001**
bp5	*6*	---------	0.000	0.500	-------	0.000	0.619	0.484	1.000
NM1 C7*	147	2.8380	0.174	0.055	0.134	0.000	0.134	0.590	0.482
bp1	*24*	---------	0.365	0.102	0.353	0.000	0.302	0.947	0.743
bp1a	*13*	---------	0.299	0.138	0.349	0.000	0.185	1.000	0.953
bp2	*12*	---------	0.409	0.081	0.470	0.000	0.234	0.813	0.930
bp3	*6*	---------	**0.829**	**0.033**	0.539	0.076	0.363	**0.070**	0.309
bp4	*2*	---------	0.000	0.500	-------	0.000	0.503	0.170	0.997
NM2 C7*	132	5.3702	0.234	0.204	0.307	0.000	0.627	0.118	0.759
bp1	*15*	---------	0.373	0.262	0.568	0.040	0.626	**0.048**	0.861
bp1a	*5*	---------	0.000	0.500	<0.001	0.000	0.758	0.661	0.364
bp2	*3*	---------	0.506	0.426	2.222	0.000	0.920	0.539	0.732
bp3-bp4	*0*								
NM3 C7	66	0.0660	0.024	0.462	0.252	0.000	0.778	0.506	0.401
bp1	*15*	---------	0.000	0.500	-------	0.000	0.656	0.393	0.347
bp1a	*14*	---------	0.087	0.429	0.424	0.000	0.628	0.385	0.344
bp2	*14*	---------	0.087	0.429	0.424	0.000	0.628	0.385	0.344
bp3	*12*	---------	0.188	0.360	0.563	0.000	0.974	0.323	0.644
bp4	*12*	---------	0.188	0.360	0.563	0.000	0.974	0.323	0.644
NM1 DTCREST	142	---------	**0.583**	**0.009**	0.306	0.000	0.884	0.387	0.809
	27								
NM2 DTCREST	132	---------	0.000	0.500	-------	0.000	0.735	0.591	0.339
	3								
NM3 DTCREST	66	---------	**1.000**	**0.033**	-------	0.000	0.656	0.588	0.955
	10								

NI1 CONG ABS	152	---------	-------	-------	-------	-------	-------	-------	-------
	0								
NP2 CONG ABS	138	---------	-------	-------	-------	-------	-------	-------	-------
	5								
NM3 CONG ABS	77	---------	-------	-------	-------	-------	-------	-------	-------
	0								

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[a]l=left; r=right; traits without a left or right designation represent the maximum of the left and right antimeric expressions; x=maxillary; n=mandibular; bp= breakpoint. All morphological trait abbreviations outlined in Appendix C. Ordinal traits were normalized and treated as continuous for the purpose for heritability estimation. Breakpoints indicate presence/absence dichotomization cutoffs for ordinal traits; each of these breakpoints was treated as an individual binary character for heritability estimation. Kurtosis is not estimated for binary character models. Certain breakpoints were omitted from the heritability analysis because expression was monomorphic across the sample. Traits marked with asterisks are associated with less stable heritability estimates because other model parameters could not be estimated, because sample size was too small, or because kurtosis values were too high after normalization. These results should be accepted with caution. Dashes are associated with incalculable parameter estimates. Traits marked with dashes for all parameters represent models that failed to converge. The traits XI1 labial convexity, XP2 double shovel, XM2 hypocone, NP1 lingual cusp variation, NP2 lingual cusp variation, NM1 protostylid, NM2 protostylid, NM3 protostylid, and NM2 C6 were removed due to high levels of intra-observer error. [b]N=sample size for heritability estimation; Count=count for dichotomized trait expression (presence) at the denoted breakpoint (bp). Count values are italicized. If a trait is binary (i.e., its original scoring standards do not include ordinal scale scoring) this value is marked on a blank row beneath the sample size “N”. [c]K=model kurtosis value. [d]h2= maximum likelihood heritability estimate. [e]All significant heritability estimates (p-value<0.05) and associated probability value estimates are bolded. [f]SE= maximum likelihood standard error estimate; this parameter estimate is typically omitted when heritability estimated equal 0.000 or 1.000. [g]c2= maximum likelihood total covariate estimate. [h]All significant probability value estimates for the covariates of age, sex, and age/sex interaction are bolded. [i]As the winging, premolar lingual cusp, and groove pattern data are categorical and not ordinal, each category was treated as a separate binary variable. [j]Peg-shaped incisor and peg-shaped molar were scored only as binary variables at the breakpoint of ASUDAS grade 2.

APPENDIX M

ANTIMERIC HERITABILITY ESTIMATE COMPARISONS

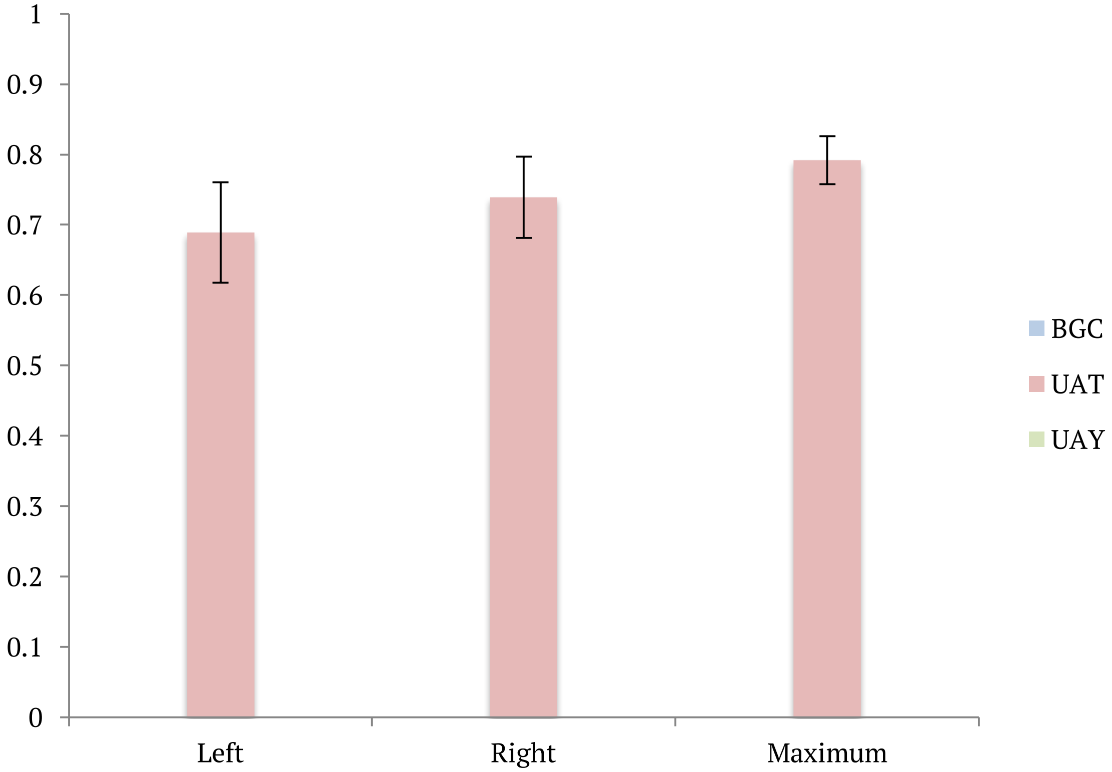


Figure 1. Antimeric h^2 estimates: c^1 shoveling.

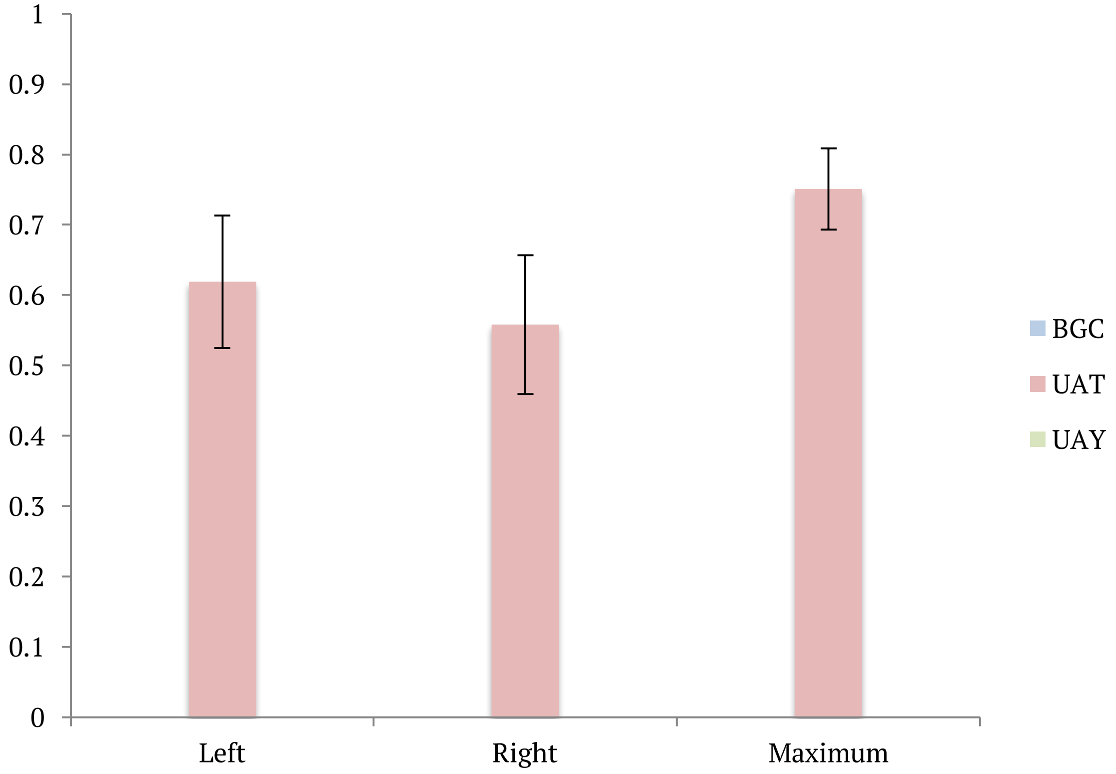


Figure 2. Antimeric h^2 estimates: c^1 double shoveling.

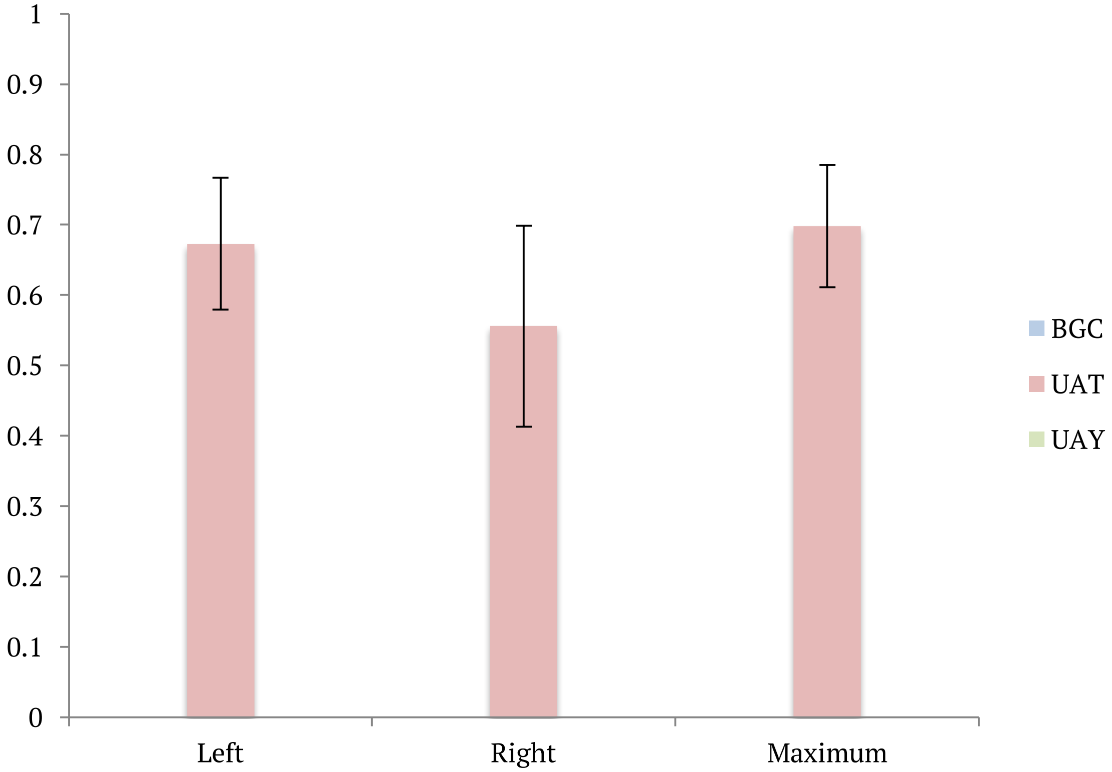


Figure 3. Antimeric h^2 estimates: i^2 tuberculum dentale.

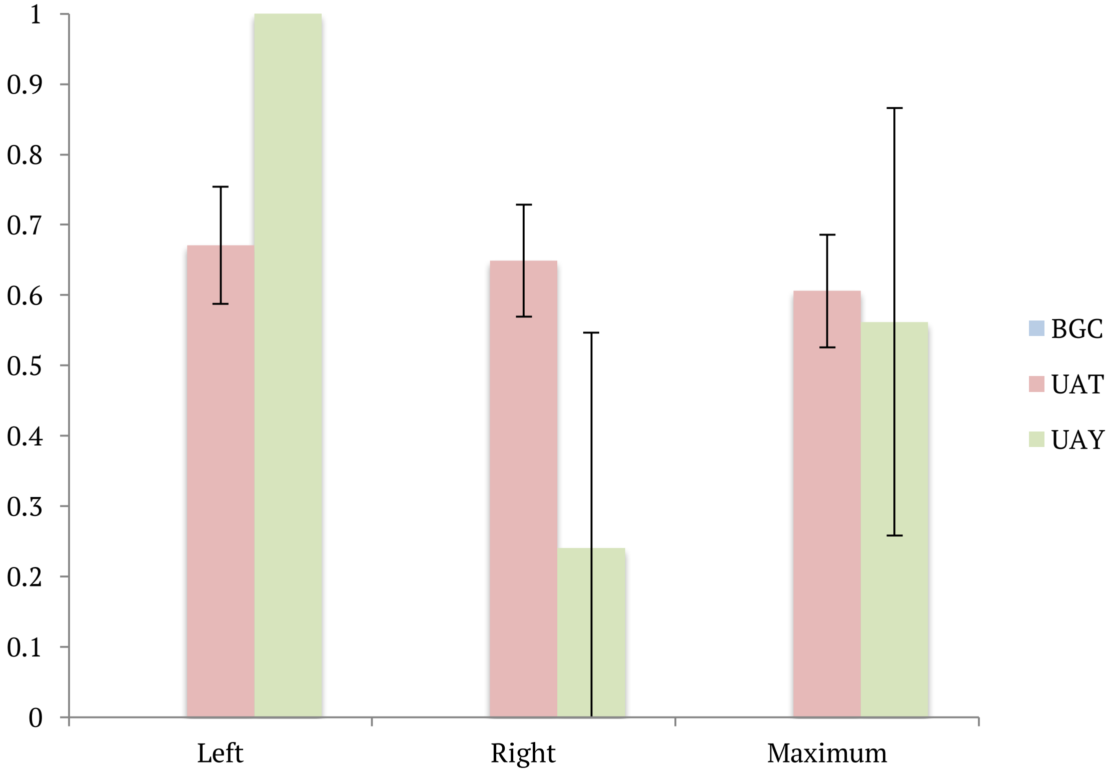


Figure 4. Antimeric h^2 estimates: c^1 tuberculum dentale.

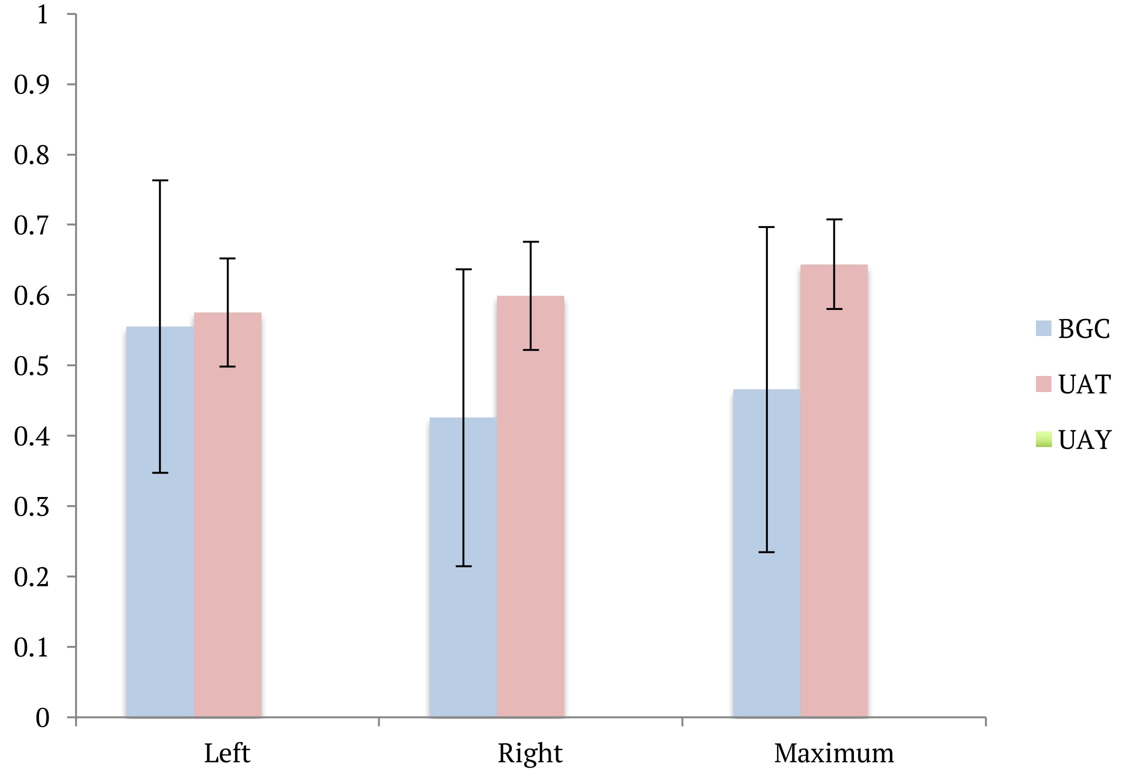


Figure 5. Antimeric h^2 estimates: m^2 metacone.

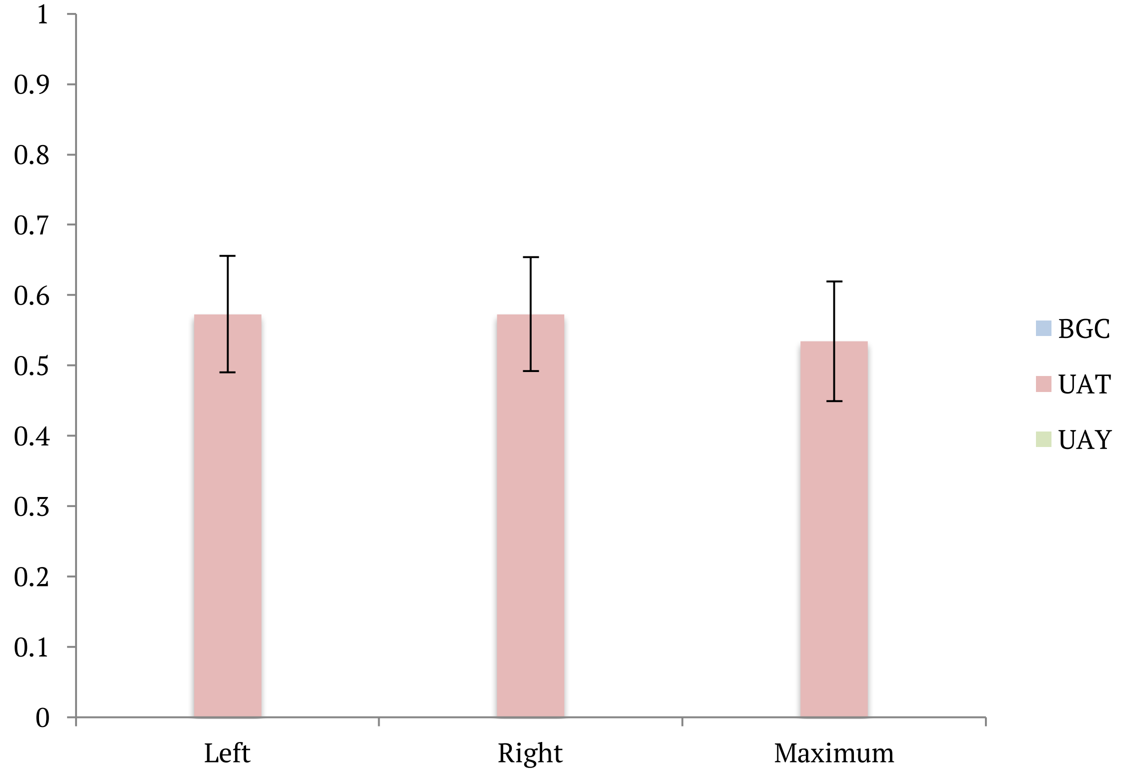


Figure 6. Antimeric h^2 estimates: m^1 hypocone.

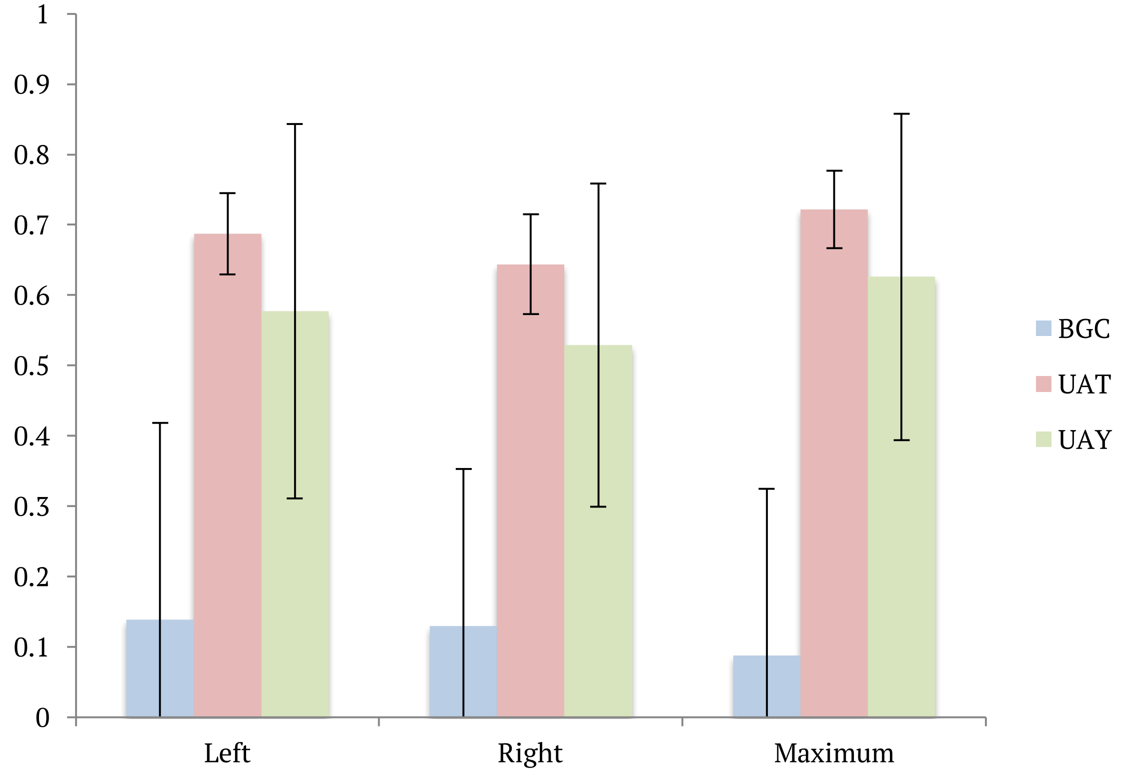


Figure 7. Antimeric *h*^{2} estimates: m^2 hypocone.

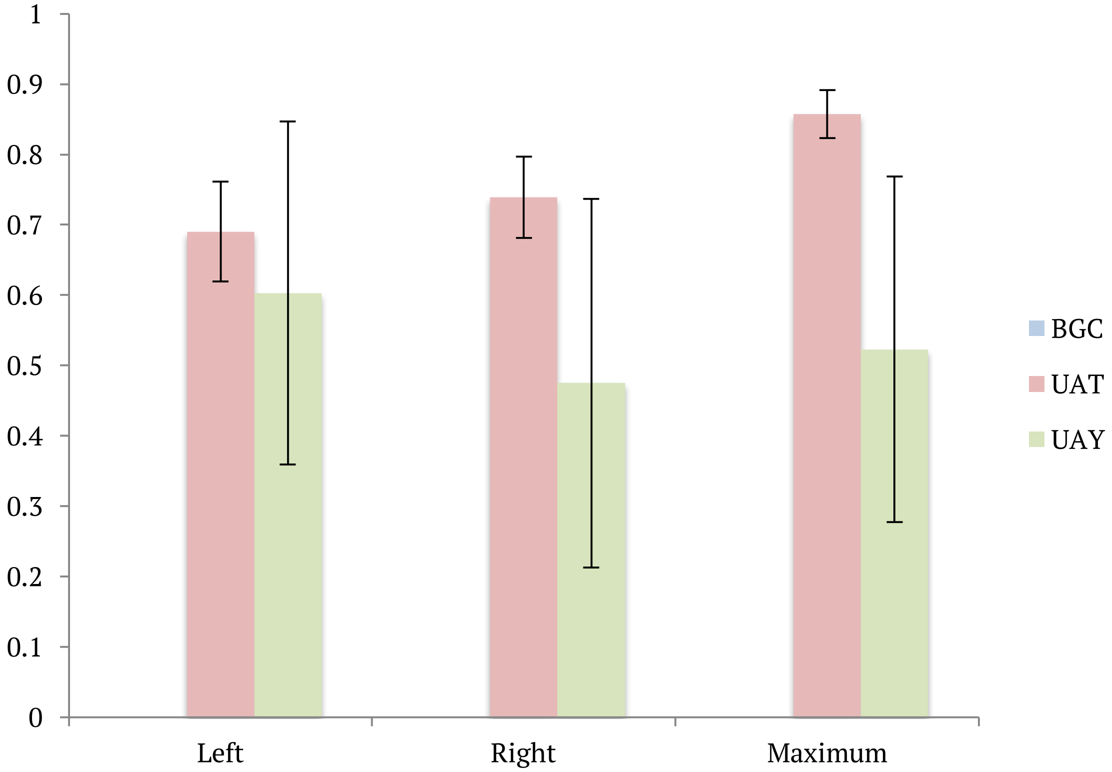


Figure 8. Antimeric h^2 estimates: m^2 Carabelli's trait.

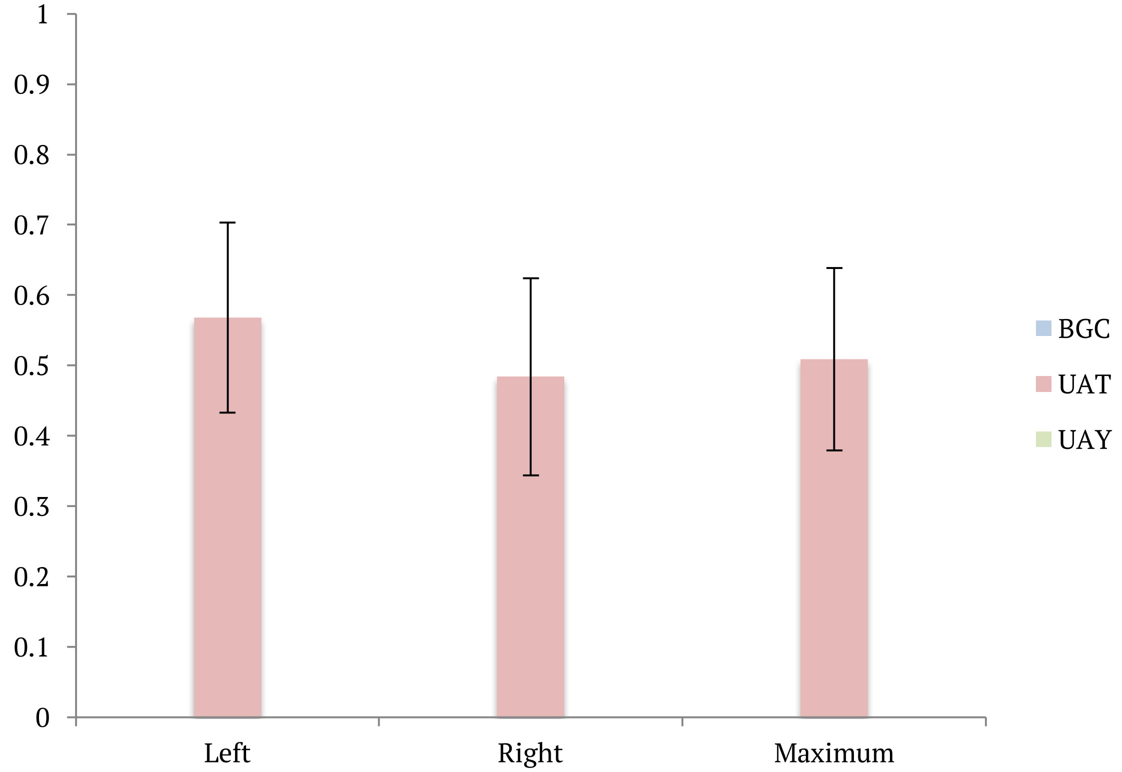


Figure 9. Antimeric h^2 estimates: i_1 shoveling.

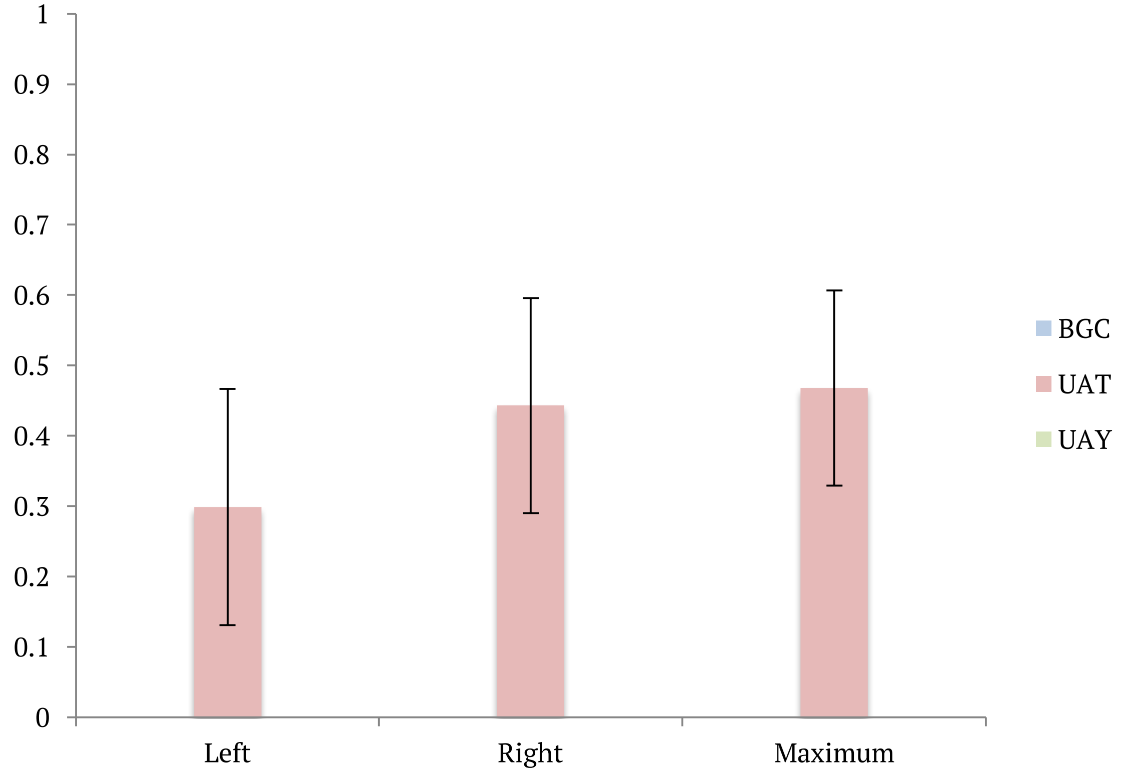


Figure 10. Antimeric h^2 estimates: c_1 distal accessory ridge.

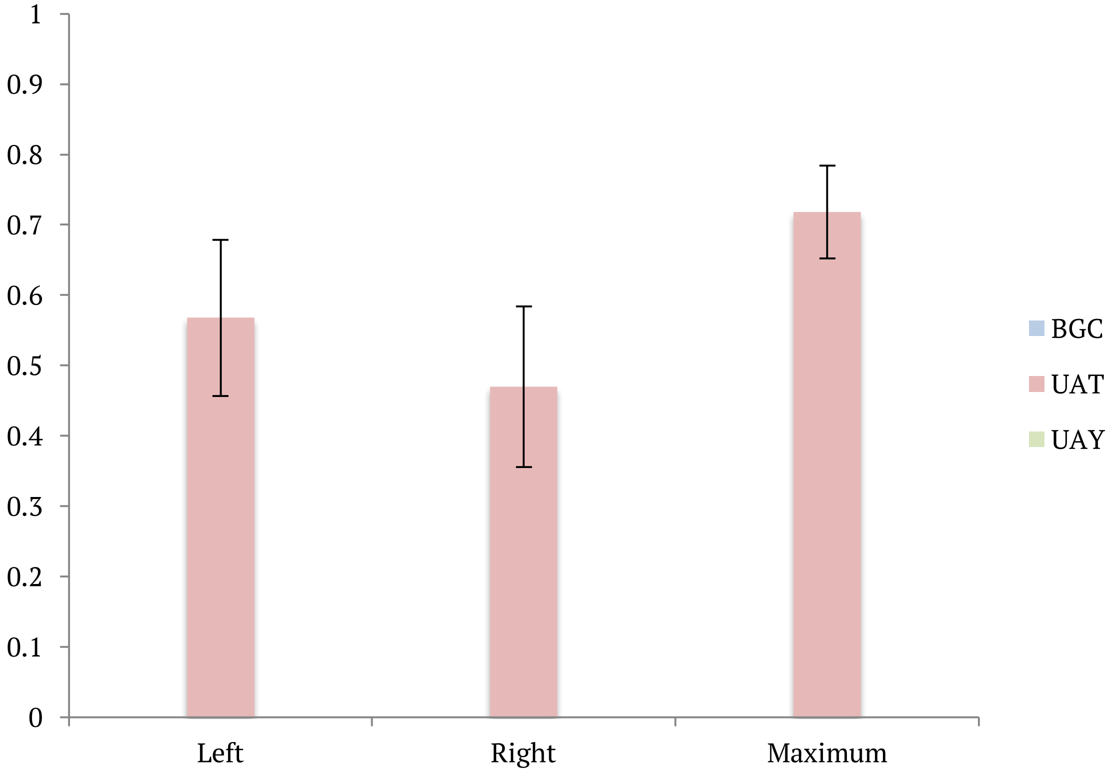


Figure 11. Antimeric h^2 estimates: m_1 cusp number.

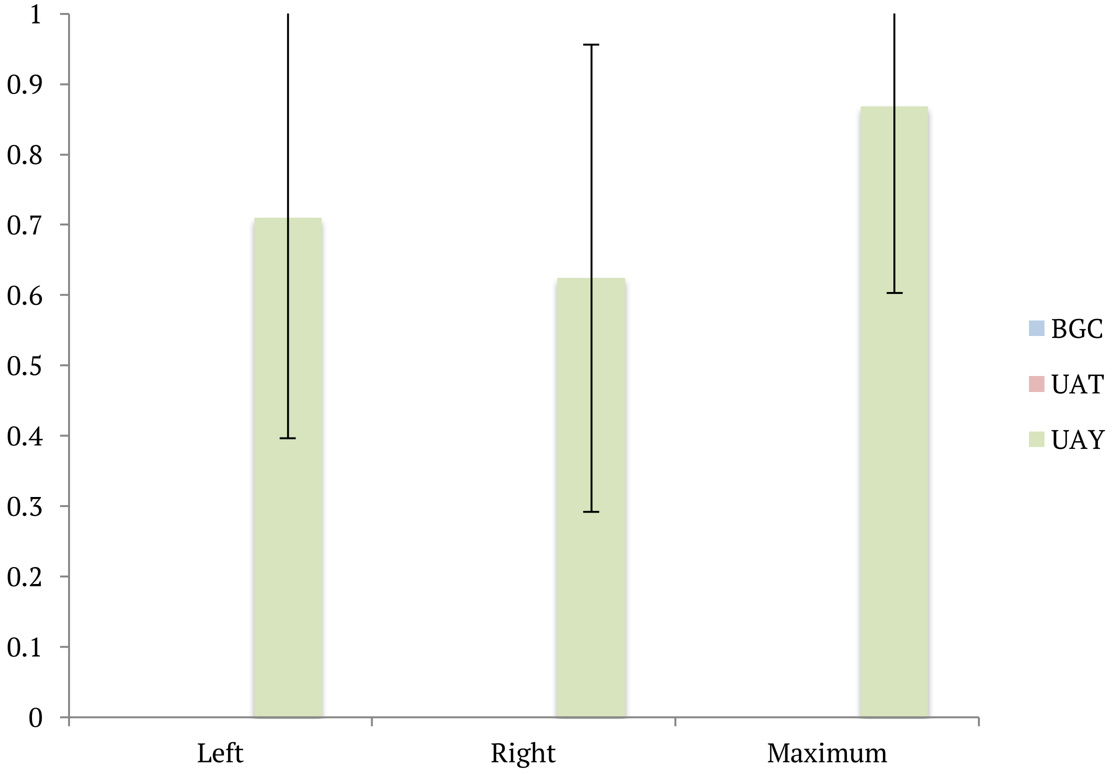


Figure 12. Antimeric h^2 estimates: m_2 cusp number.

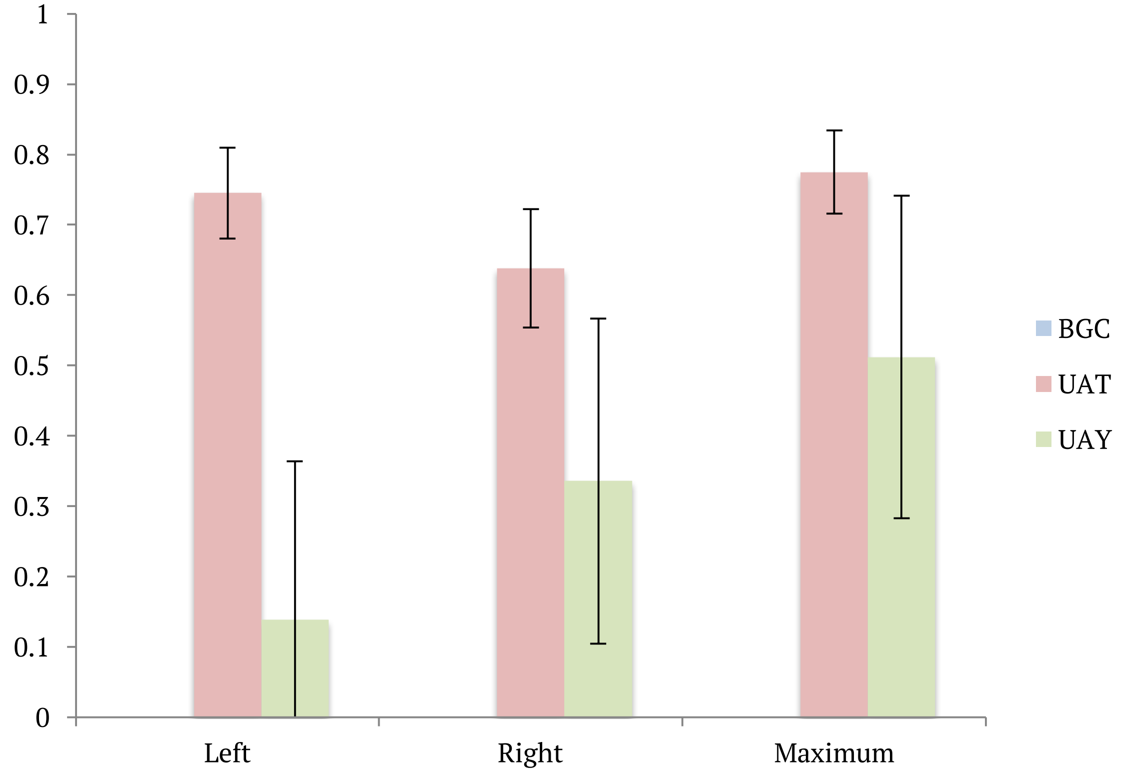


Figure 13. Antimeric h^2 estimates: m_2 deflecting wrinkle.

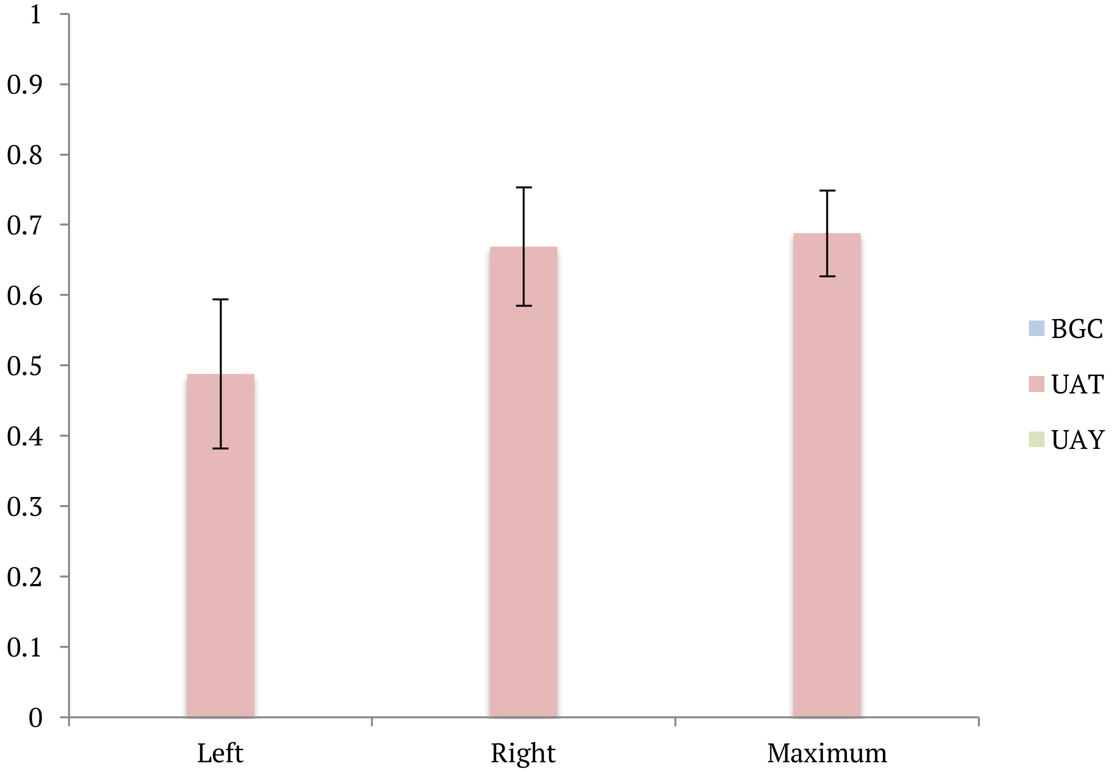


Figure 14. Antimeric h^2 estimates: m_1 cusp 5.

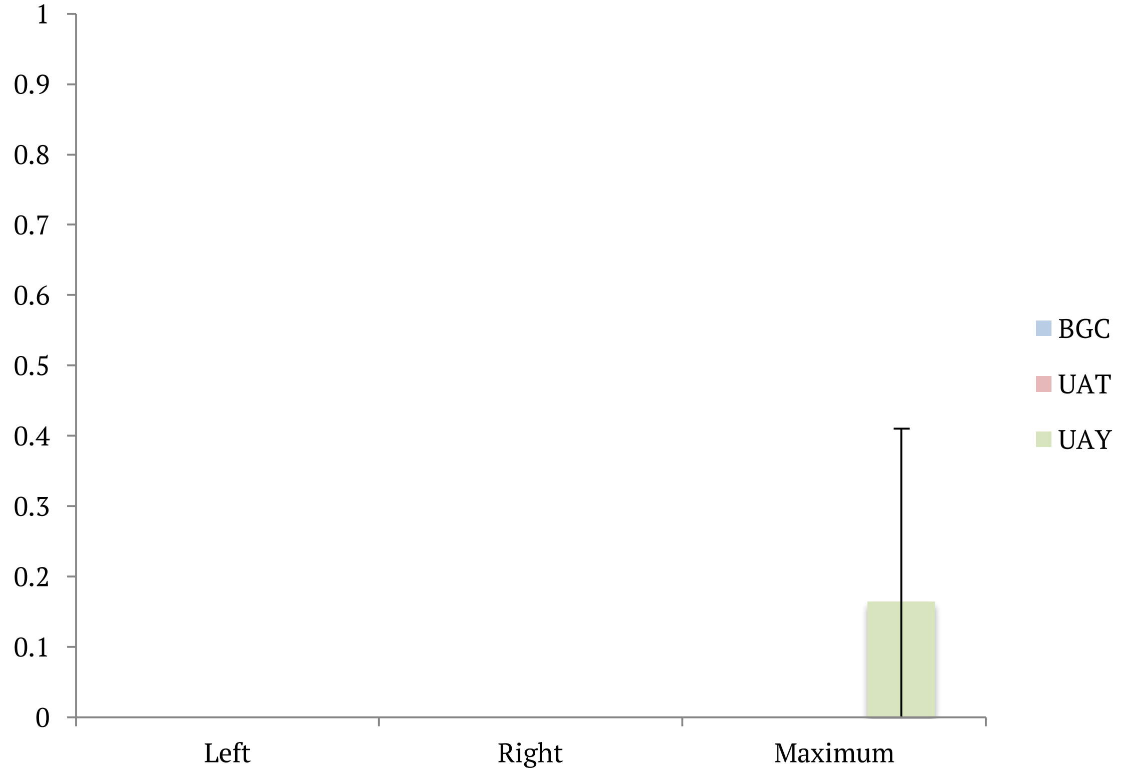


Figure 15. Antimeric h^2 estimates: m_2 cusp 5.

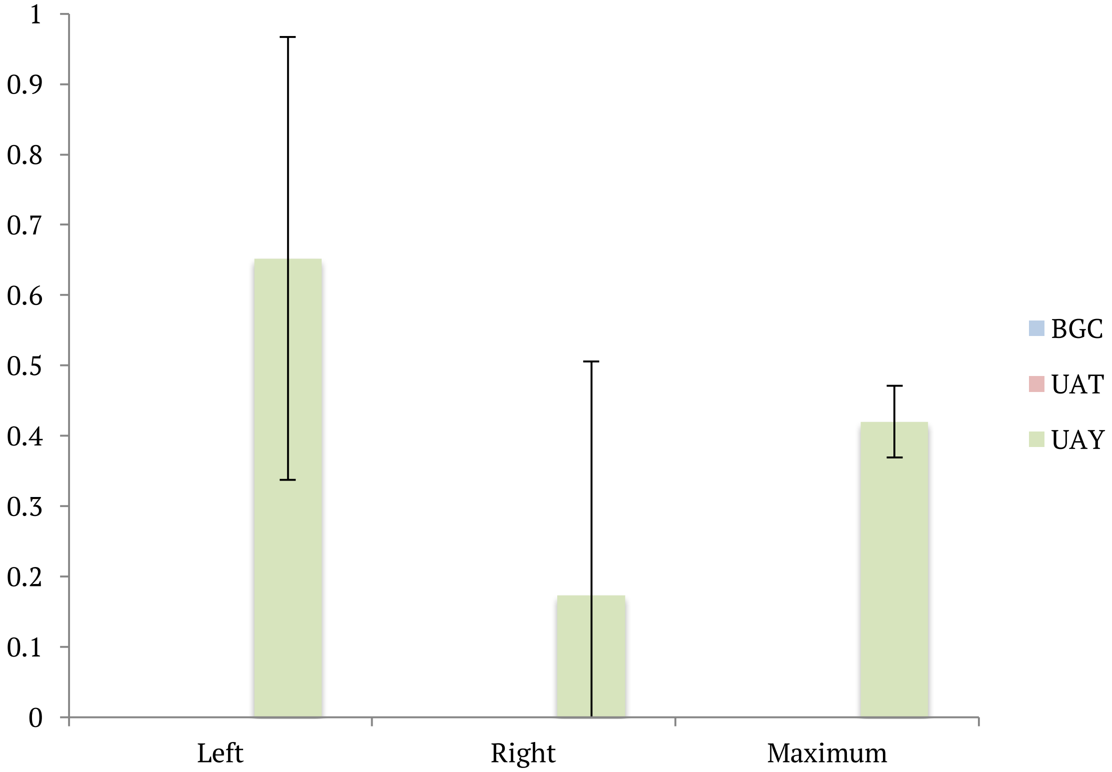


Figure 16. Antimeric h^2 estimates: m_2 cusp 6.

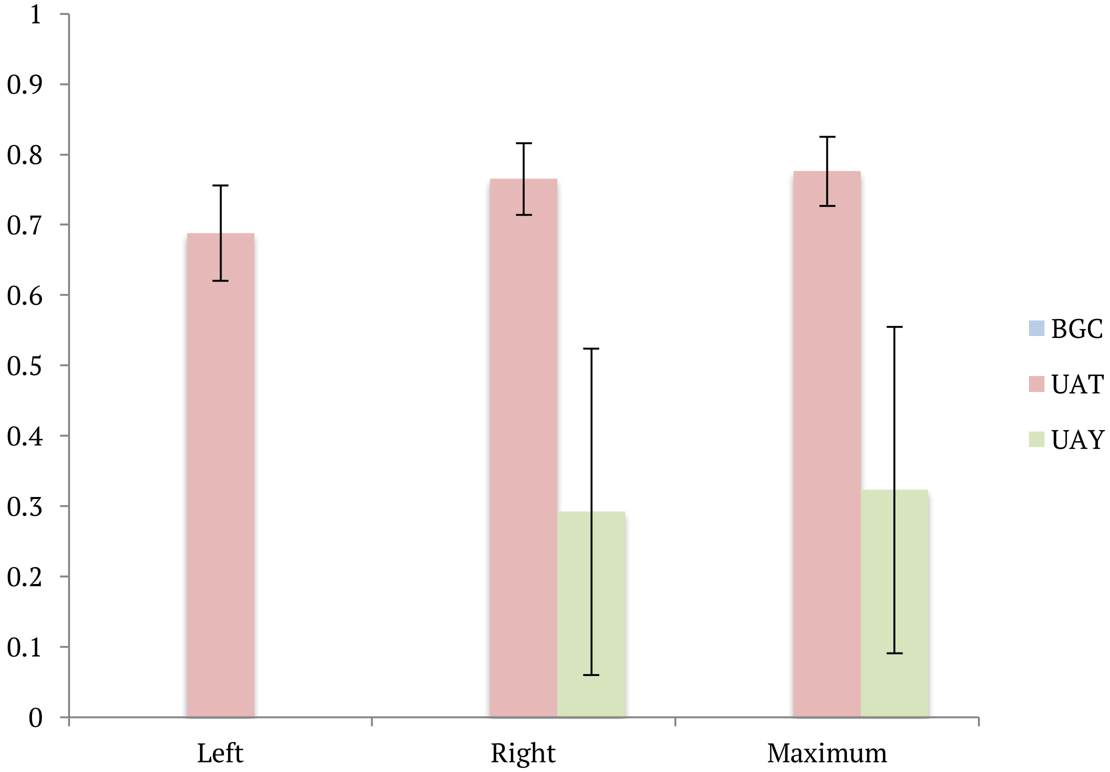


Figure 17. Antimeric h^2 estimates: m_2 cusp 7.

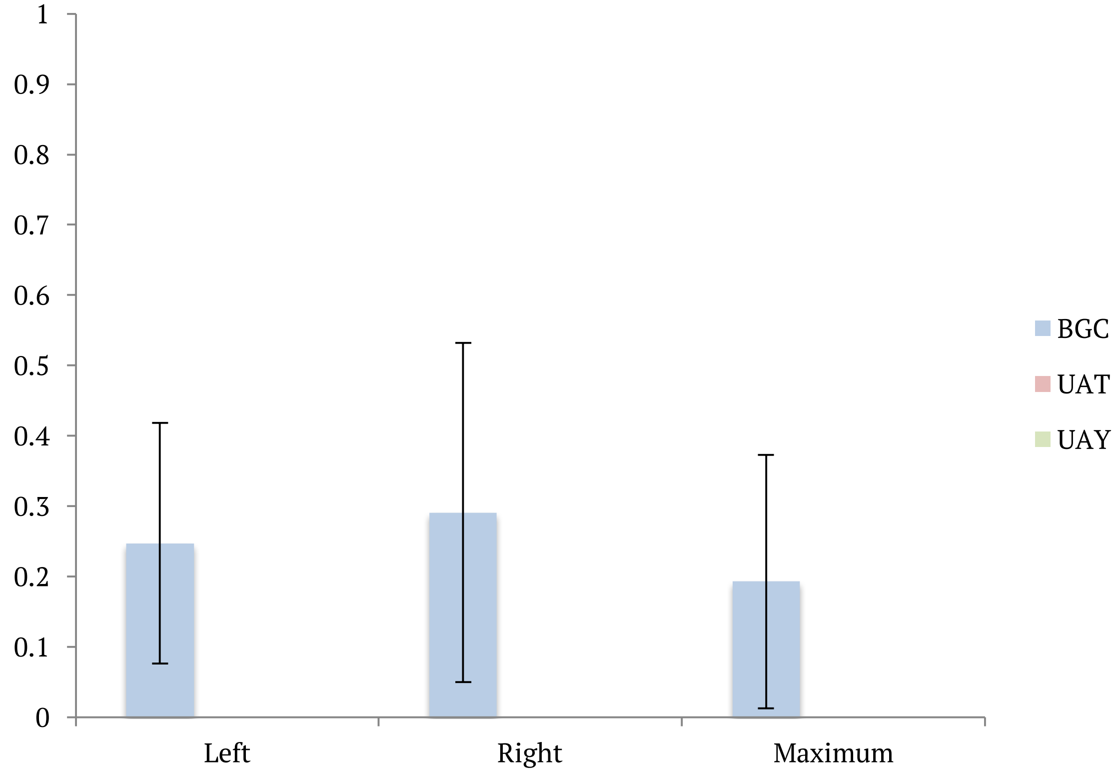


Figure 18. Antimeric h^2 estimates: I^1 Labial Convexity.

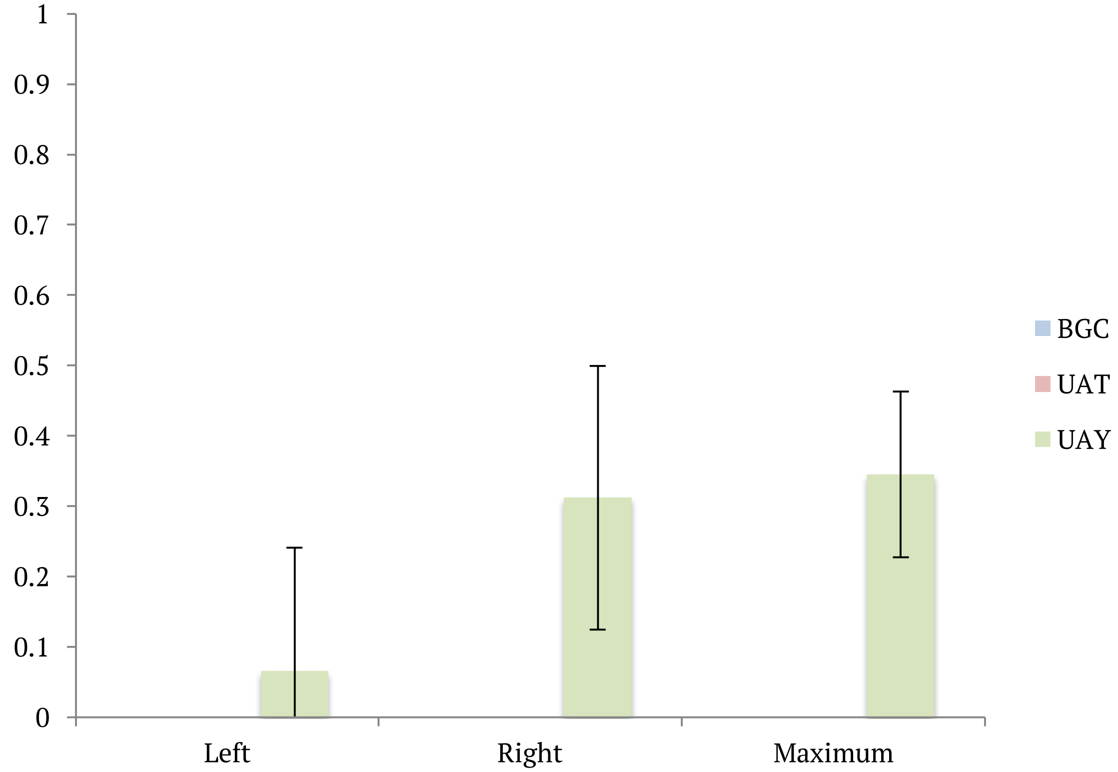


Figure 19. Antimeric *h^2* estimates: I^1 Shoveling.

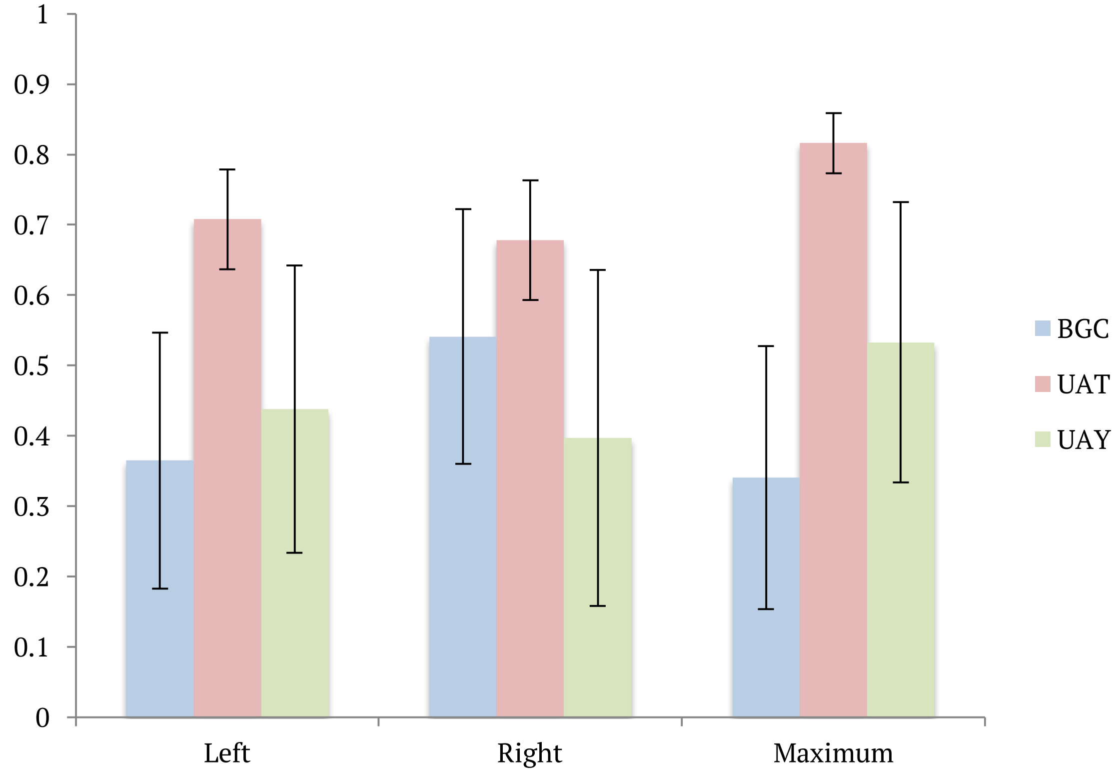


Figure 20. Antimeric h^2 estimates: I^2 Shoveling.

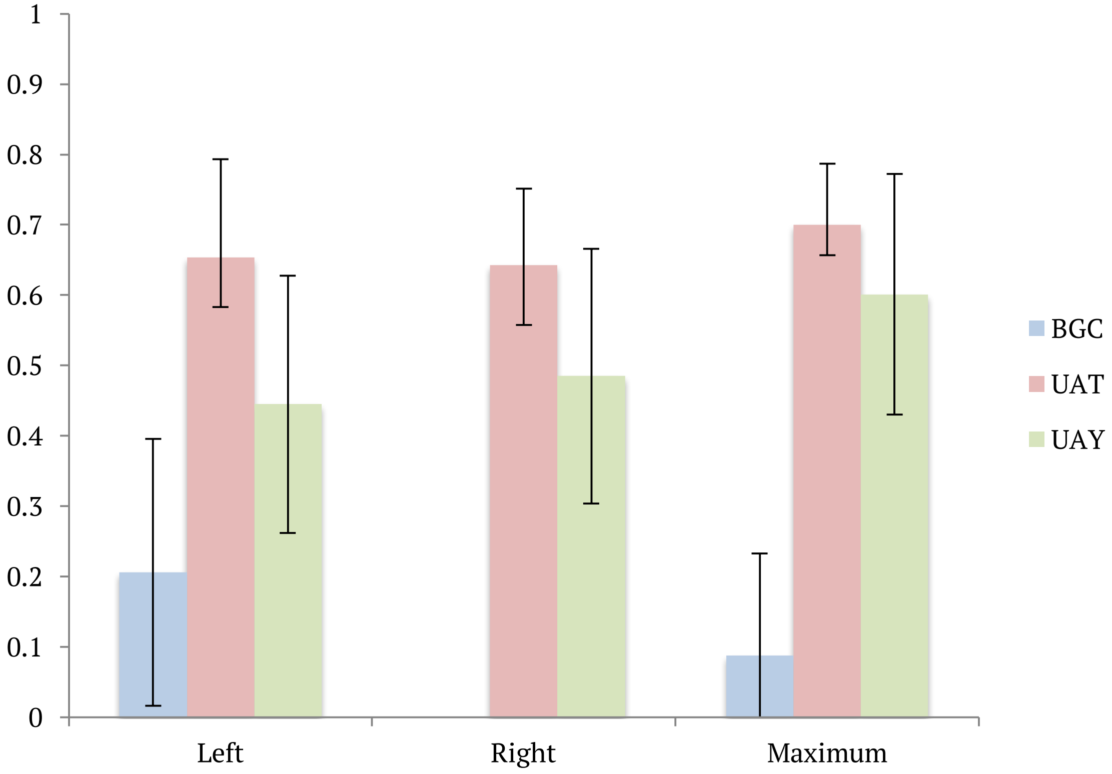


Figure 21. Antimeric *h*^{2} estimates: C^1 Shoveling.

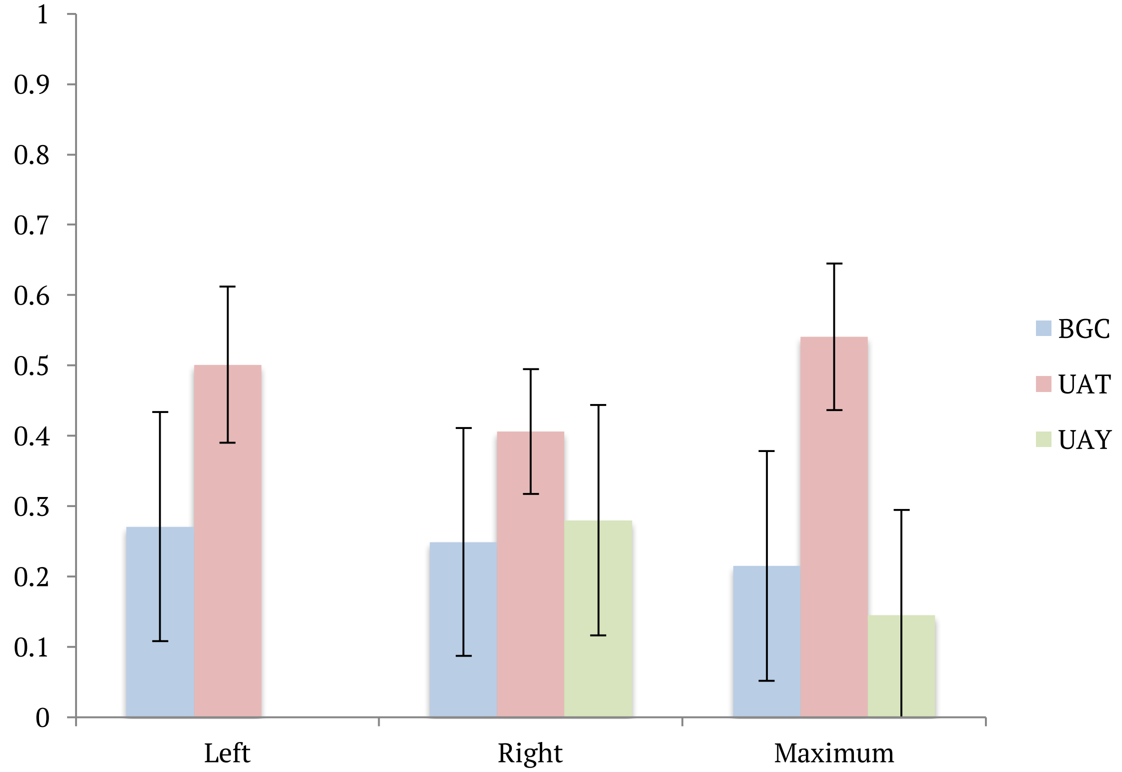


Figure 22. Antimeric h^2 estimates: I^1 Double Shoveling.

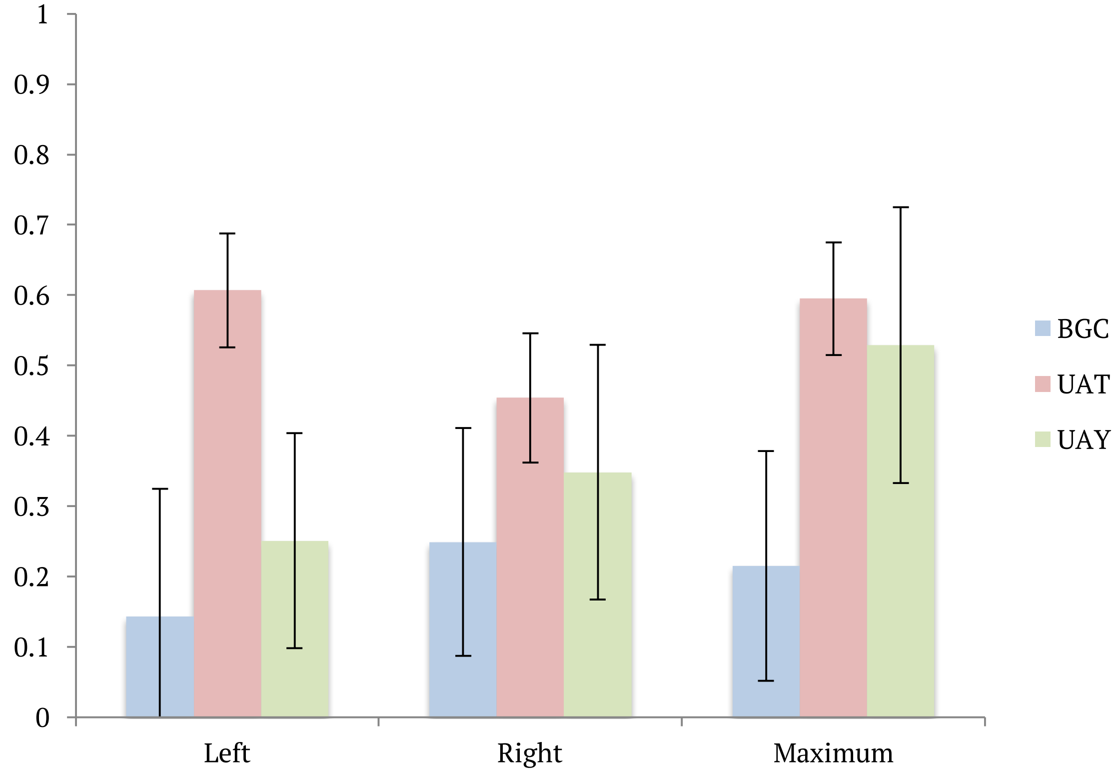


Figure 23. Antimeric h^2 estimates: I^2 Double Shoveling.

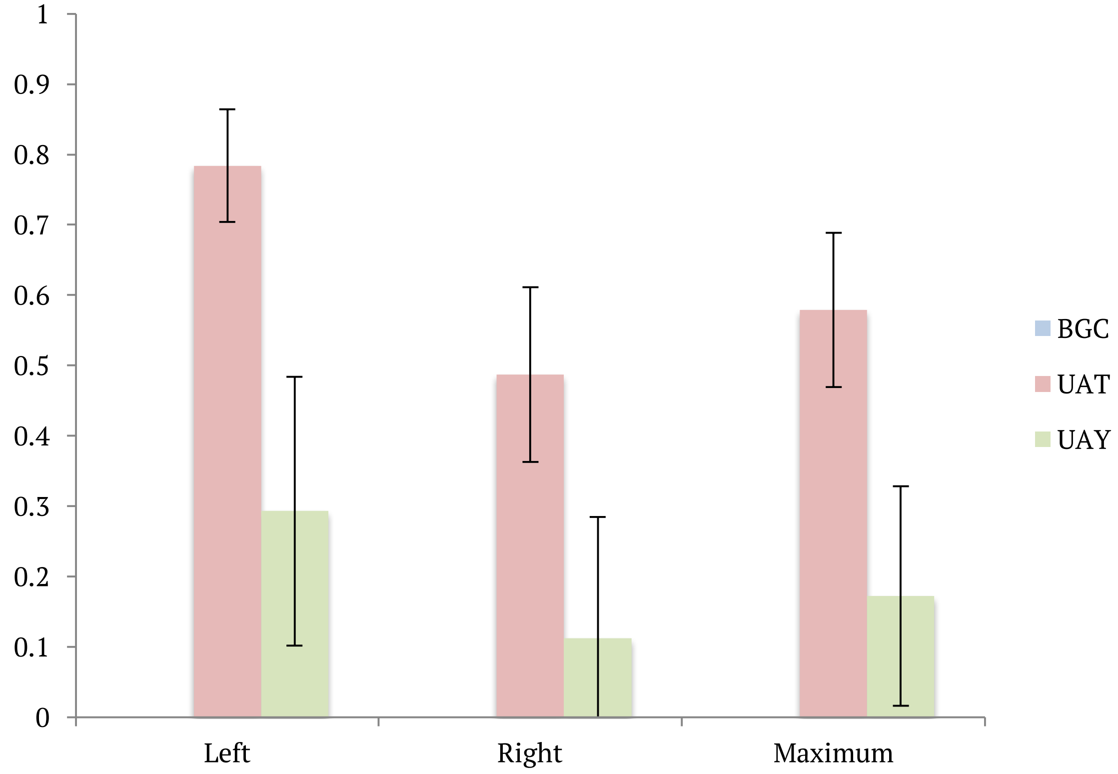


Figure 24. Antimeric h^2 estimates: C^1 Double Shoveling.

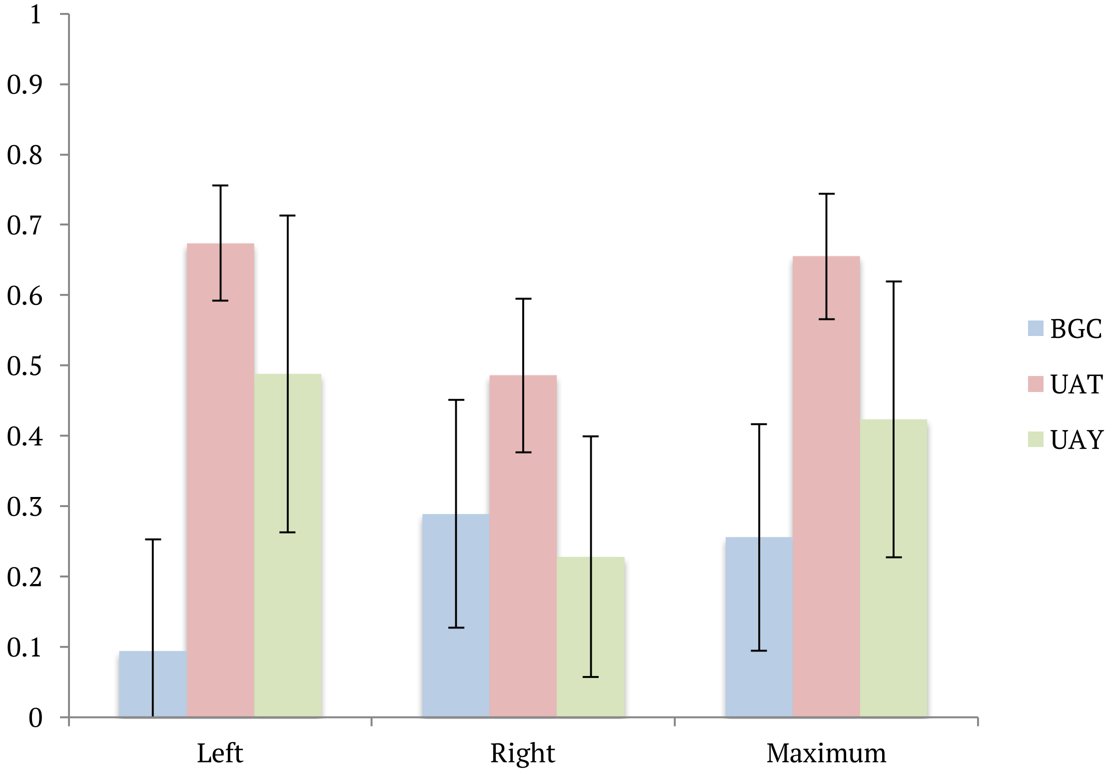


Figure 25. Antimeric h^2 estimates: P^1 Double Shoveling.

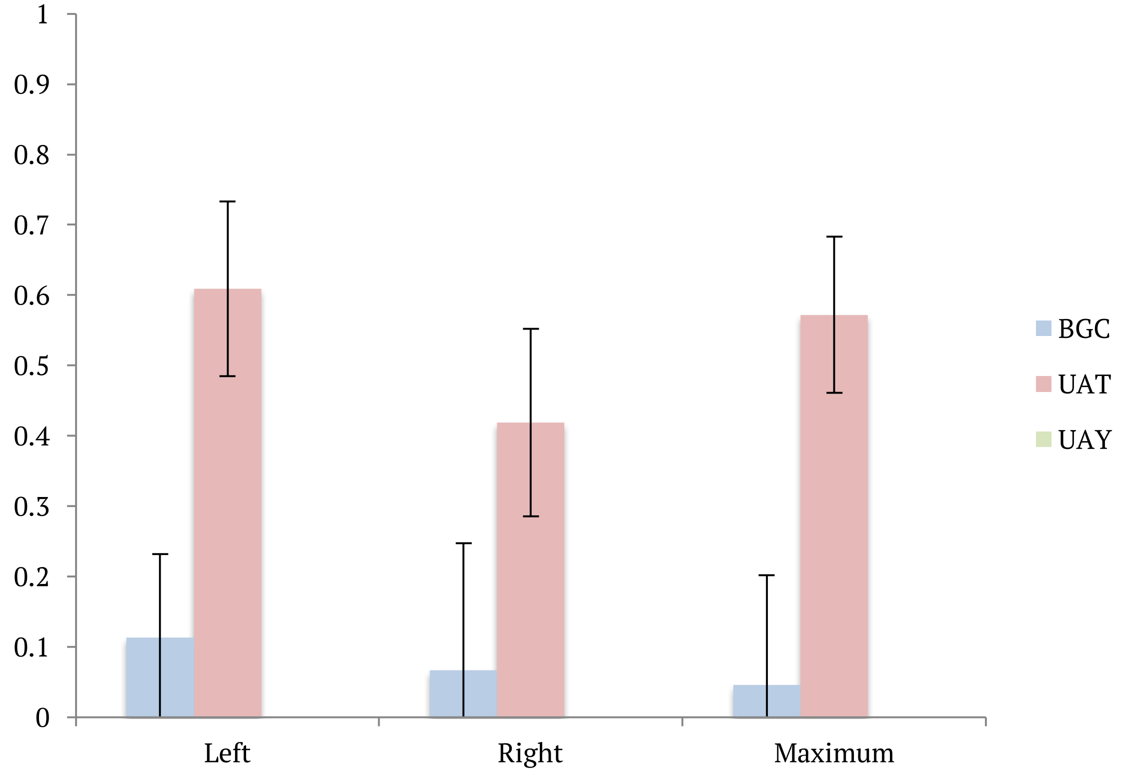


Figure 26. Antimeric h^2 estimates: P^2 Double Shoveling.

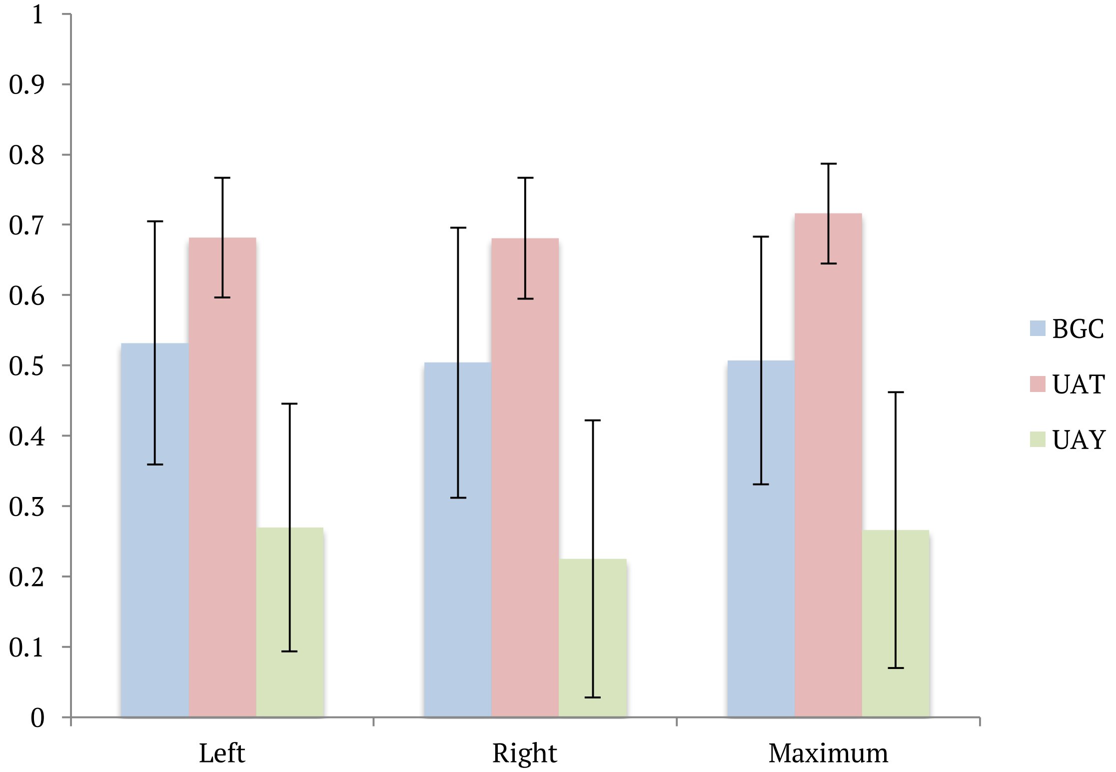


Figure 27. Antimeric h^2 estimates: I^1 Tuberculum Dentale.

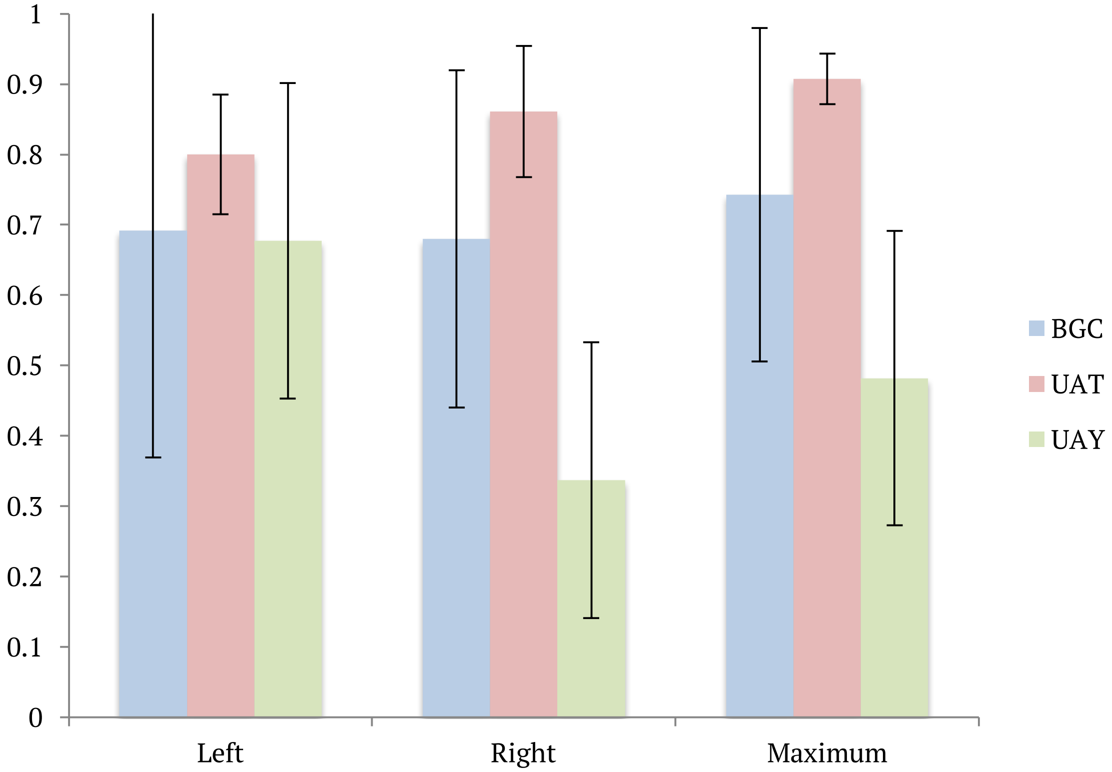


Figure 28. Antimeric h^2 estimates: I^2 Tuberculum Dentale.

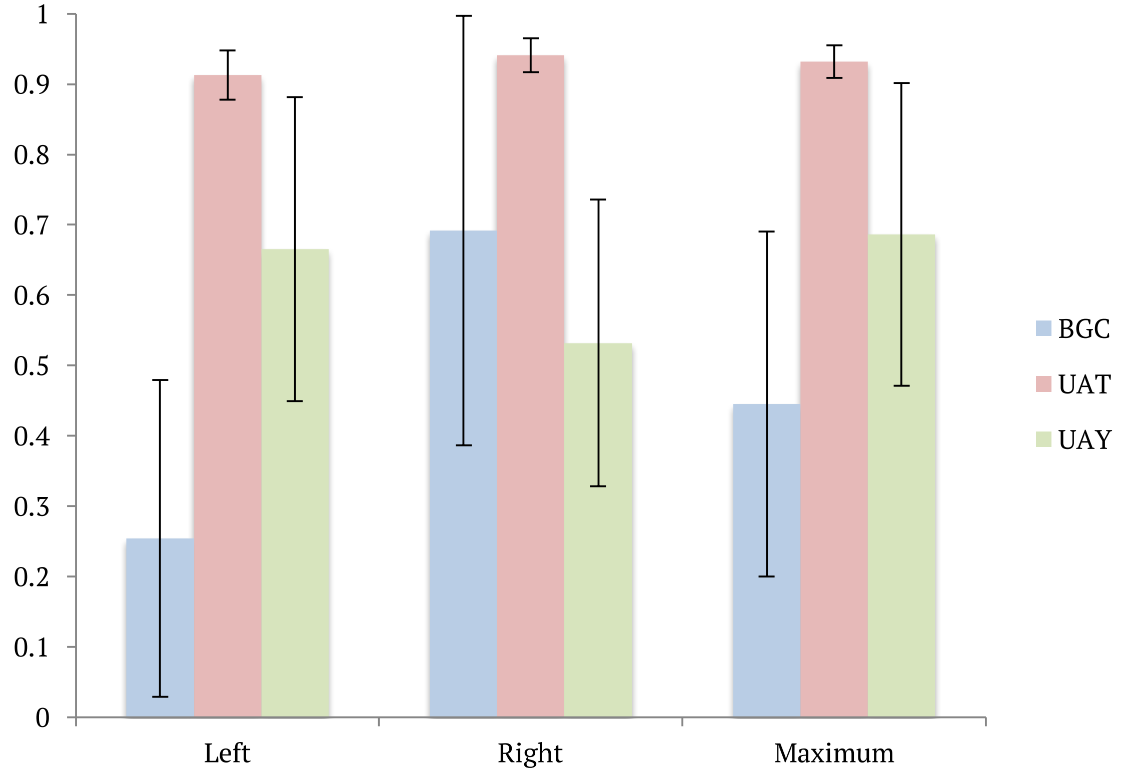


Figure 29. Antimeric h^2 estimates: C^1 Tuberculum Dentale.

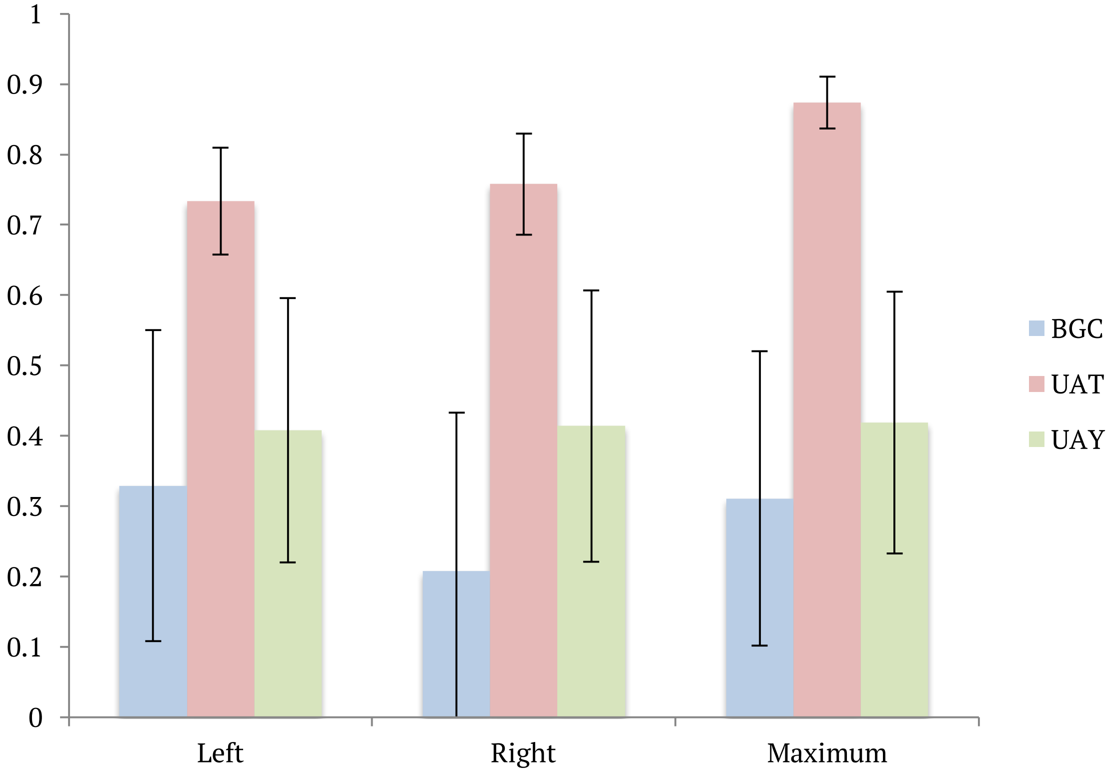


Figure 30. Antimeric h^2 estimates: C^1 Distal Accessory Ridge.

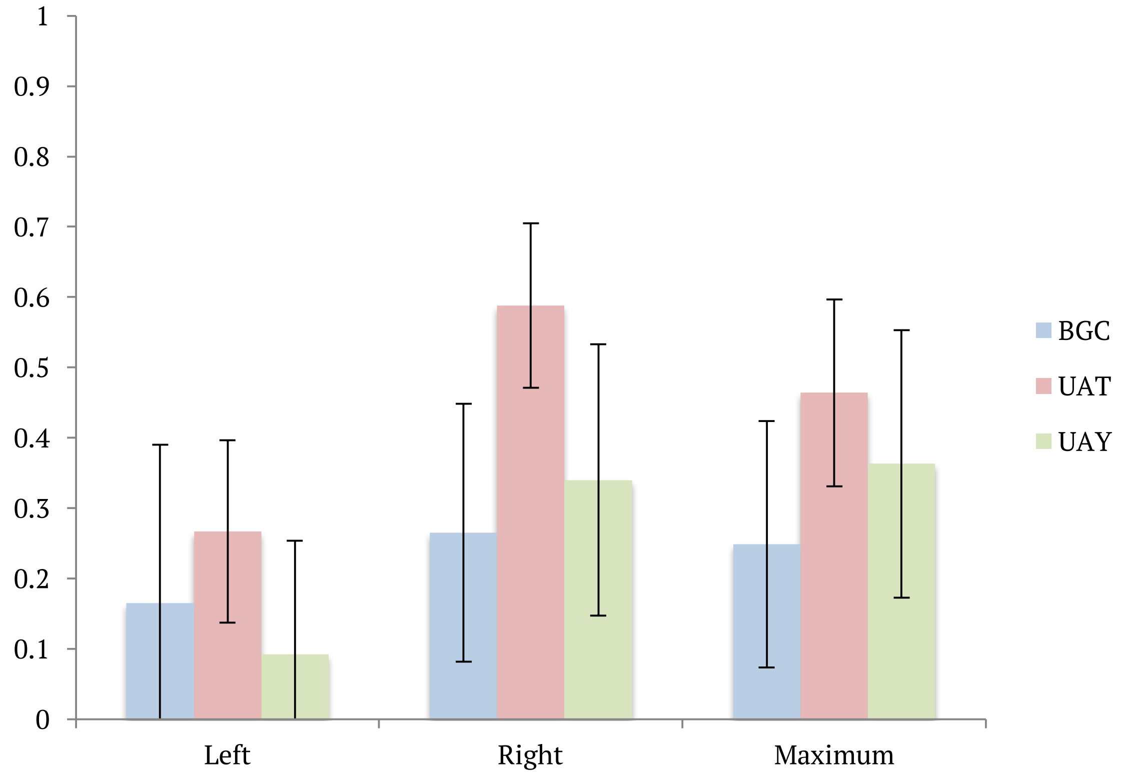


Figure 31. Antimeric h^2 estimates: M^2 Metacone.

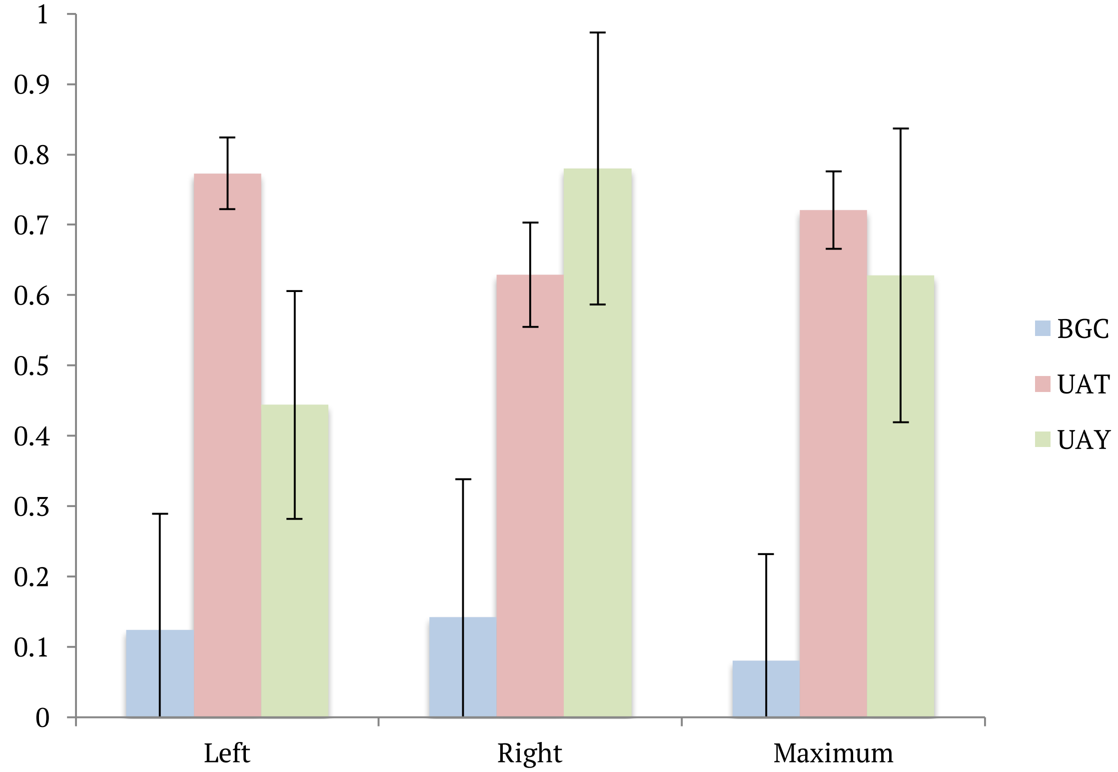


Figure 32. Antimeric h^2 estimates: M^1 Hypocone.

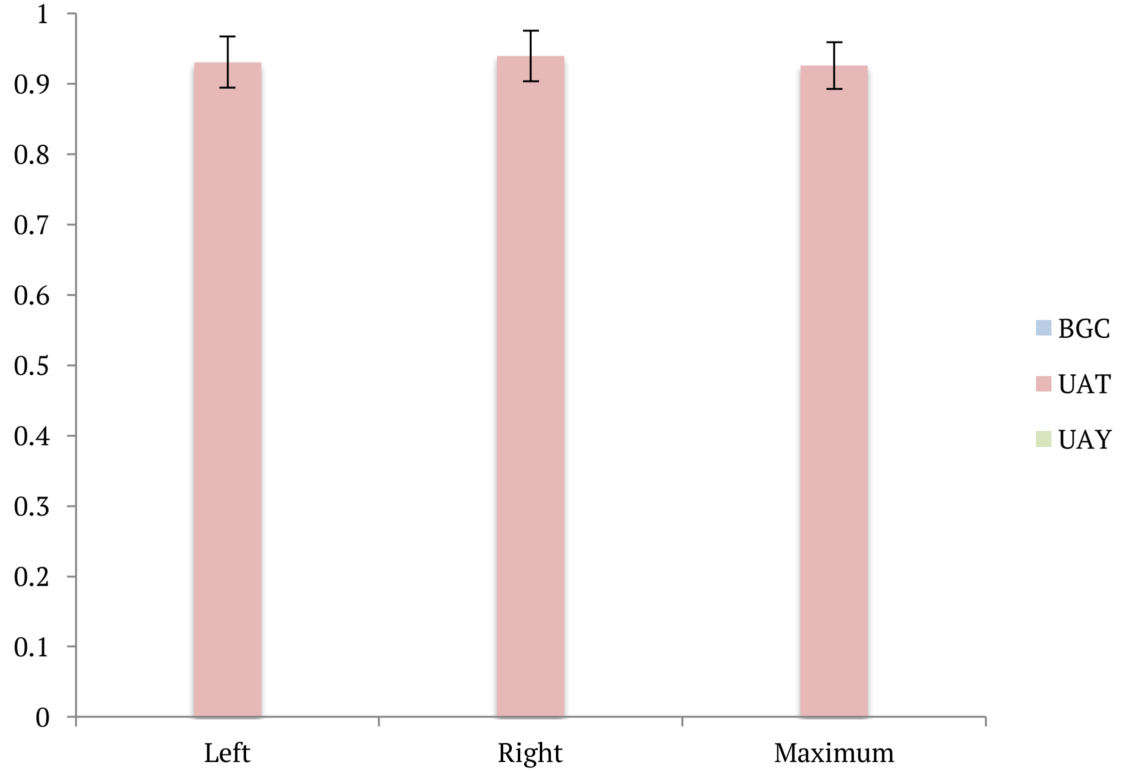


Figure 33. Antimeric h^2 estimates: M^2 Hypocone.

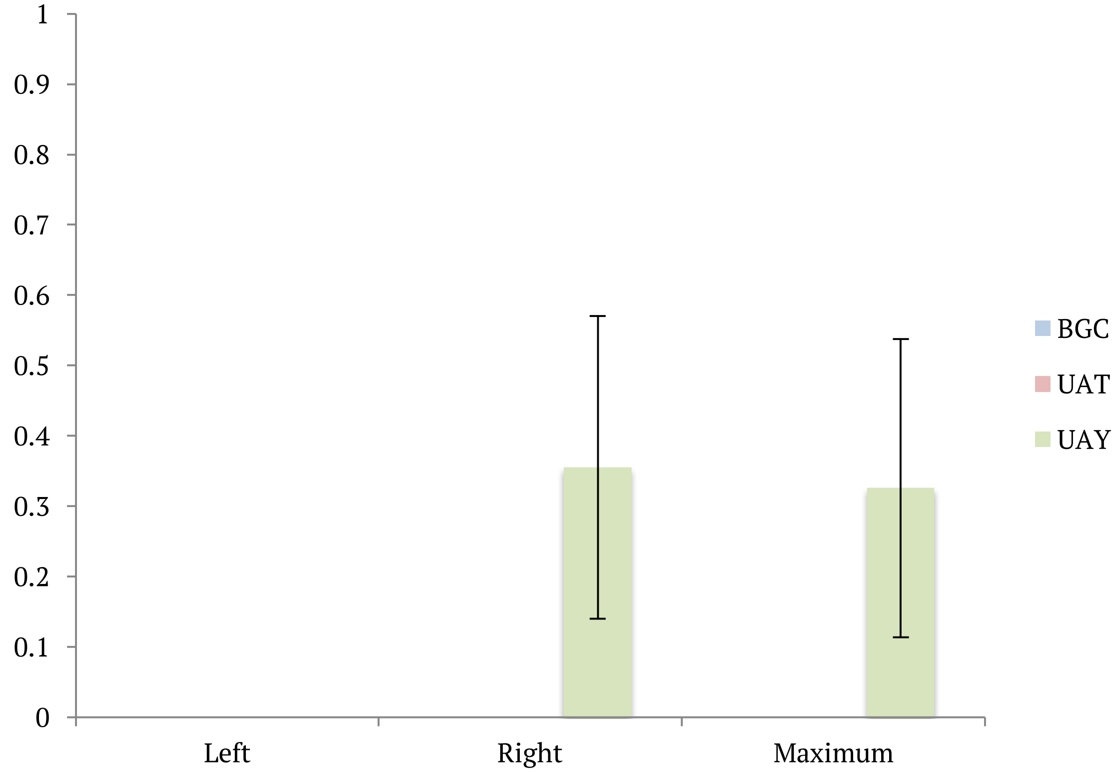


Figure 34. Antimeric h^2 estimates: M^1 Cusp 5.

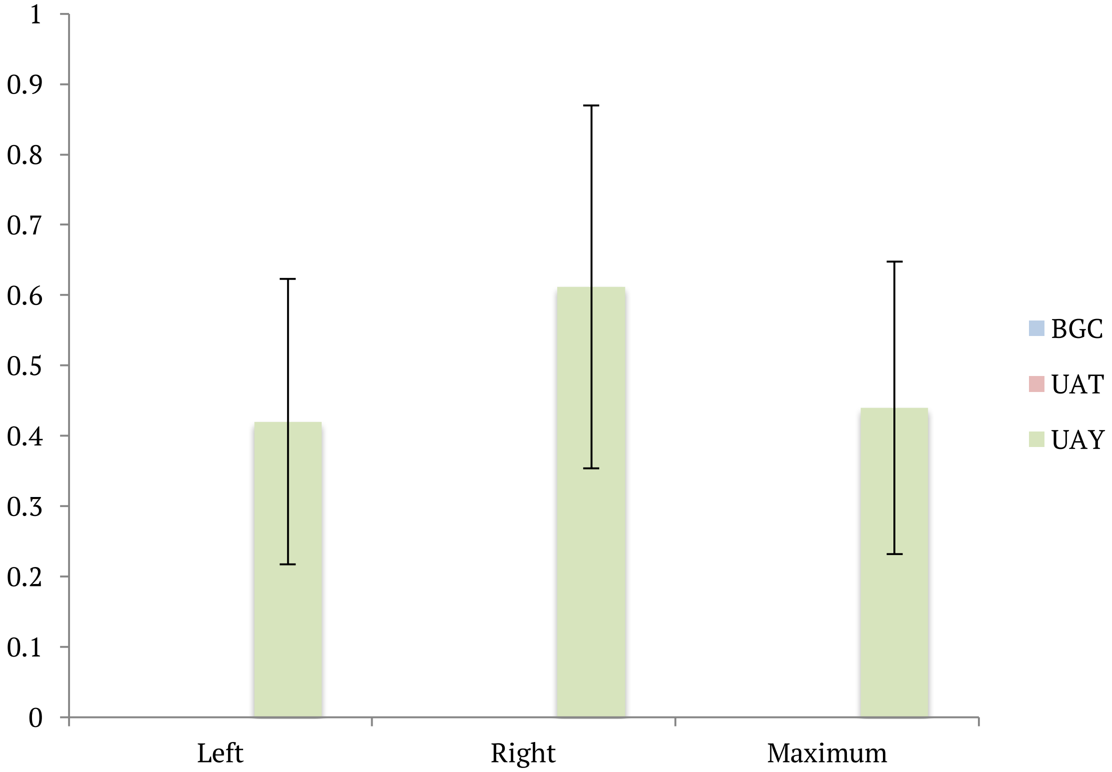


Figure 35. Antimeric h^2 estimates: M^2 Cusp 5.

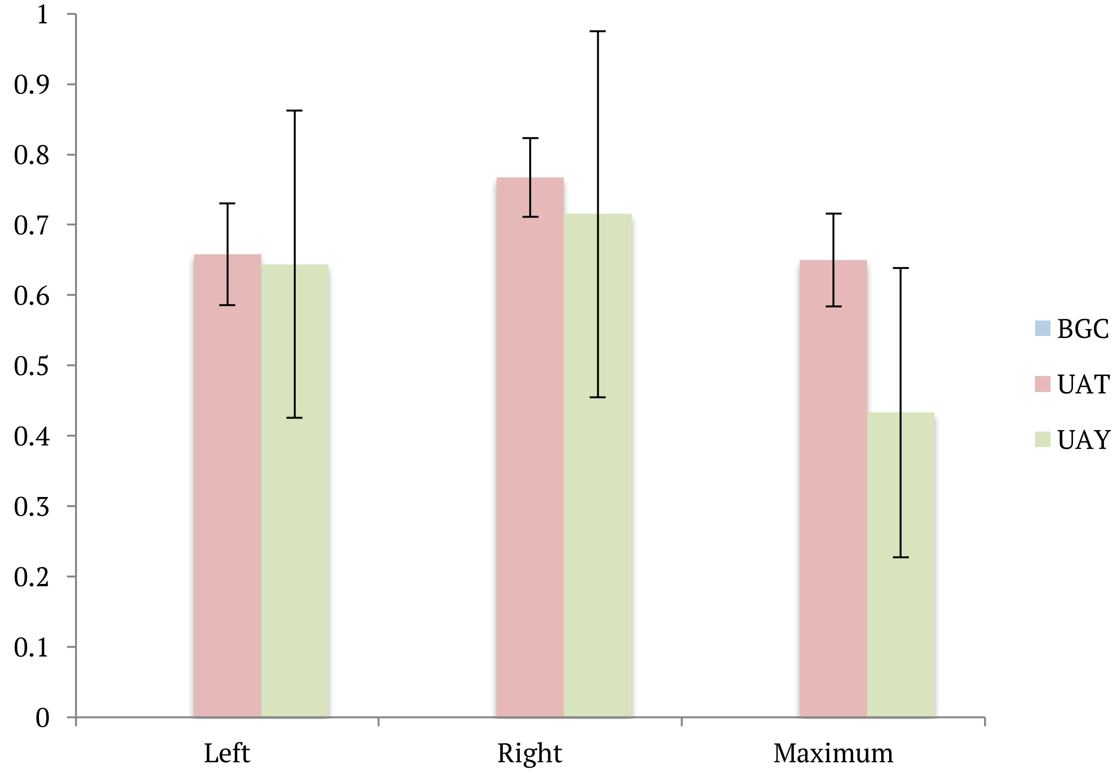


Figure 36. Antimeric h^2 estimates: M^1 Carabelli's Trait.

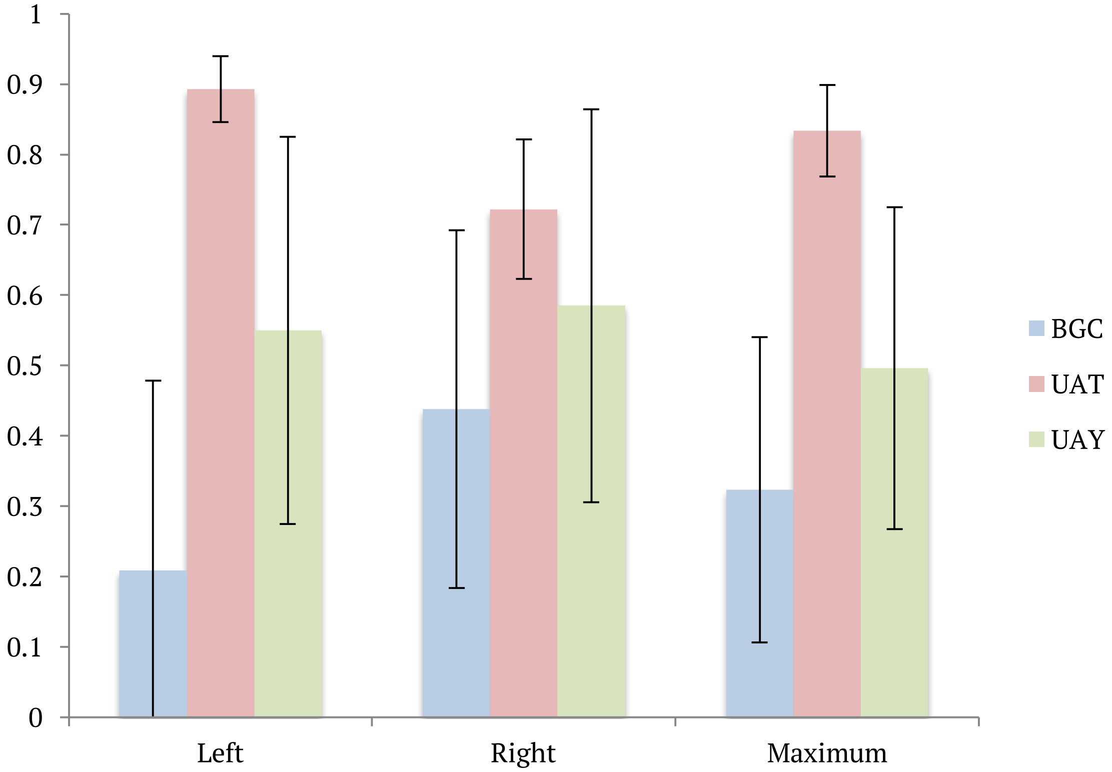


Figure 37. Antimeric h^2 estimates: M^2 Carabelli's Trait.

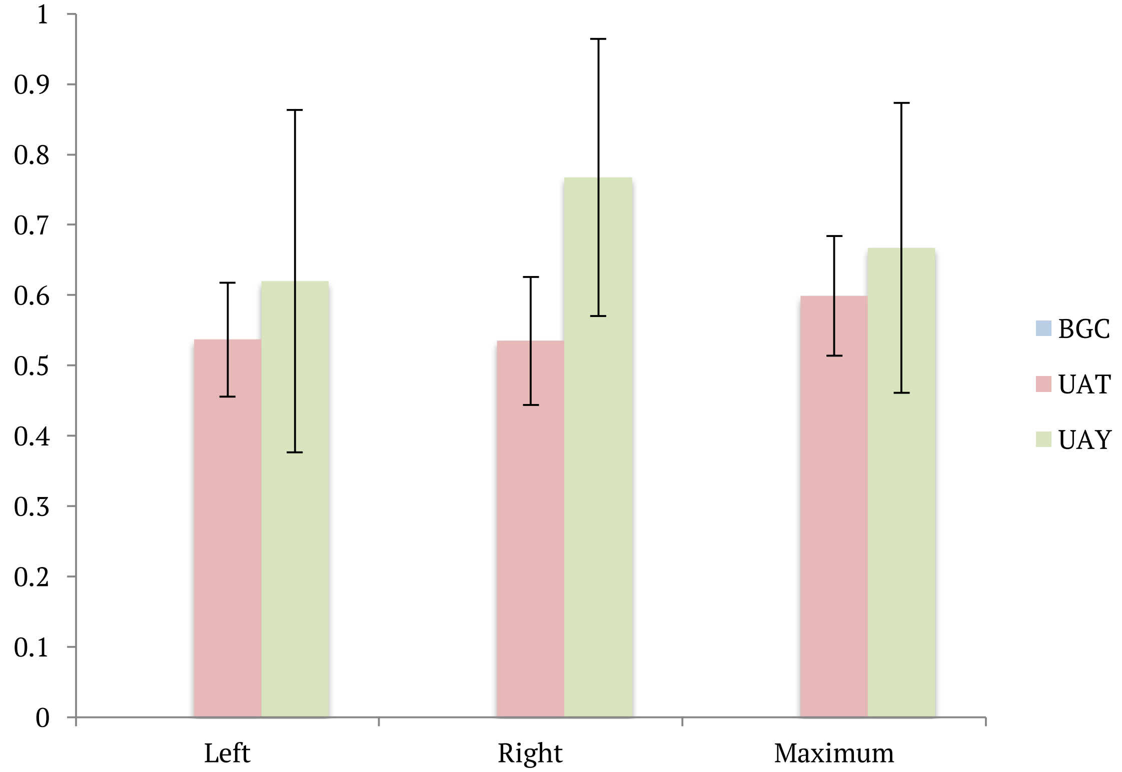


Figure 38. Antimeric h^2 estimates: I_1 Shoveling.

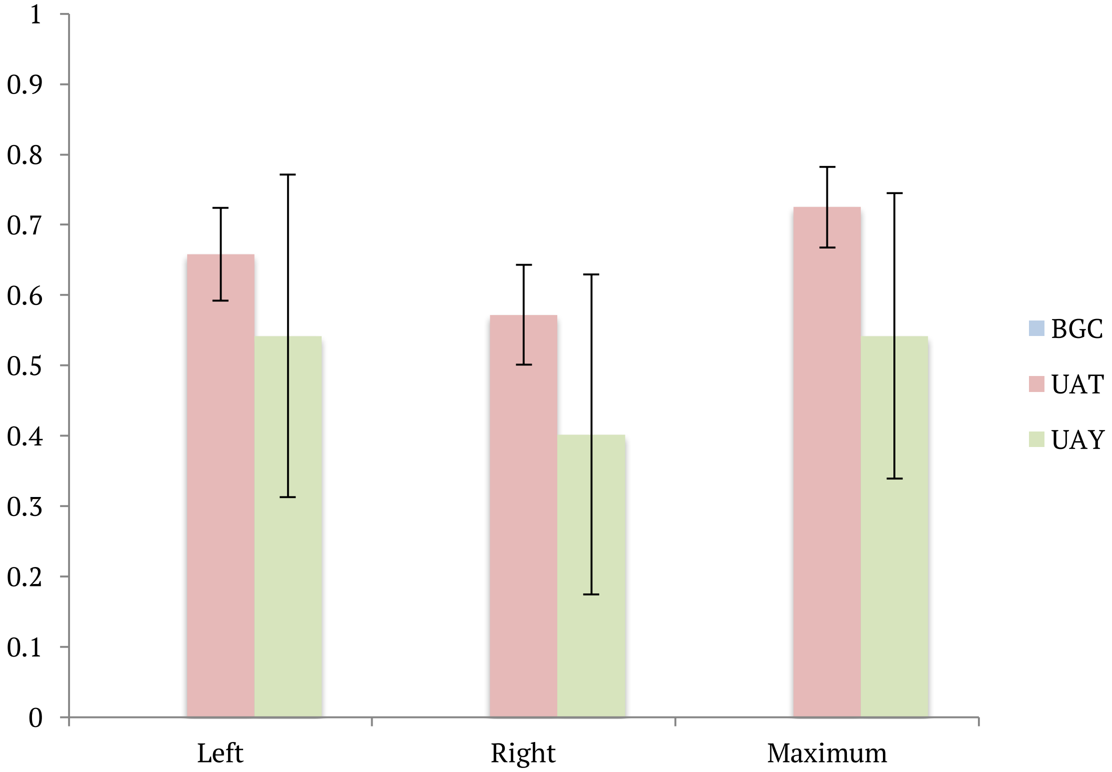


Figure 39. Antimeric h^2 estimates: I_2 Shoveling.

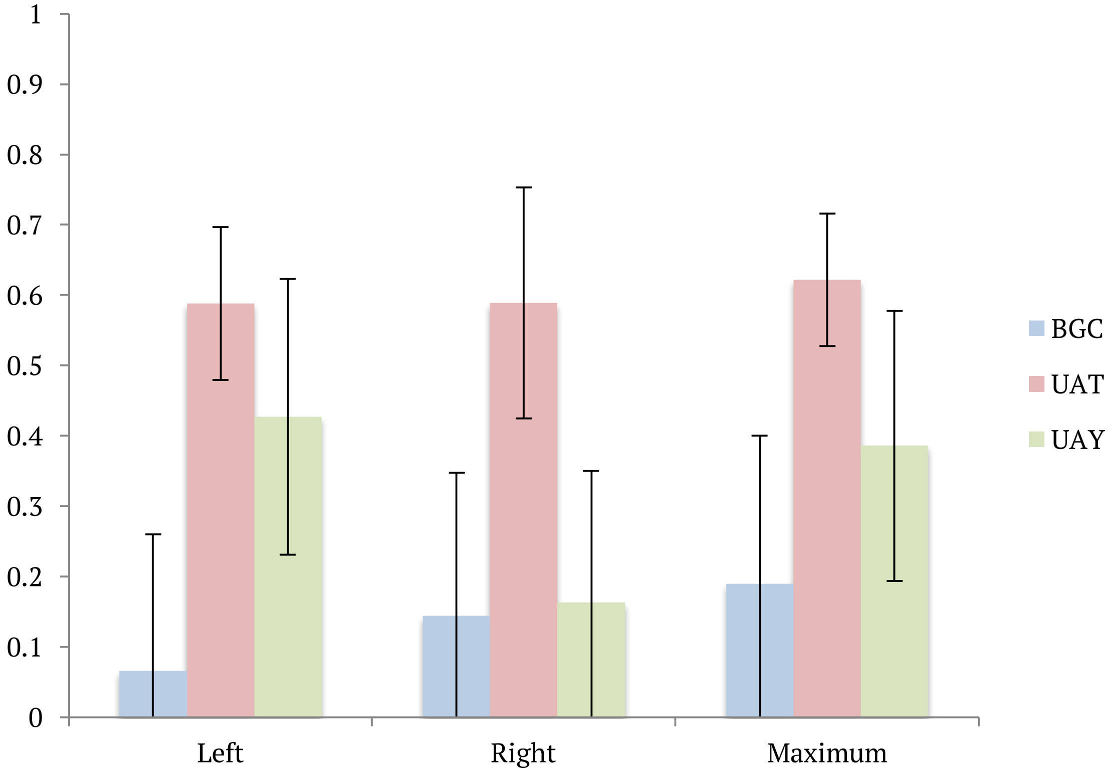


Figure 40. Antimeric h^2 estimates: C_1 Distal Accessory Ridge.

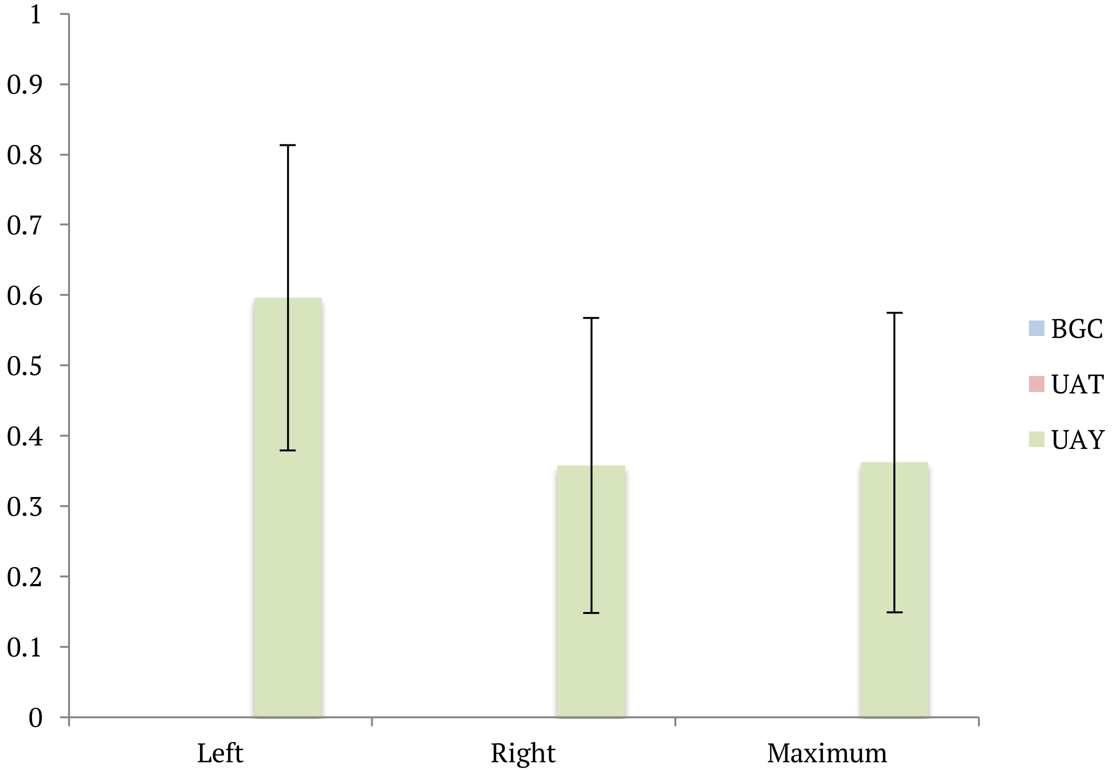


Figure 41. Antimeric h^2 estimates: M_1 Anterior Fovea.

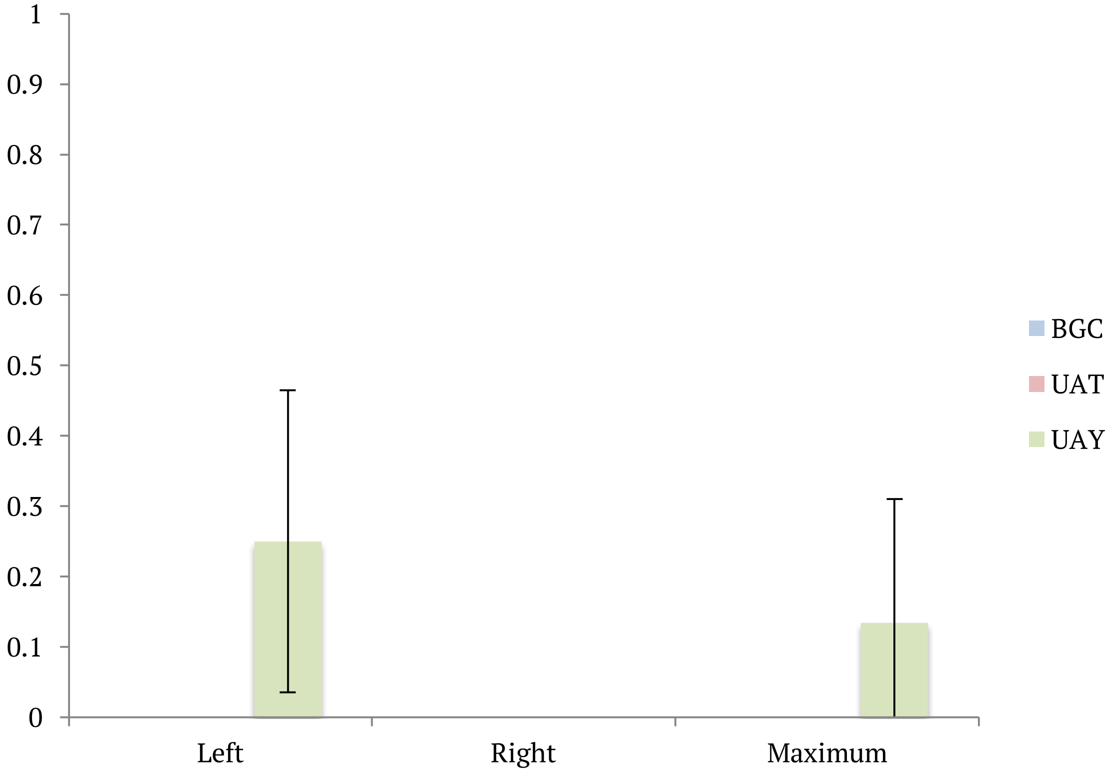


Figure 42. Antimeric h^2 estimates: M_2 Cusp Number.

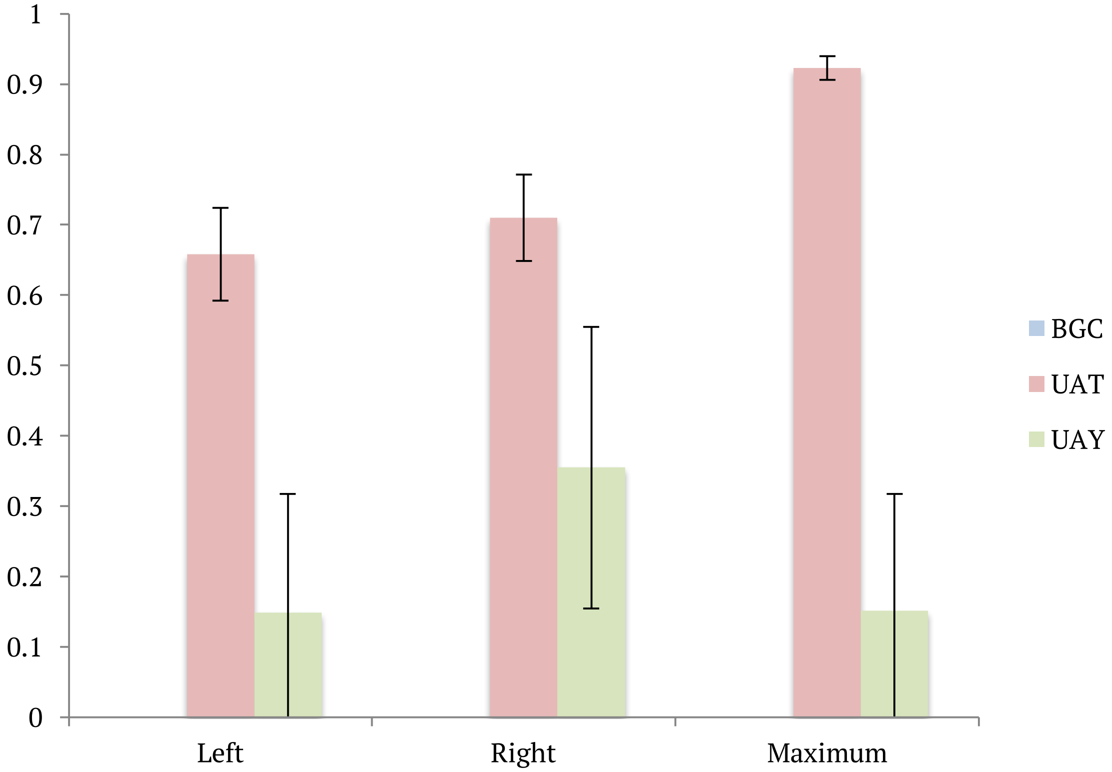


Figure 43. Antimeric h^2 estimates: M_1 Deflecting Wrinkle.

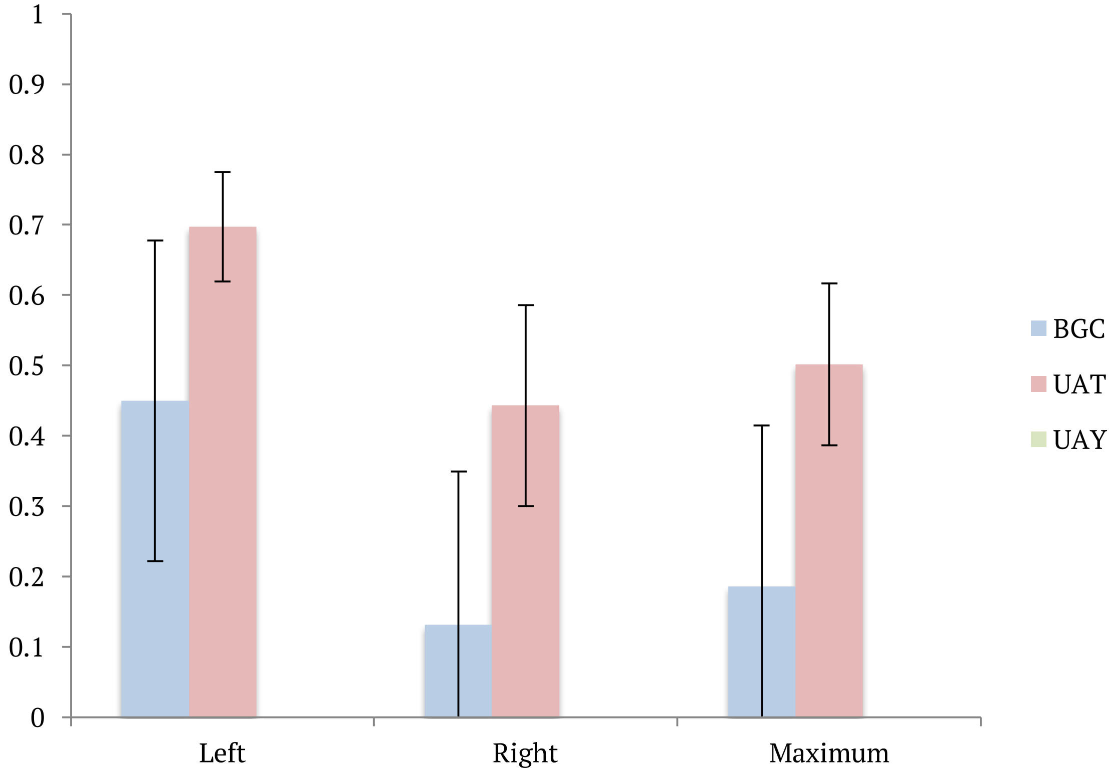


Figure 44. Antimeric h^2 estimates: M_1 Protostylid.

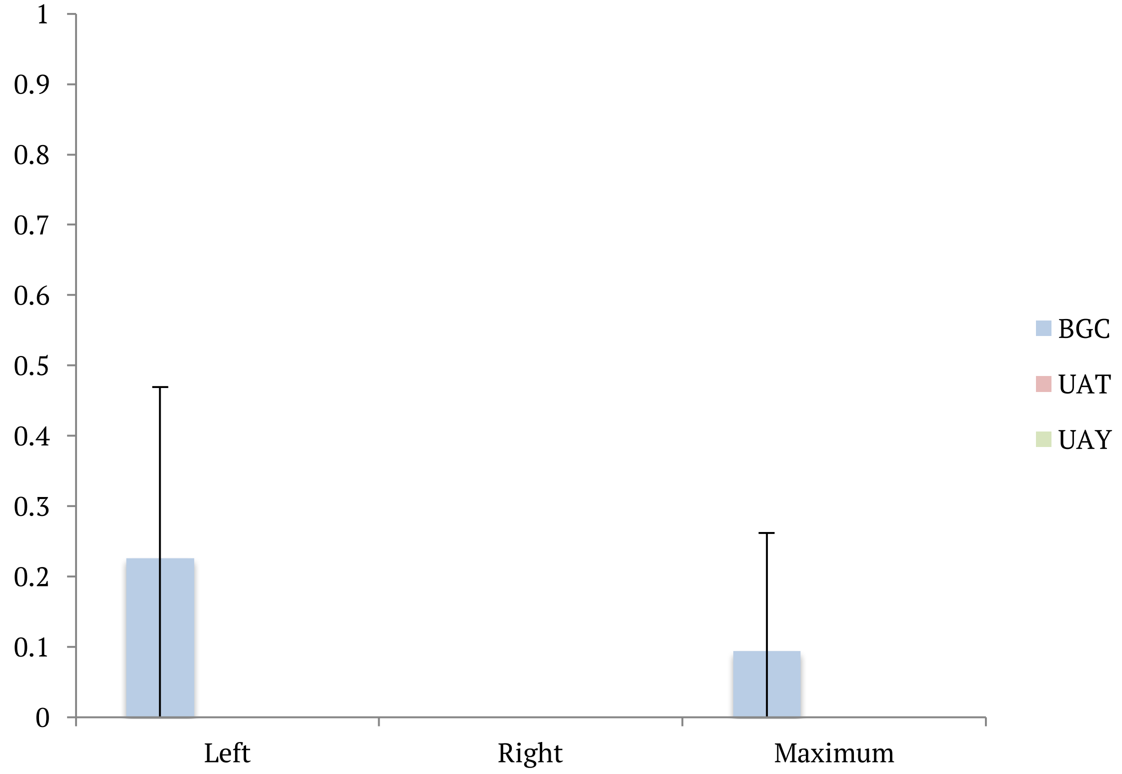


Figure 45. Antimeric h^2 estimates: M_2 Protostylid.

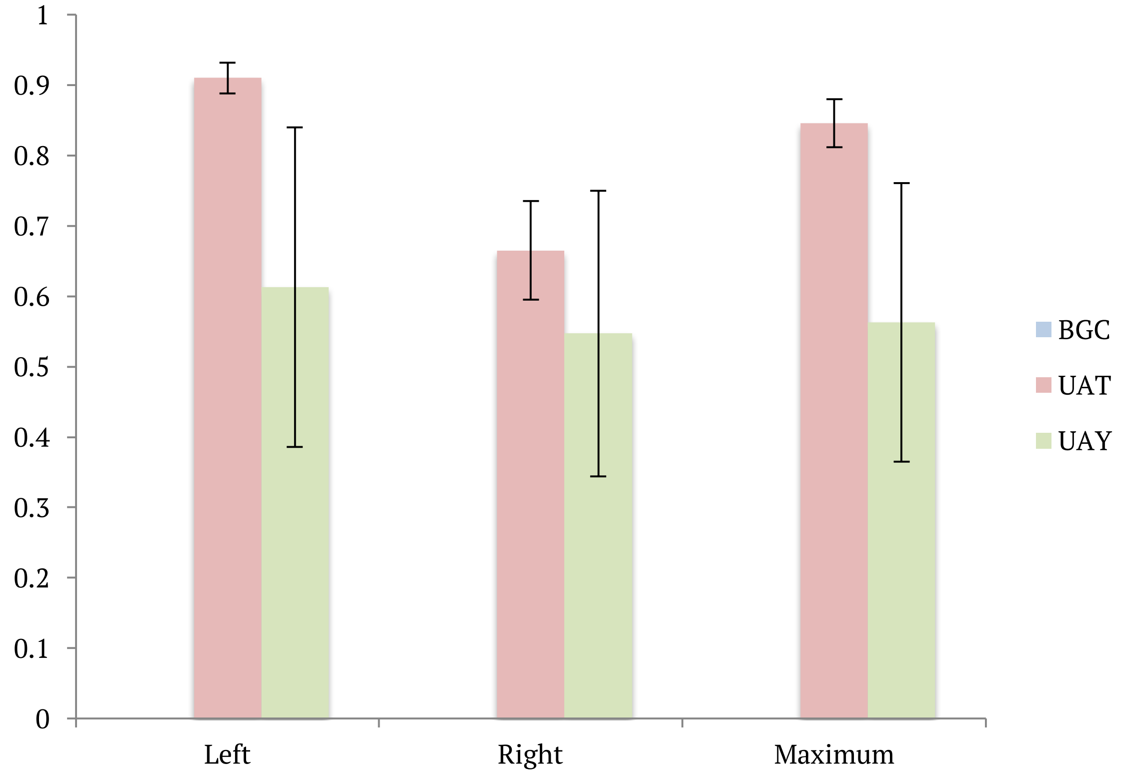


Figure 46. Antimeric h^2 estimates: M_1 Cusp 5.

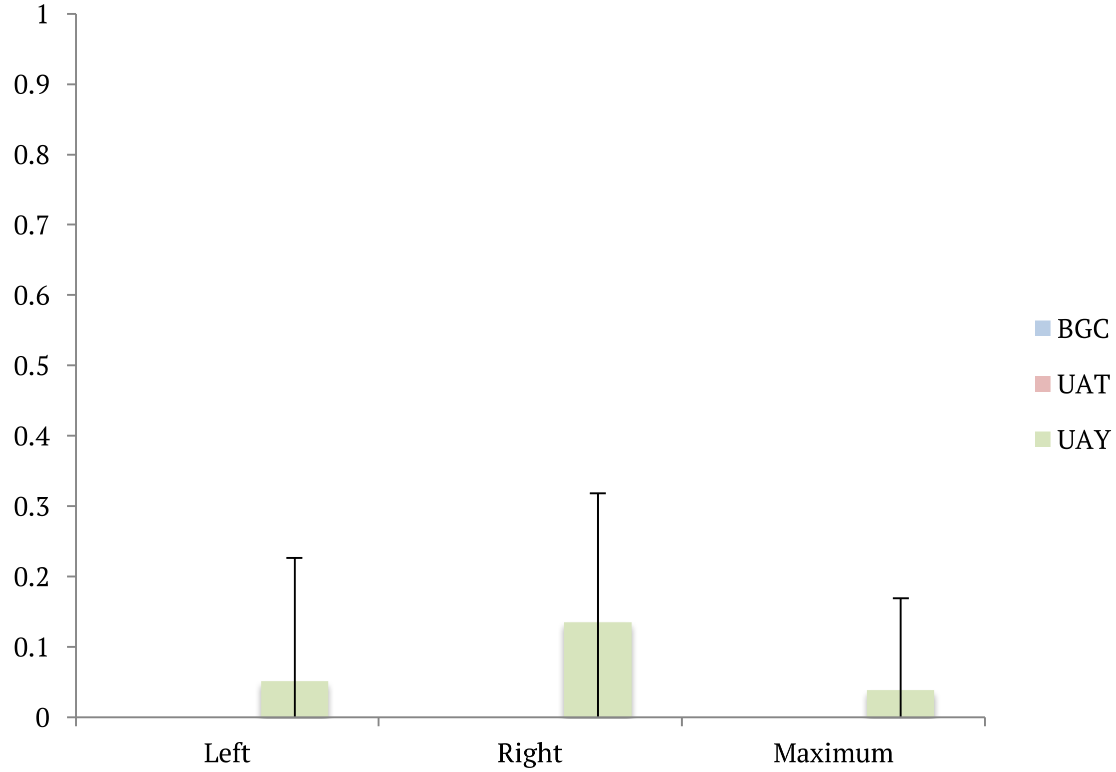


Figure 47. Antimeric h^2 estimates: M_2 Cusp 5.

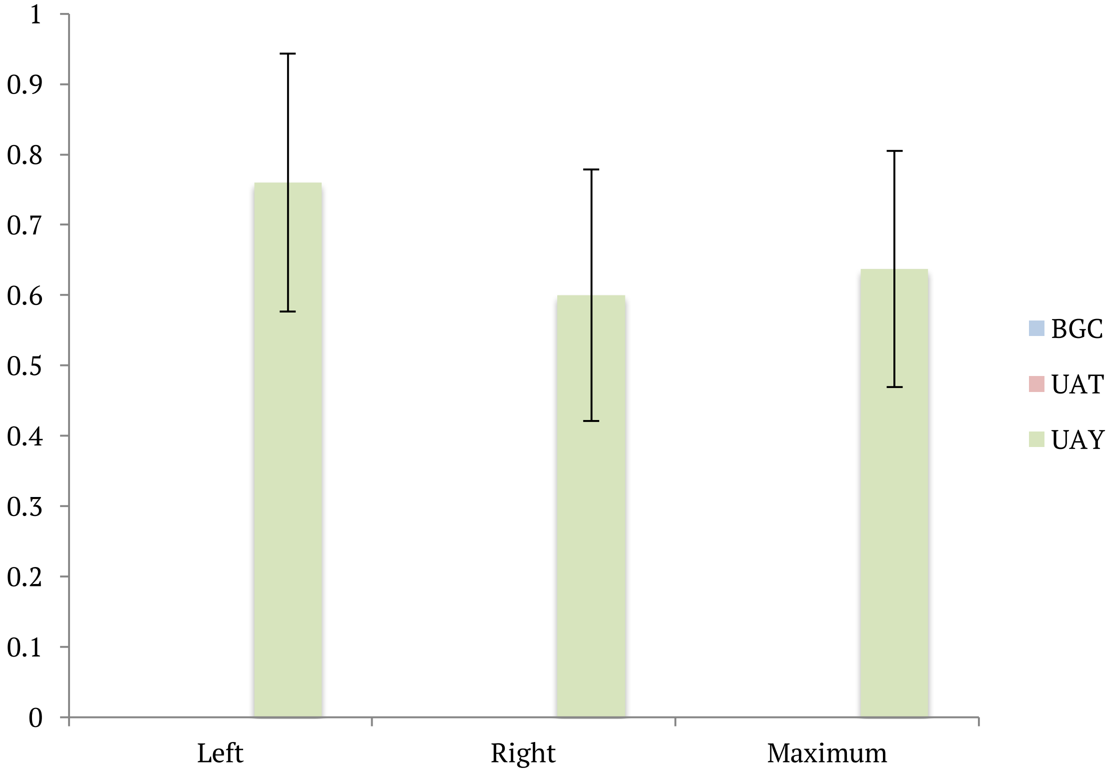
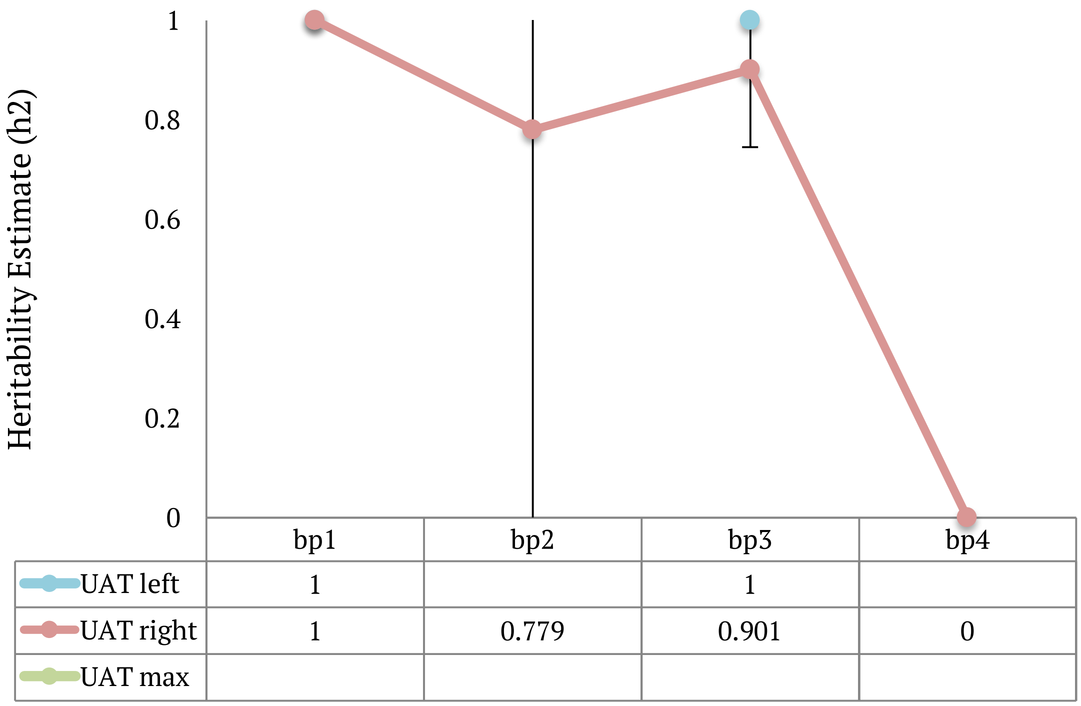


Figure 48. Antimeric *h*^{2} estimates: M_1 Cusp 6.

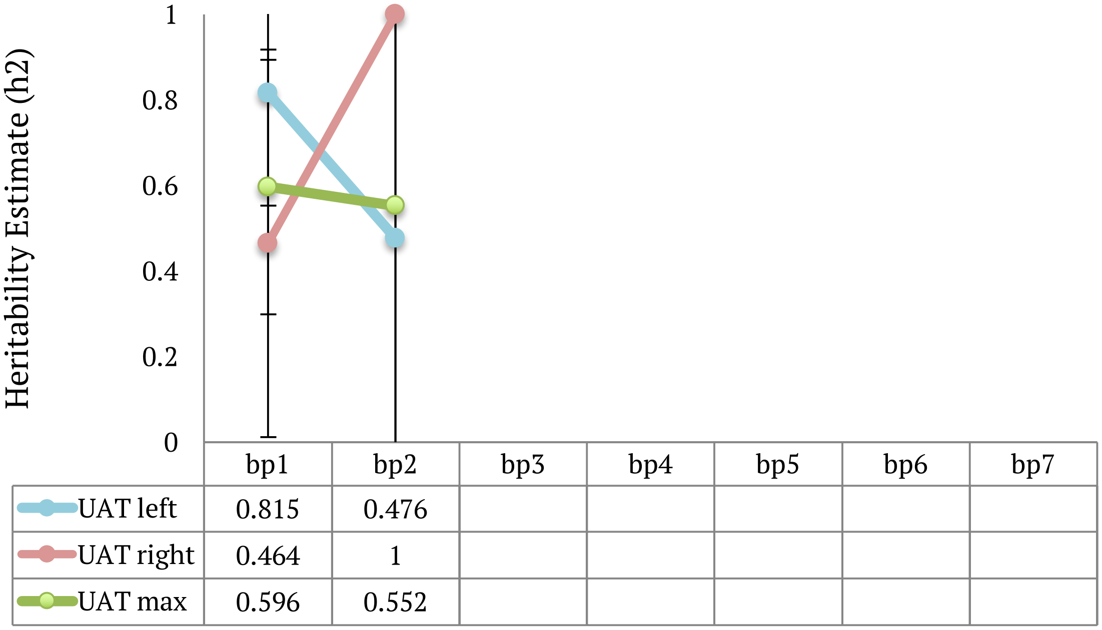
APPENDIX N

DICHOTOMIZATION BREAKPOINT HERITABILITY ESTIMATE COMPARISONS



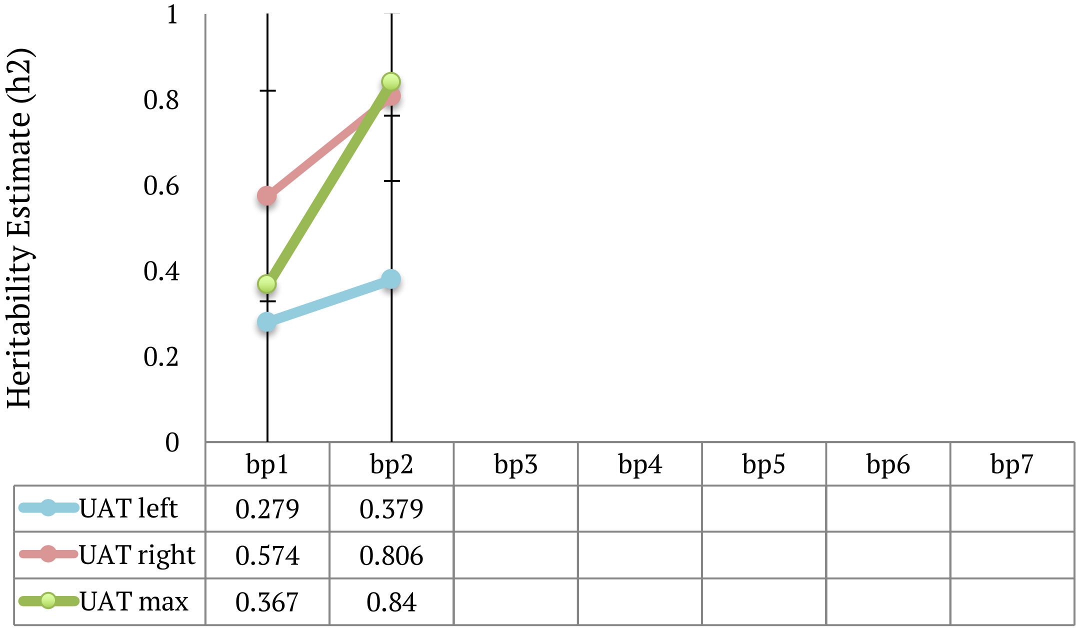
	bp1	bp2	bp3	bp4
UAT left	1		1	
UAT right	1	0.779	0.901	0
UAT max				

Figure 1. Breakpoint h^2 estimates: i^1 winging.



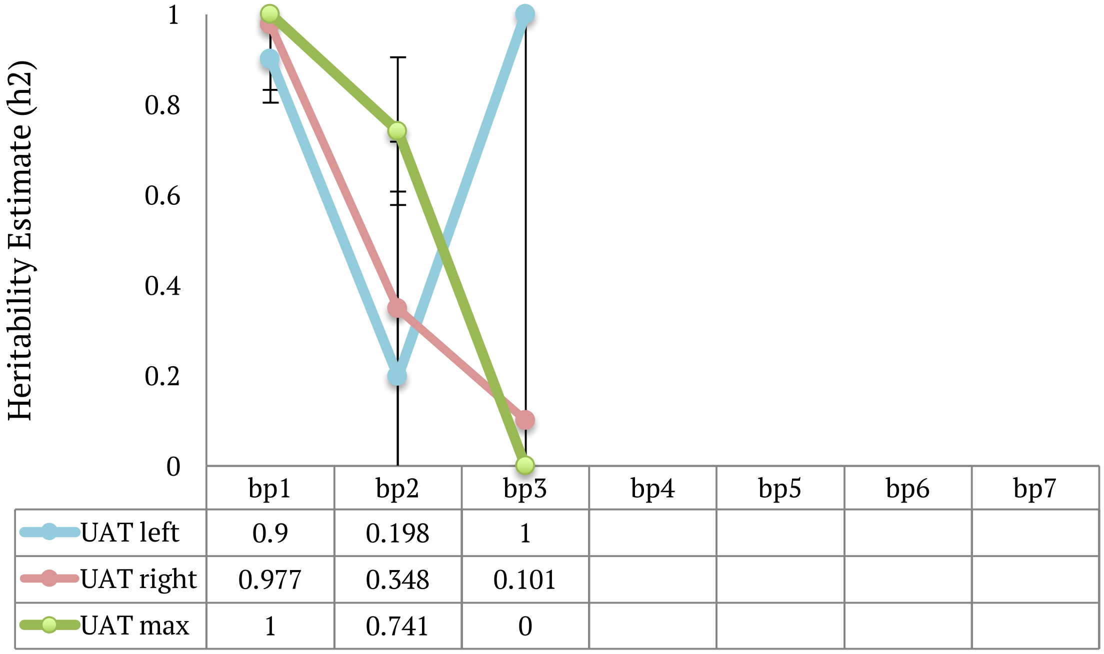
	bp1	bp2	bp3	bp4	bp5	bp6	bp7
UAT left	0.815	0.476					
UAT right	0.464	1					
UAT max	0.596	0.552					

Figure 2. Breakpoint h^2 estimates: i^1 shoveling.



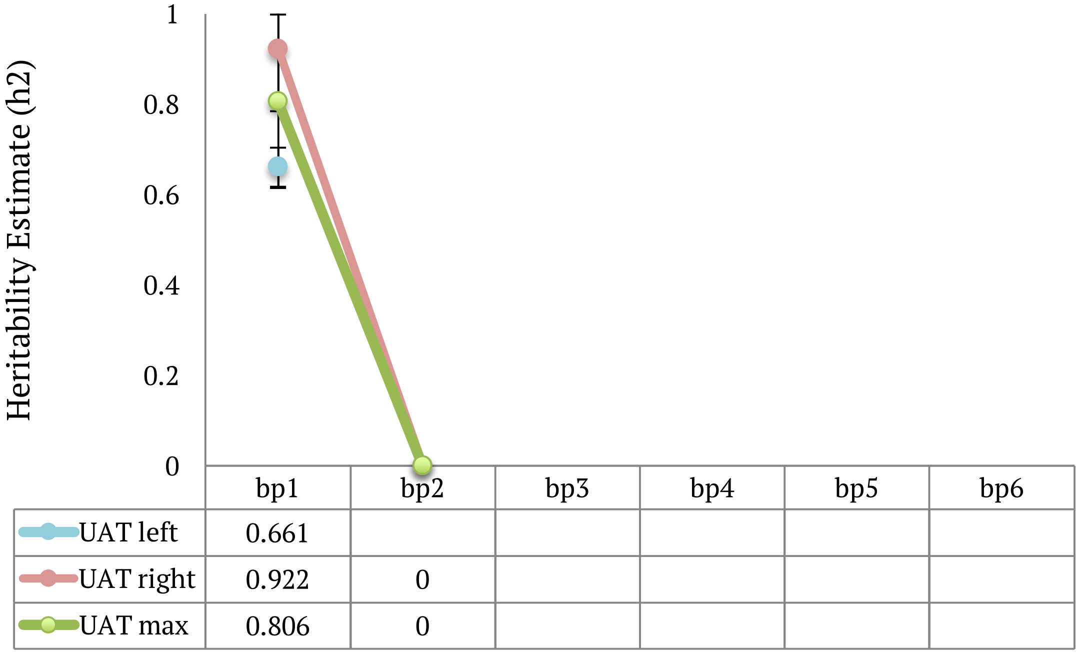
	bp1	bp2	bp3	bp4	bp5	bp6	bp7
UAT left	0.279	0.379					
UAT right	0.574	0.806					
UAT max	0.367	0.84					

Figure 3. Breakpoint *h*^{2} estimates: i^2 shoveling.



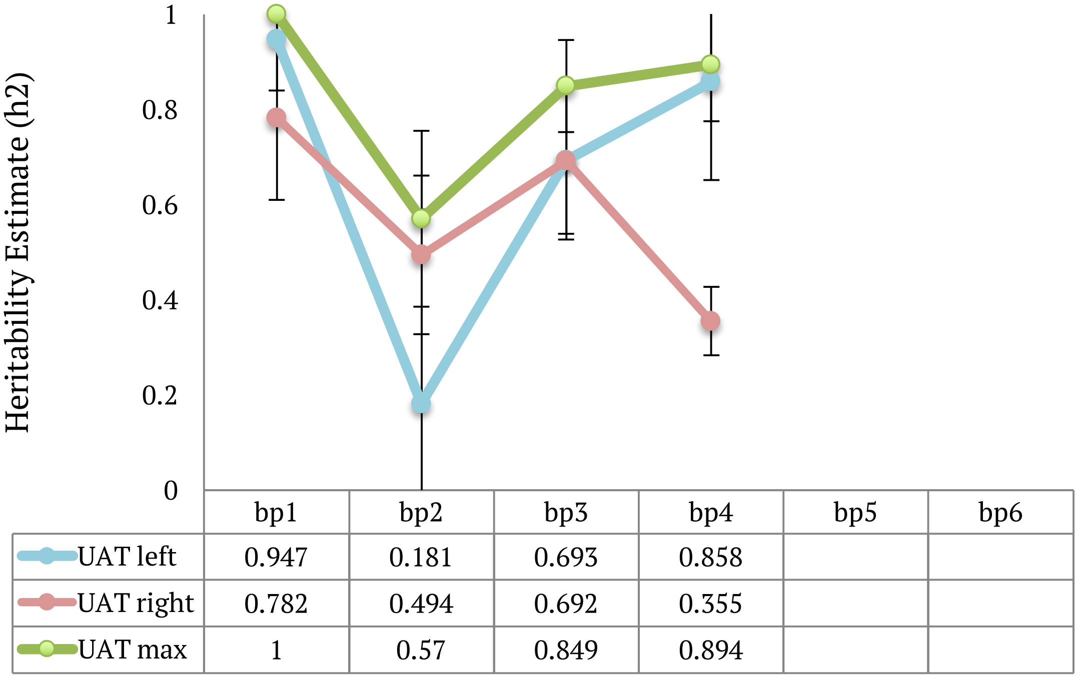
	bp1	bp2	bp3	bp4	bp5	bp6	bp7
UAT left	0.9	0.198	1				
UAT right	0.977	0.348	0.101				
UAT max	1	0.741	0				

Figure 4. Breakpoint *h*^{2} estimates: c^1 shoveling.



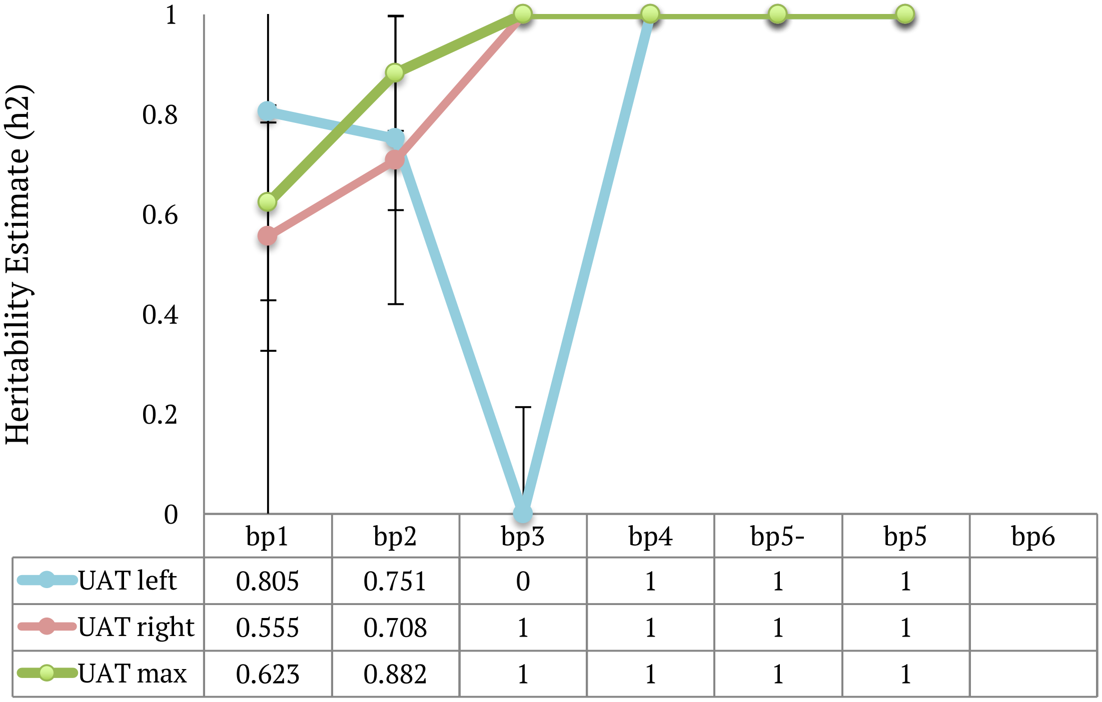
	bp1	bp2	bp3	bp4	bp5	bp6
UAT left	0.661					
UAT right	0.922	0				
UAT max	0.806	0				

Figure 5. Breakpoint h^2 estimates: i^1 double shoveling.



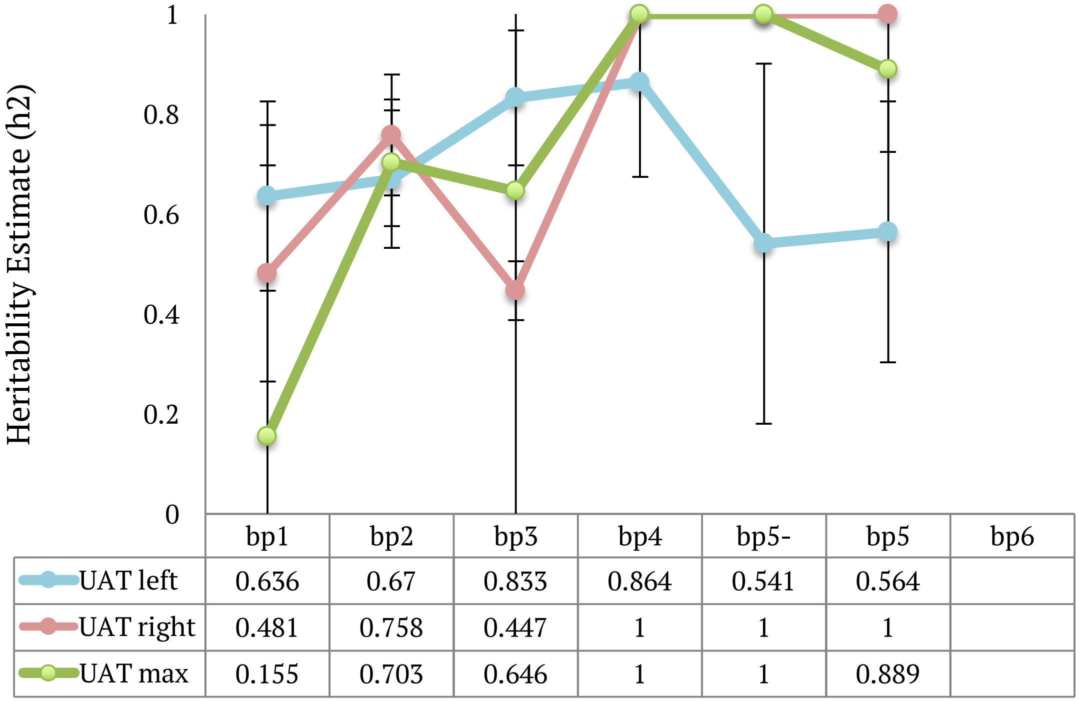
	bp1	bp2	bp3	bp4	bp5	bp6
UAT left	0.947	0.181	0.693	0.858		
UAT right	0.782	0.494	0.692	0.355		
UAT max	1	0.57	0.849	0.894		

Figure 6. Breakpoint *h*^{2} estimates: c^1 double shoveling.



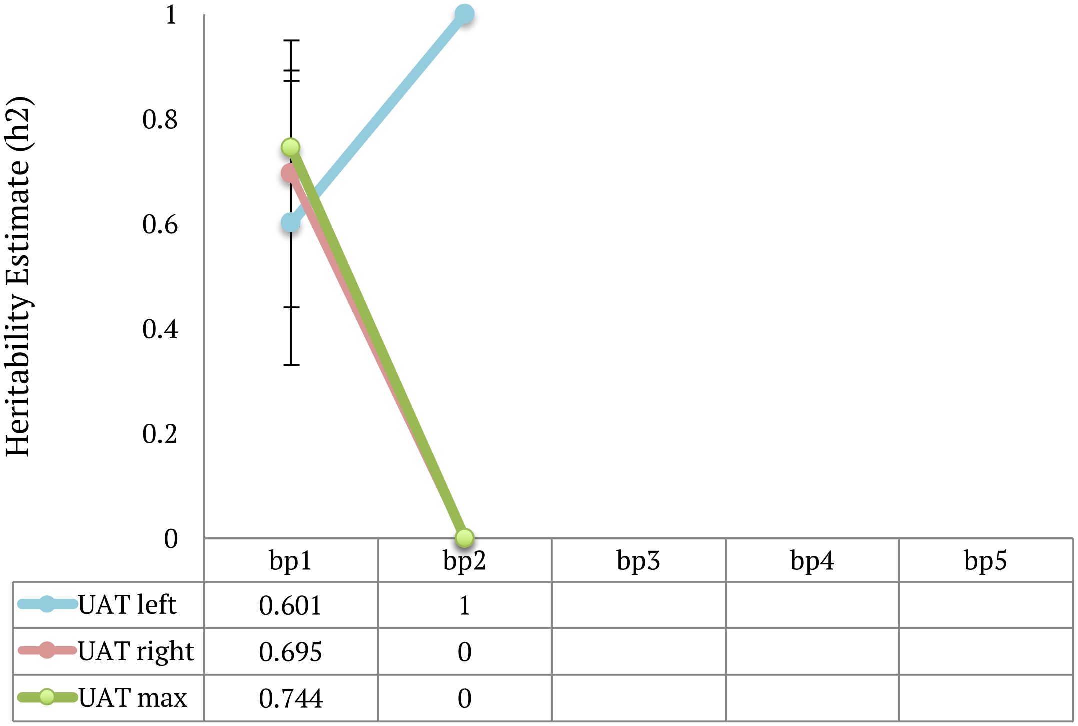
	bp1	bp2	bp3	bp4	bp5-	bp5	bp6
UAT left	0.805	0.751	0	1	1	1	
UAT right	0.555	0.708	1	1	1	1	
UAT max	0.623	0.882	1	1	1	1	

Figure 7. Breakpoint *h*^{2} estimates: i^1 tuberculum dentale.



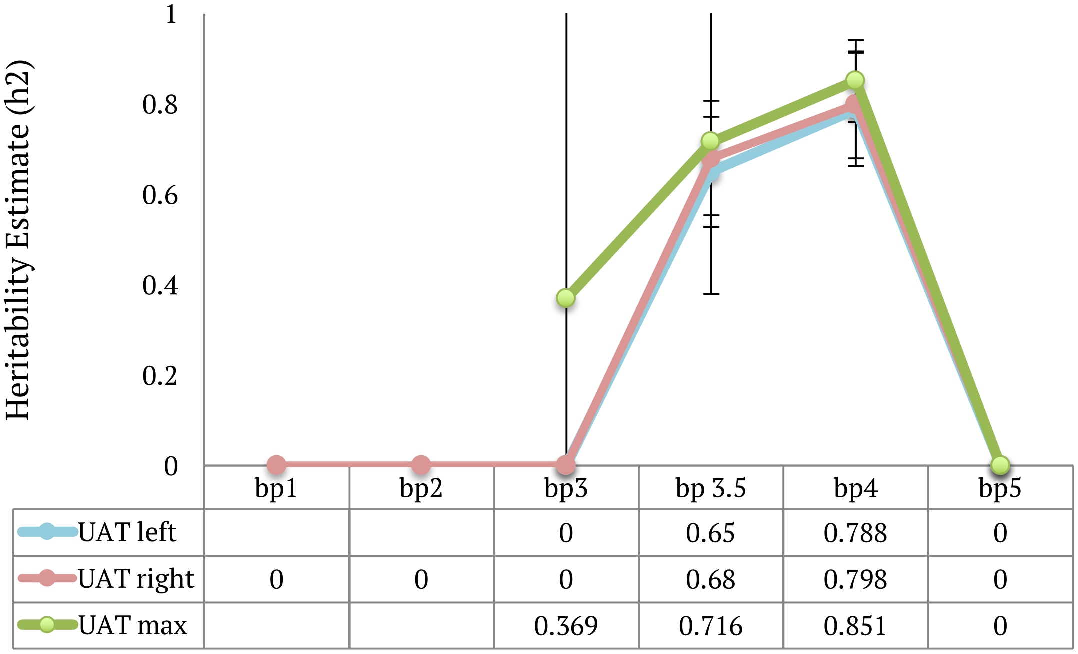
	bp1	bp2	bp3	bp4	bp5-	bp5	bp6
UAT left	0.636	0.67	0.833	0.864	0.541	0.564	
UAT right	0.481	0.758	0.447	1	1	1	
UAT max	0.155	0.703	0.646	1	1	0.889	

Figure 8. Breakpoint h^2 estimates: c^1 tuberculum dentale.



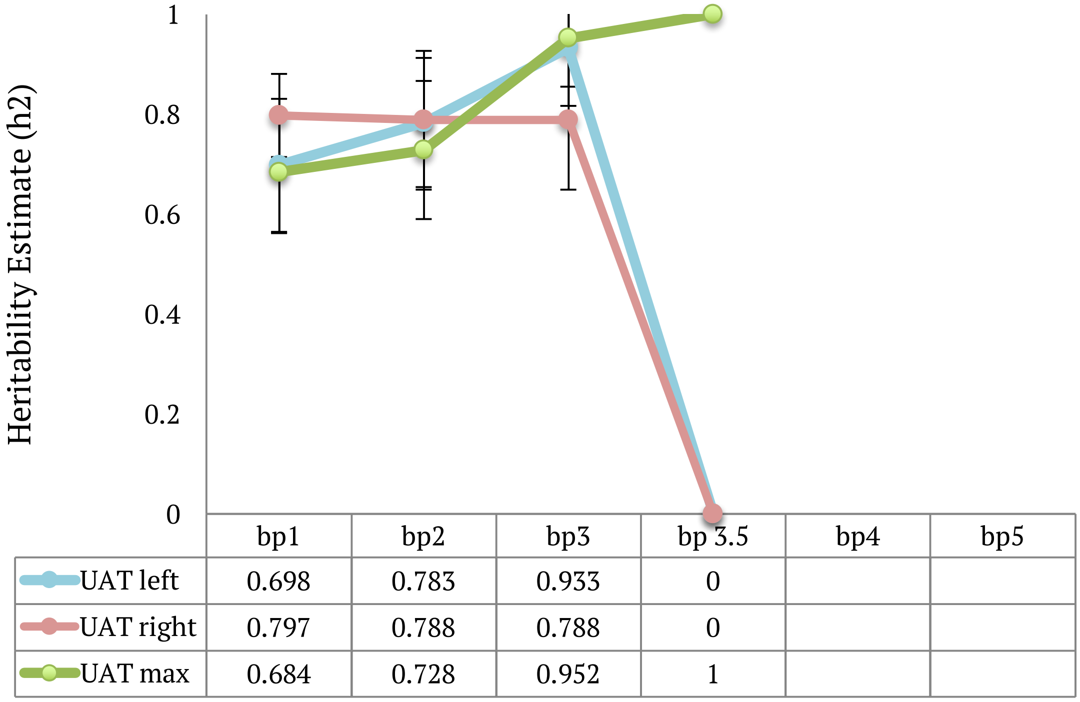
	bp1	bp2	bp3	bp4	bp5
UAT left	0.601	1			
UAT right	0.695	0			
UAT max	0.744	0			

Figure 9. Breakpoint h^2 estimates: c^1 distal accessory ridge.



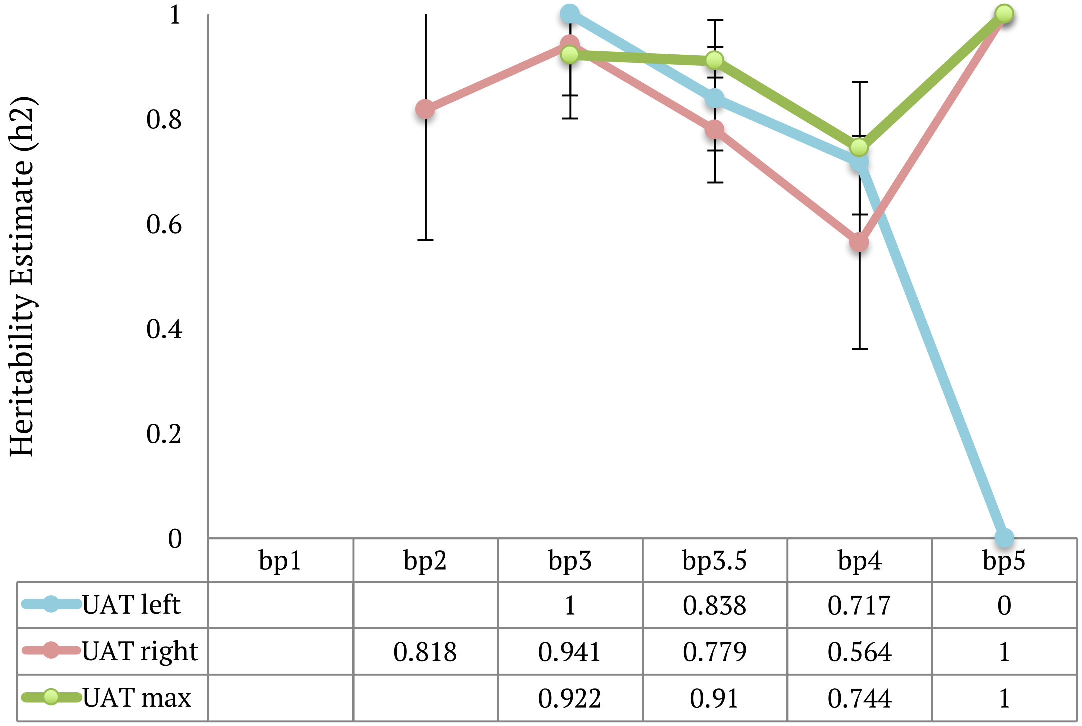
	bp1	bp2	bp3	bp 3.5	bp4	bp5
UAT left			0	0.65	0.788	0
UAT right	0	0	0	0.68	0.798	0
UAT max			0.369	0.716	0.851	0

Figure 10. Breakpoint *h*^{2} estimates: m^2 metacone.



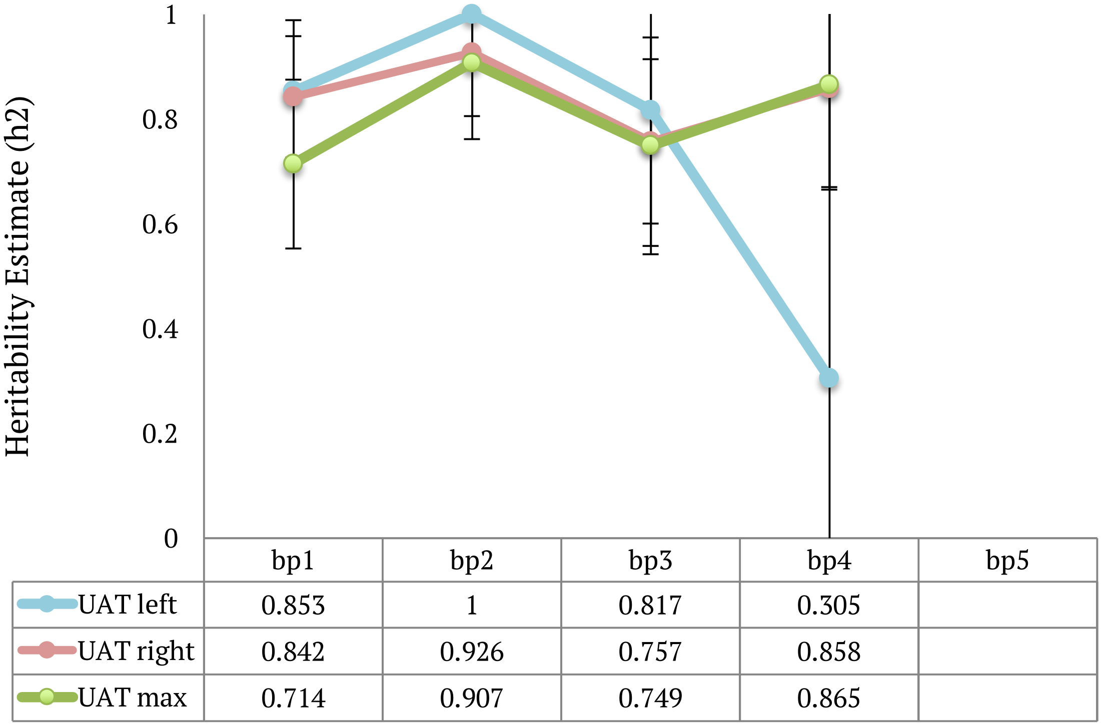
	bp1	bp2	bp3	bp 3.5	bp4	bp5
UAT left	0.698	0.783	0.933	0		
UAT right	0.797	0.788	0.788	0		
UAT max	0.684	0.728	0.952	1		

Figure 11. Breakpoint h^2 estimates: m^1 hypocone.



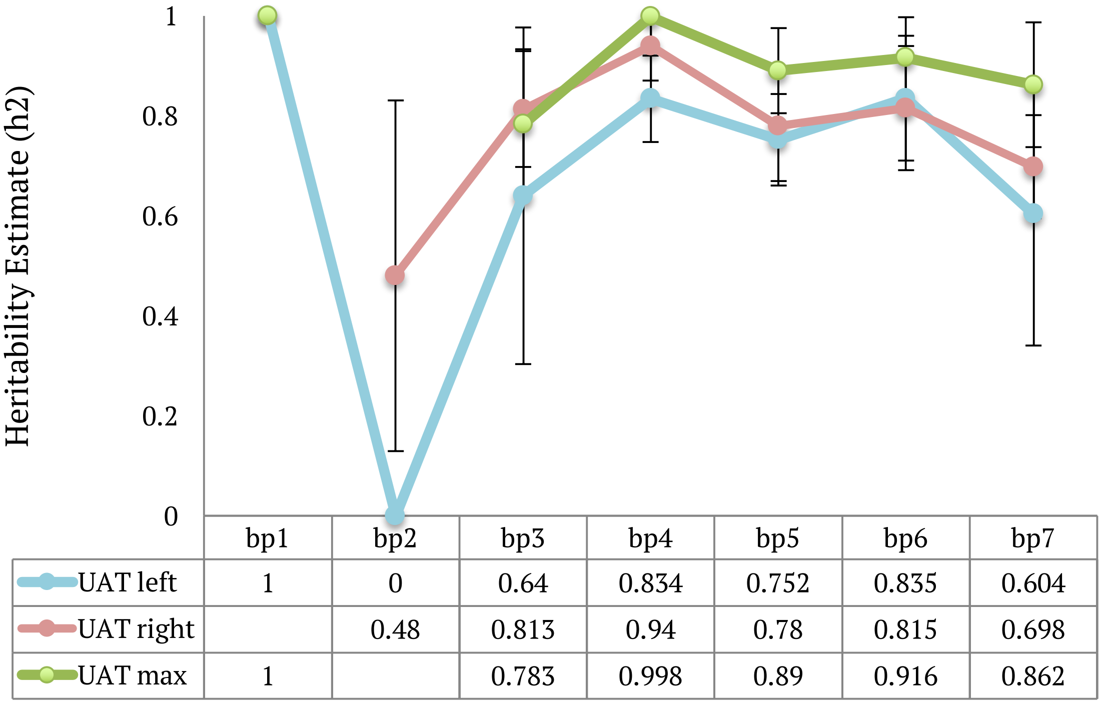
	bp1	bp2	bp3	bp3.5	bp4	bp5
UAT left			1	0.838	0.717	0
UAT right		0.818	0.941	0.779	0.564	1
UAT max			0.922	0.91	0.744	1

Figure 12. Breakpoint h^2 estimates: m^2 hypocone.



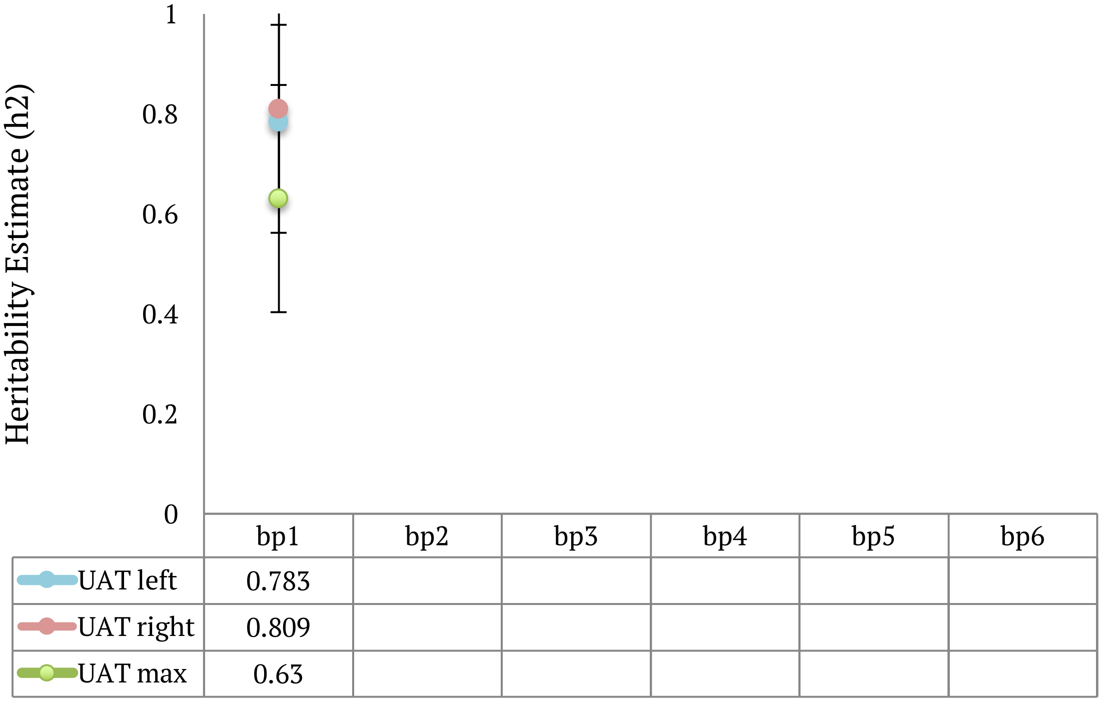
	bp1	bp2	bp3	bp4	bp5
UAT left	0.853	1	0.817	0.305	
UAT right	0.842	0.926	0.757	0.858	
UAT max	0.714	0.907	0.749	0.865	

Figure 13. Breakpoint h^2 estimates: m^2 cusp 5.



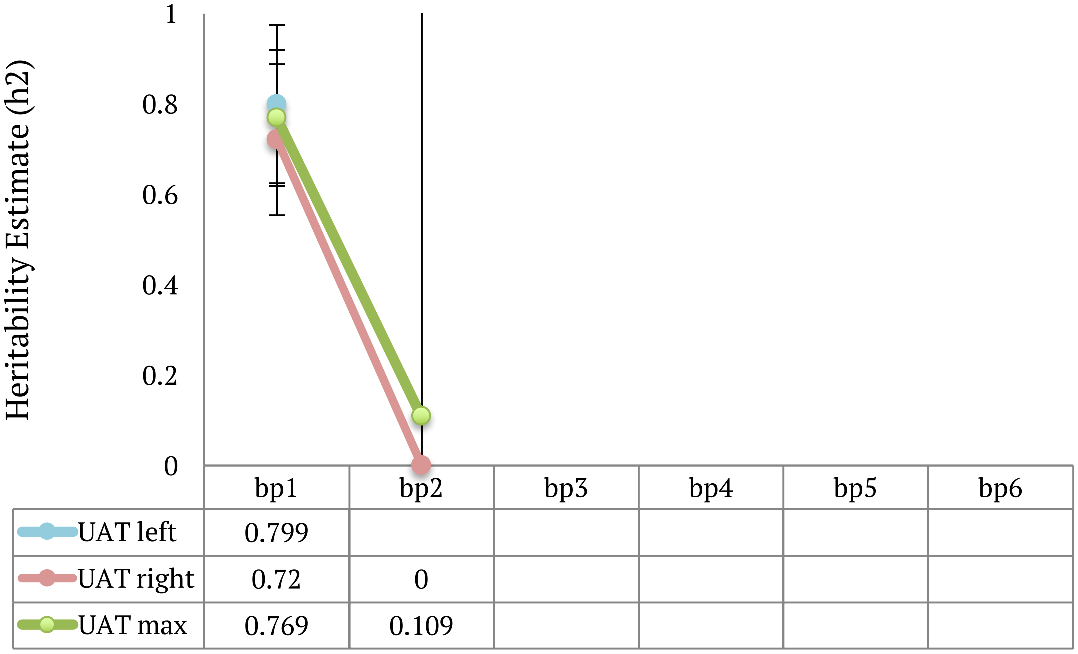
	bp1	bp2	bp3	bp4	bp5	bp6	bp7
UAT left	1	0	0.64	0.834	0.752	0.835	0.604
UAT right		0.48	0.813	0.94	0.78	0.815	0.698
UAT max	1		0.783	0.998	0.89	0.916	0.862

Figure 14. Breakpoint *h^2* estimates: m^2 Carabelli’s trait.



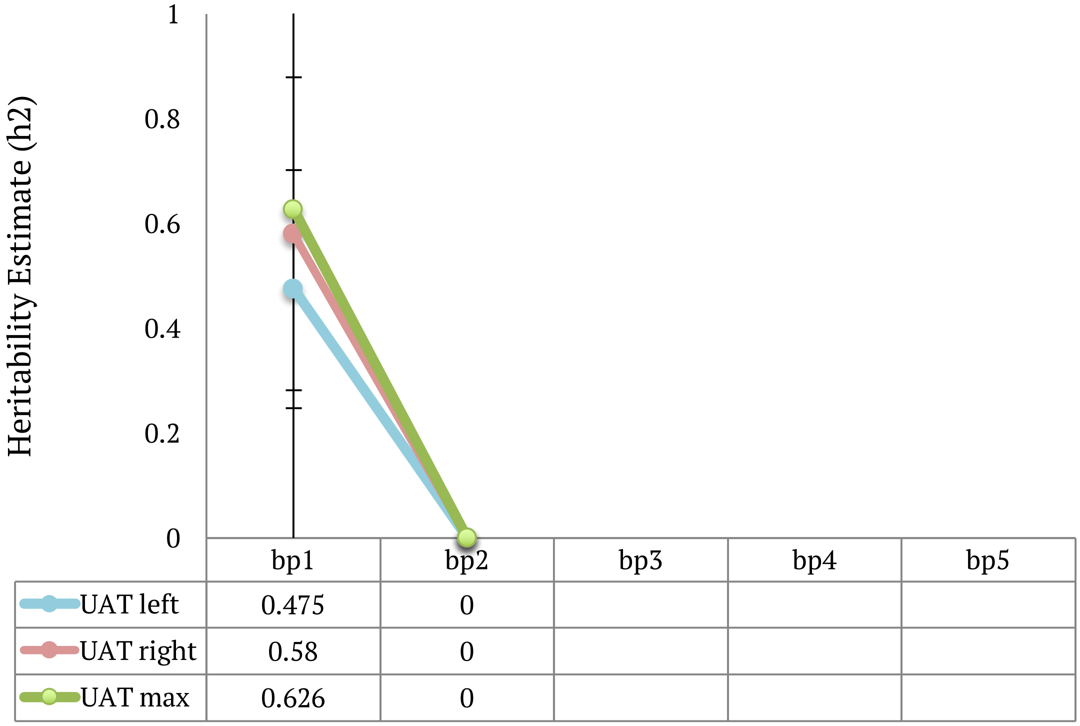
	bp1	bp2	bp3	bp4	bp5	bp6
UAT left	0.783					
UAT right	0.809					
UAT max	0.63					

Figure 15. Breakpoint h^2 estimates: i_1 shoveling.



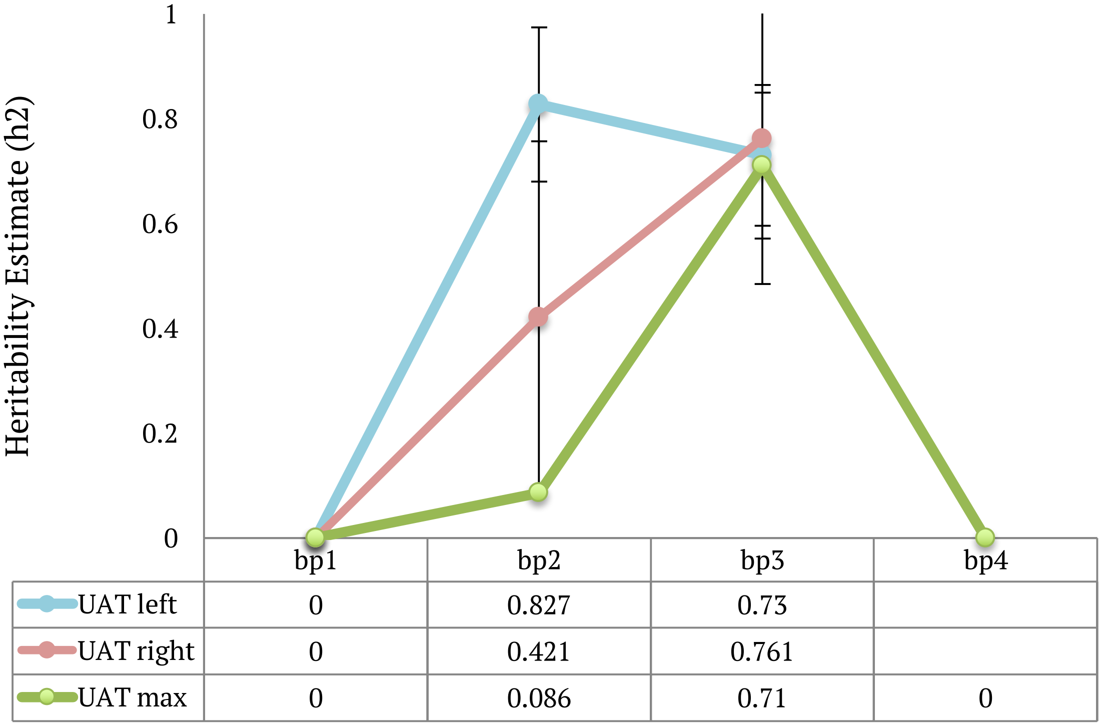
	bp1	bp2	bp3	bp4	bp5	bp6
UAT left	0.799					
UAT right	0.72	0				
UAT max	0.769	0.109				

Figure 16. Breakpoint h^2 estimates: i_2 shoveling.



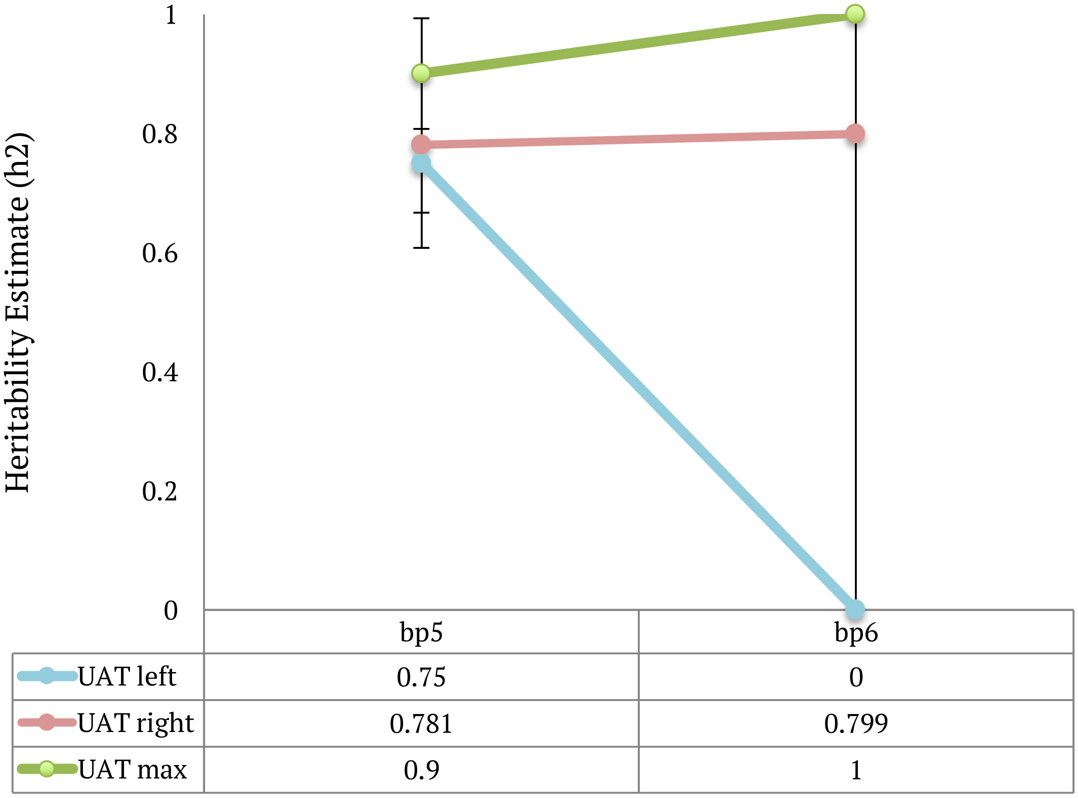
	bp1	bp2	bp3	bp4	bp5
UAT left	0.475	0			
UAT right	0.58	0			
UAT max	0.626	0			

Figure 17. Breakpoint h^2 estimates: c_1 distal accessory ridge.



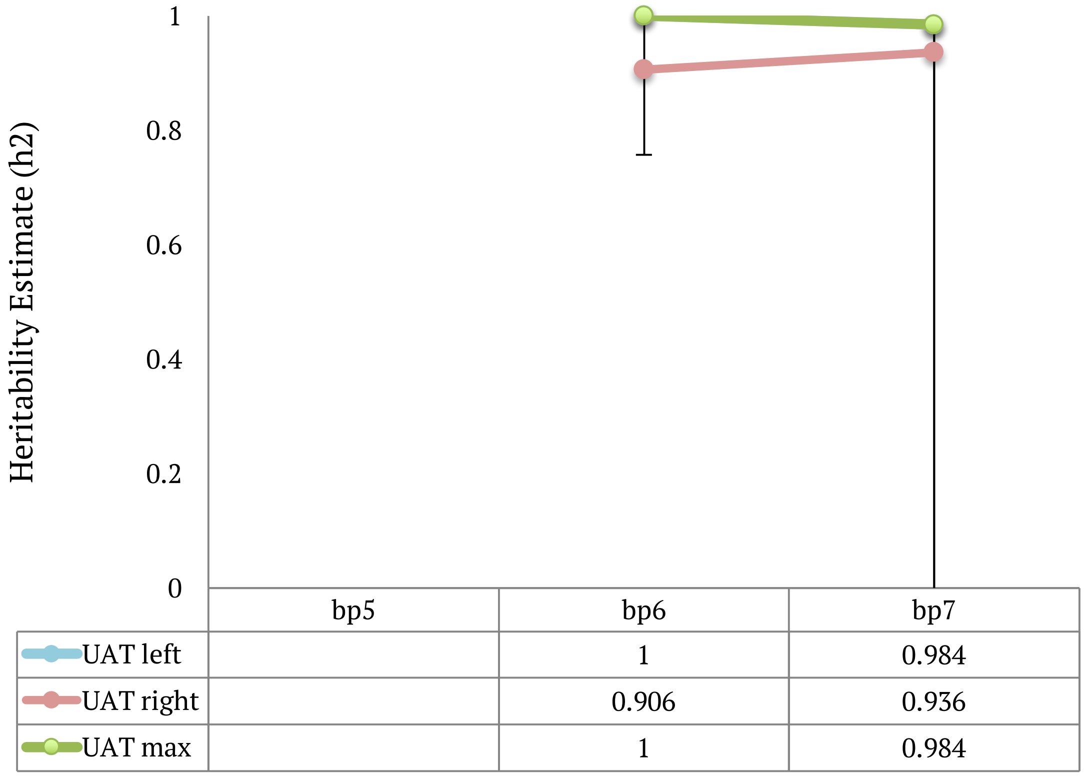
	bp1	bp2	bp3	bp4
UAT left	0	0.827	0.73	
UAT right	0	0.421	0.761	
UAT max	0	0.086	0.71	0

Figure 18. Breakpoint h^2 estimates: m_2 anterior fovea.



	bp5	bp6
UAT left	0.75	0
UAT right	0.781	0.799
UAT max	0.9	1

Figure 19. Breakpoint h^2 estimates: m_1 cusp number.



	bp5	bp6	bp7
UAT left		1	0.984
UAT right		0.906	0.936
UAT max		1	0.984

Figure 20. Breakpoint h^2 estimates: m_2 cusp number.

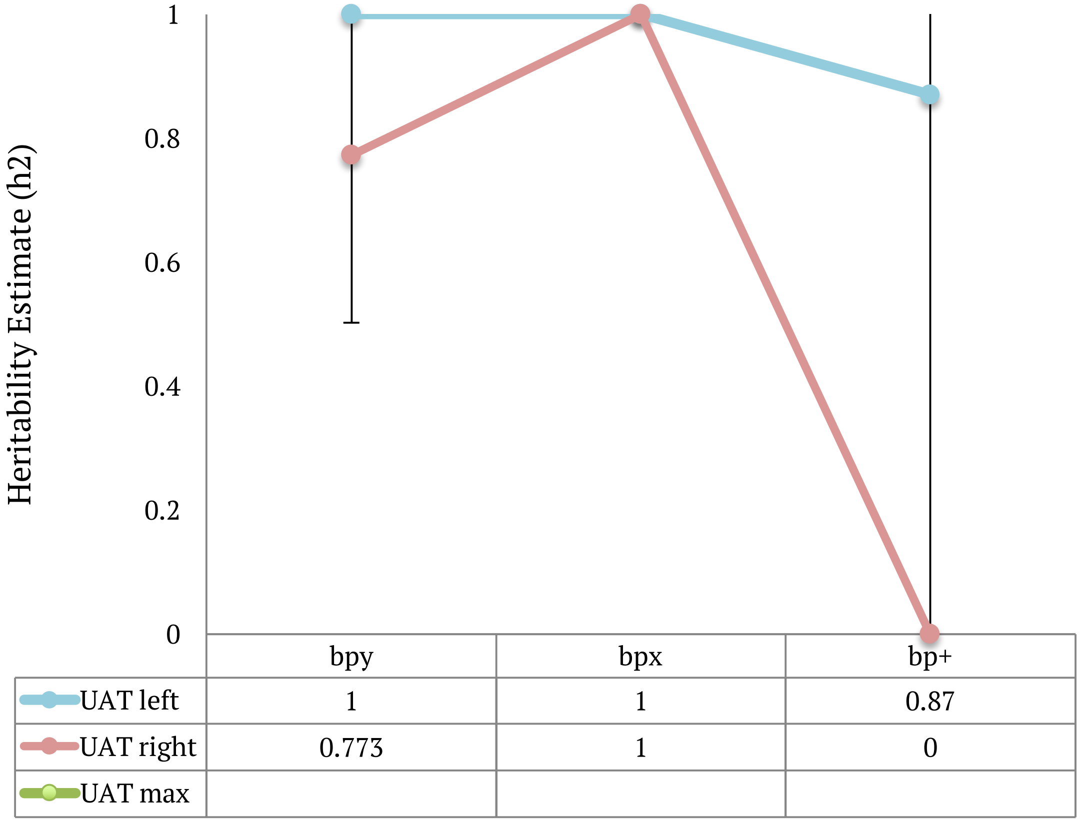
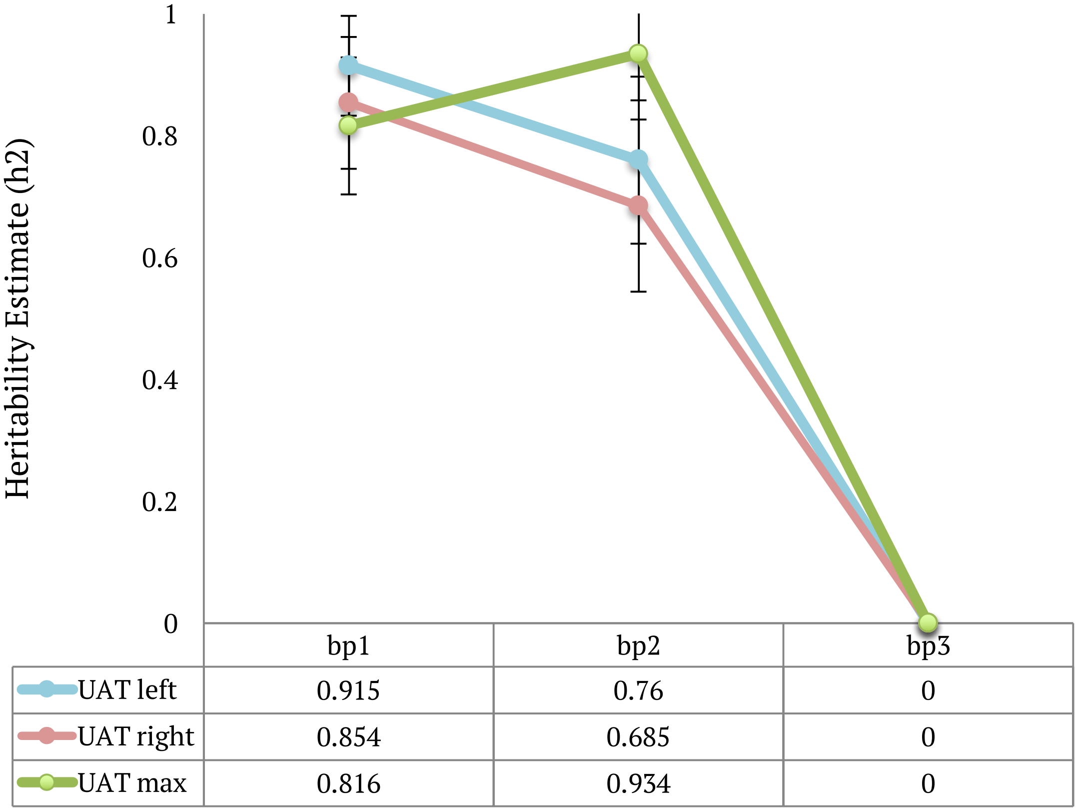
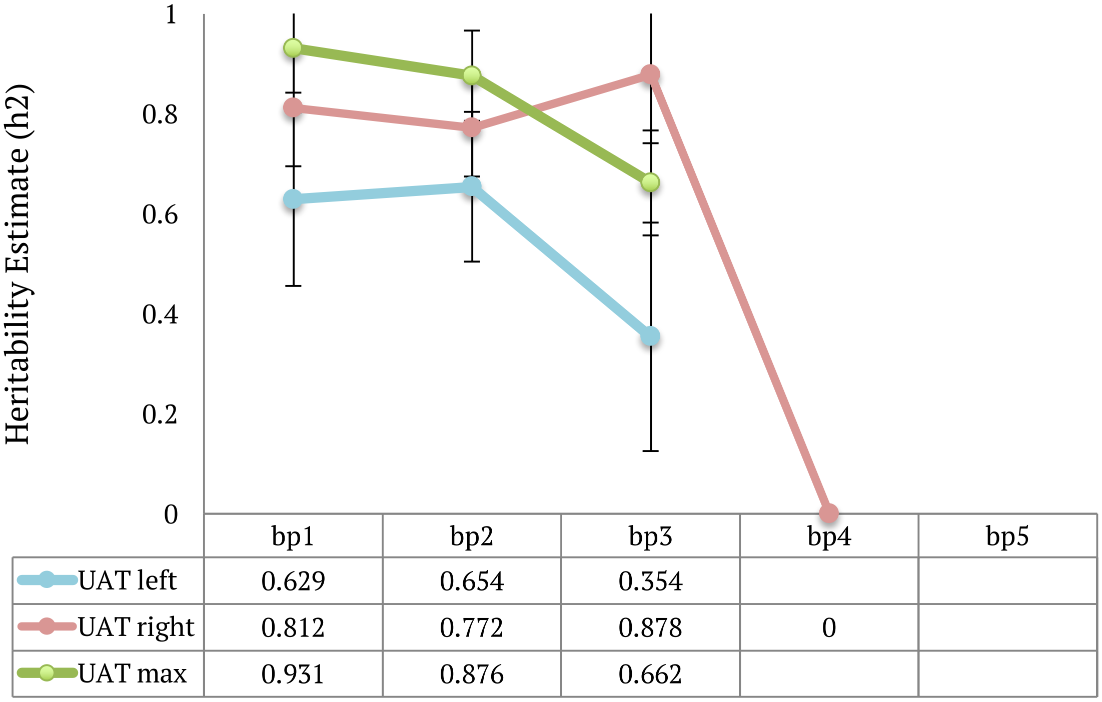


Figure 21. Breakpoint h^2 estimates: m_2 groove pattern.



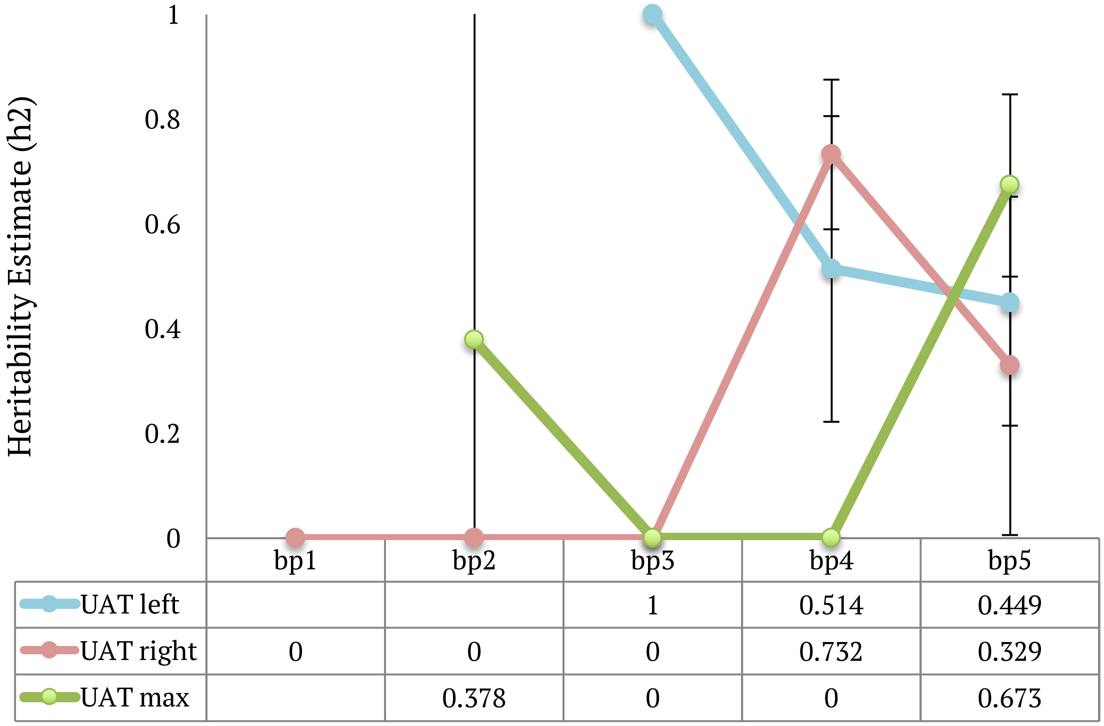
	bp1	bp2	bp3
● UAT left	0.915	0.76	0
● UAT right	0.854	0.685	0
● UAT max	0.816	0.934	0

Figure 22. Breakpoint h^2 estimates: m_2 deflecting wrinkle.



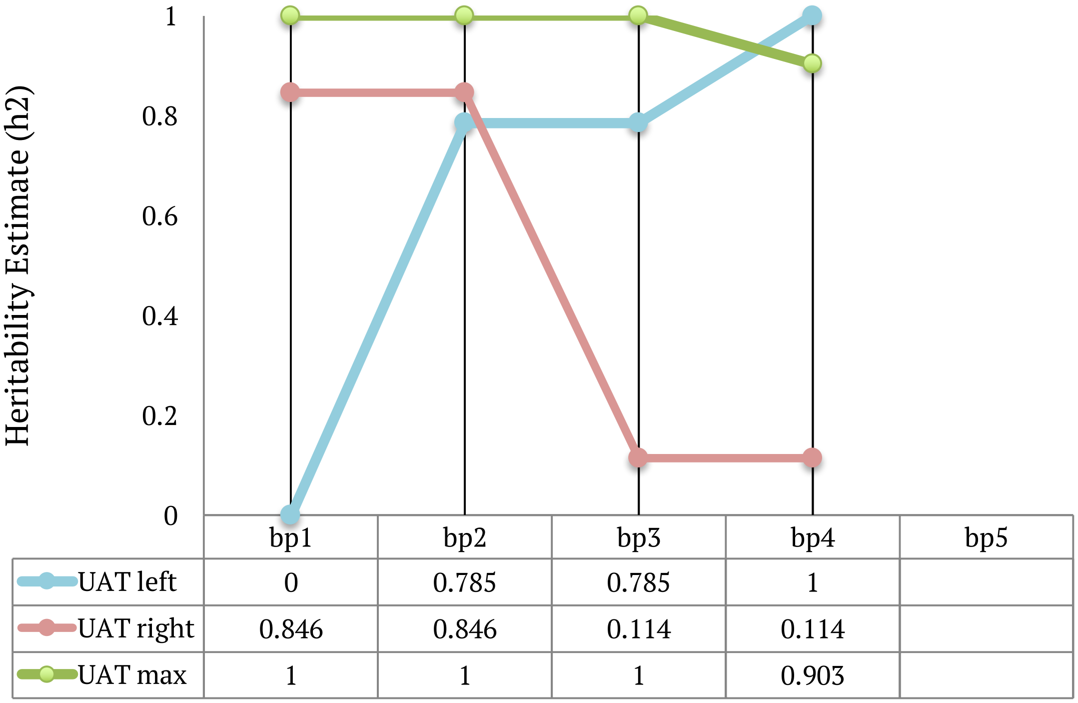
	bp1	bp2	bp3	bp4	bp5
UAT left	0.629	0.654	0.354		
UAT right	0.812	0.772	0.878	0	
UAT max	0.931	0.876	0.662		

Figure 23. Breakpoint *h*^{2} estimates: m$_1$ cusp 5.



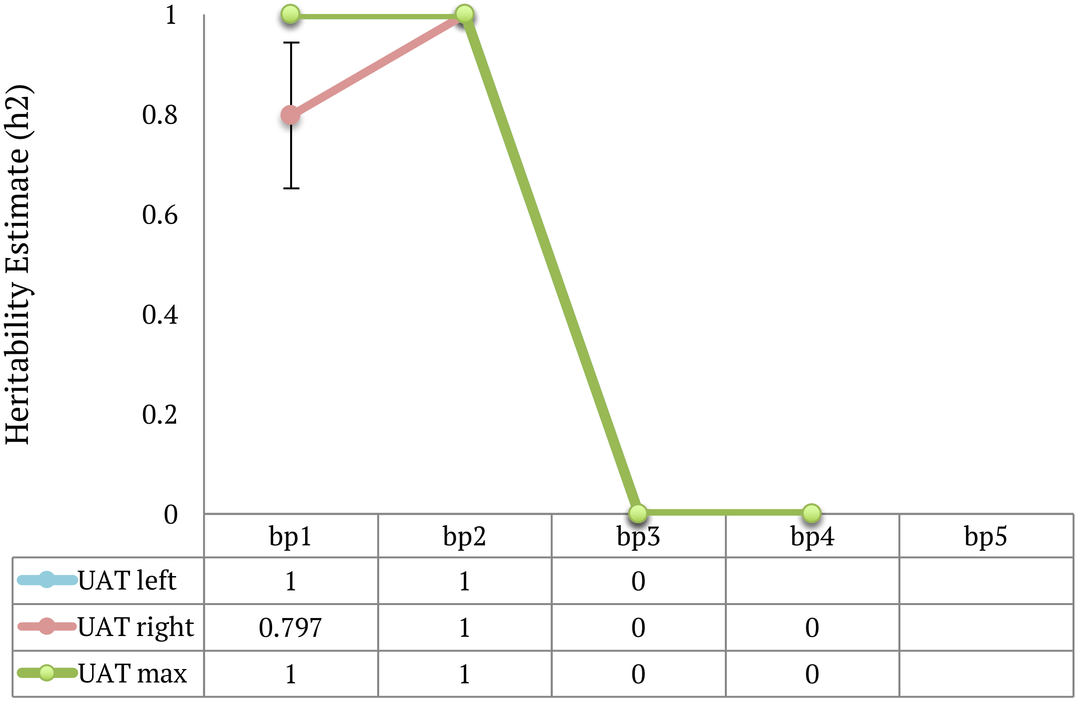
	bp1	bp2	bp3	bp4	bp5
UAT left			1	0.514	0.449
UAT right	0	0	0	0.732	0.329
UAT max		0.378	0	0	0.673

Figure 24. Breakpoint h^2 estimates: m_2 cusp 5.



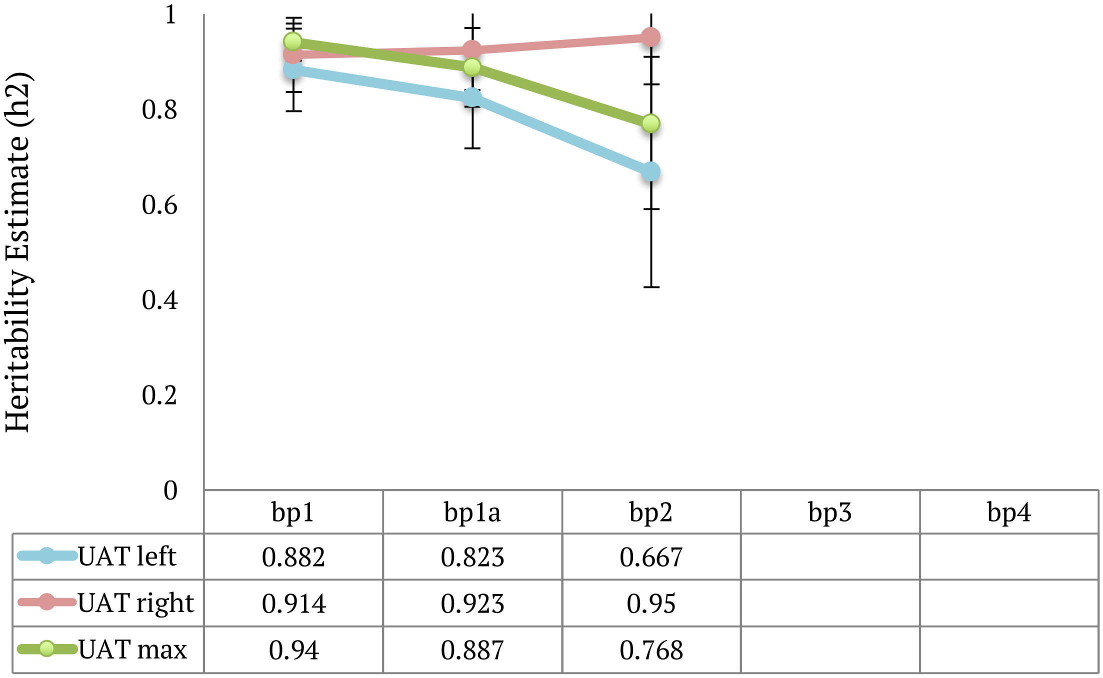
	bp1	bp2	bp3	bp4	bp5
UAT left	0	0.785	0.785	1	
UAT right	0.846	0.846	0.114	0.114	
UAT max	1	1	1	0.903	

Figure 25. Breakpoint h^2 estimates: m_1 cusp 6.



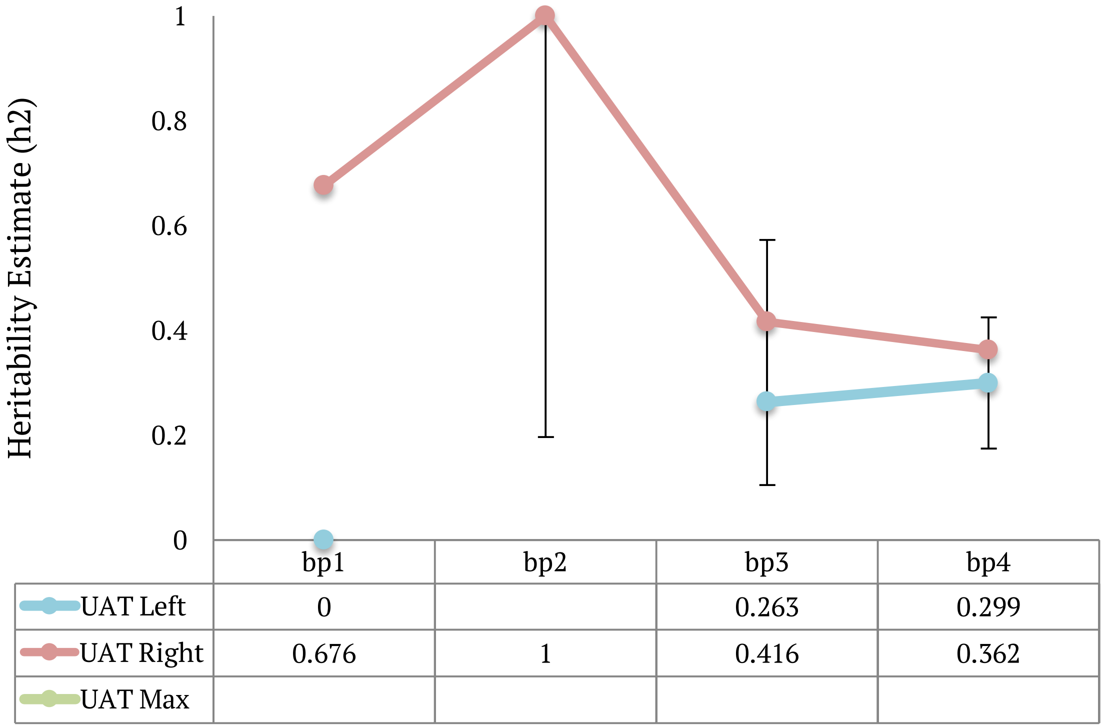
	bp1	bp2	bp3	bp4	bp5
UAT left	1	1	0		
UAT right	0.797	1	0	0	
UAT max	1	1	0	0	

Figure 26. Breakpoint h^2 estimates: m_2 cusp 6.



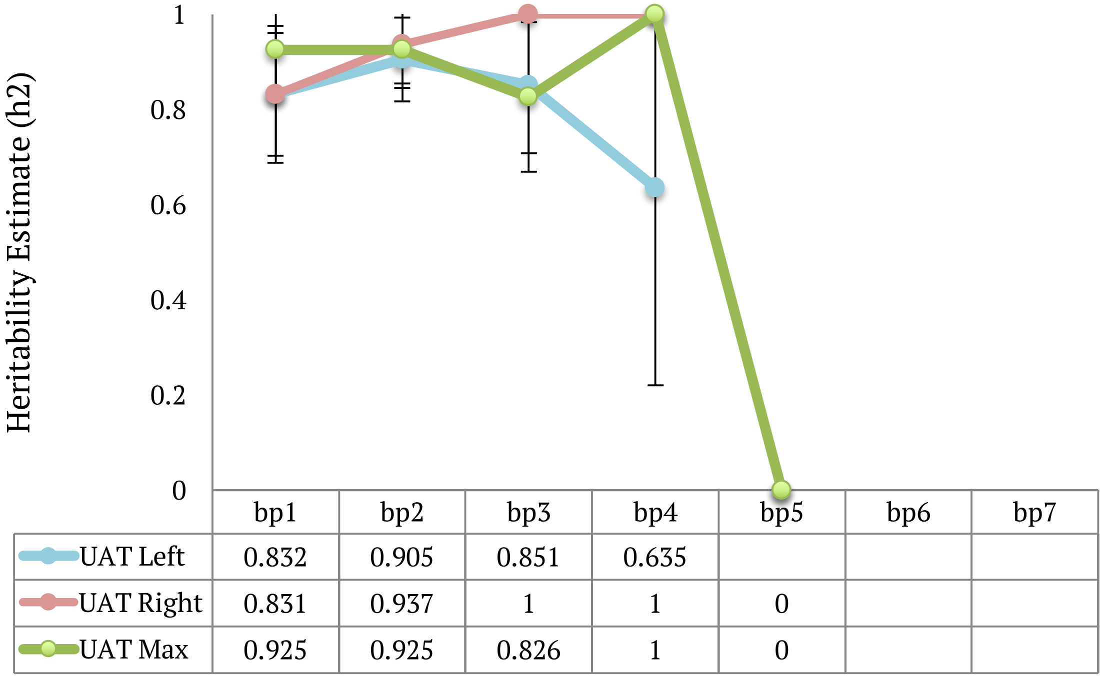
	bp1	bp1a	bp2	bp3	bp4
UAT left	0.882	0.823	0.667		
UAT right	0.914	0.923	0.95		
UAT max	0.94	0.887	0.768		

Figure 27. Breakpoint h^2 estimates: m_2 cusp 7.



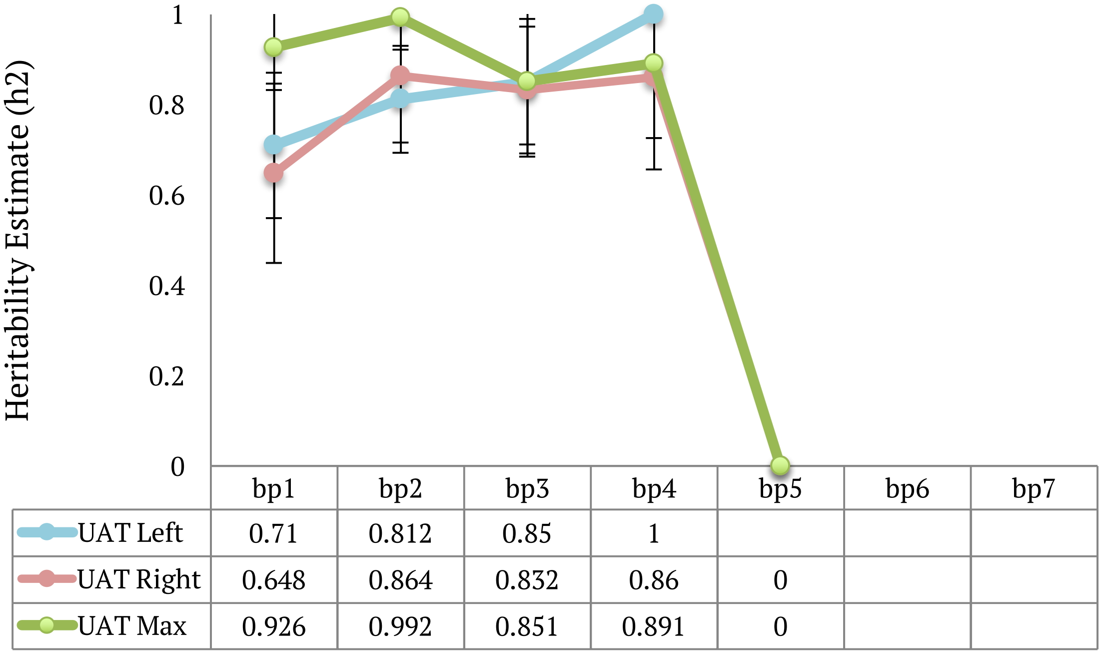
	bp1	bp2	bp3	bp4
UAT Left	0		0.263	0.299
UAT Right	0.676	1	0.416	0.362
UAT Max				

Figure 28. Breakpoint h^2 estimates: I^1 Winging.



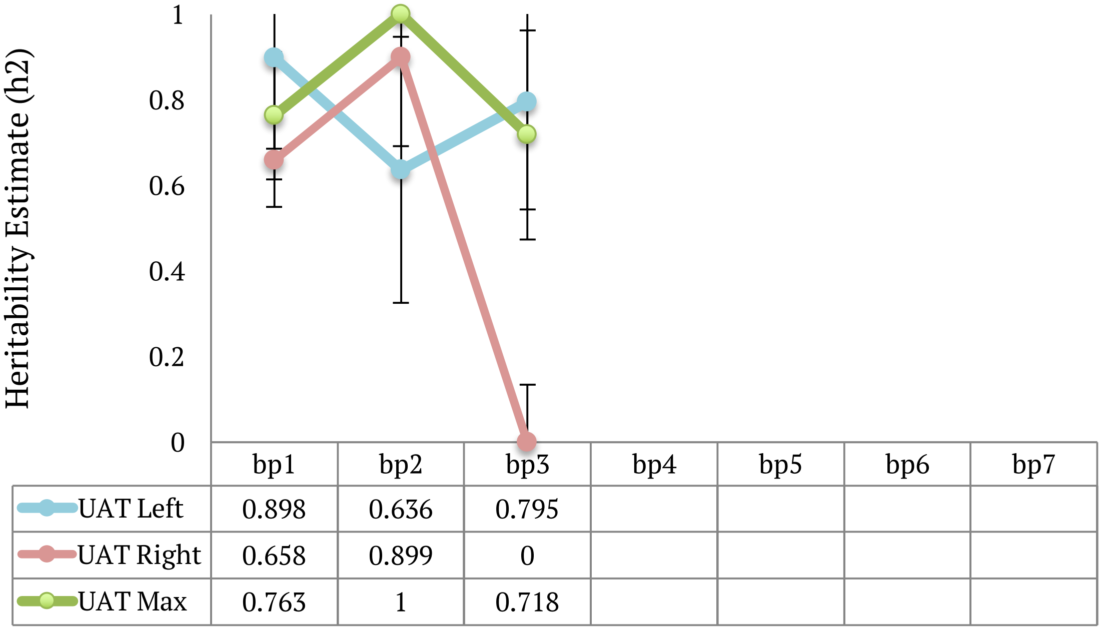
	bp1	bp2	bp3	bp4	bp5	bp6	bp7
UAT Left	0.832	0.905	0.851	0.635			
UAT Right	0.831	0.937	1	1	0		
UAT Max	0.925	0.925	0.826	1	0		

Figure 29. Breakpoint h^2 estimates: I^1 Shoveling.



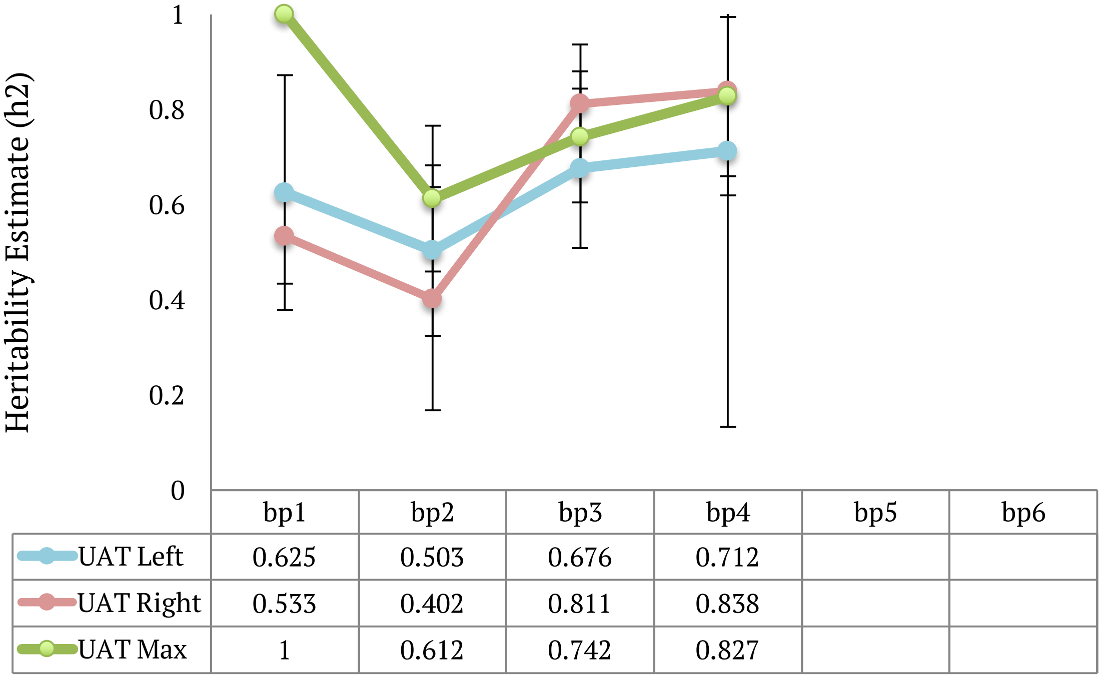
	bp1	bp2	bp3	bp4	bp5	bp6	bp7
UAT Left	0.71	0.812	0.85	1			
UAT Right	0.648	0.864	0.832	0.86	0		
UAT Max	0.926	0.992	0.851	0.891	0		

Figure 30. Breakpoint *h*^{2} estimates: I^2 Shoveling.



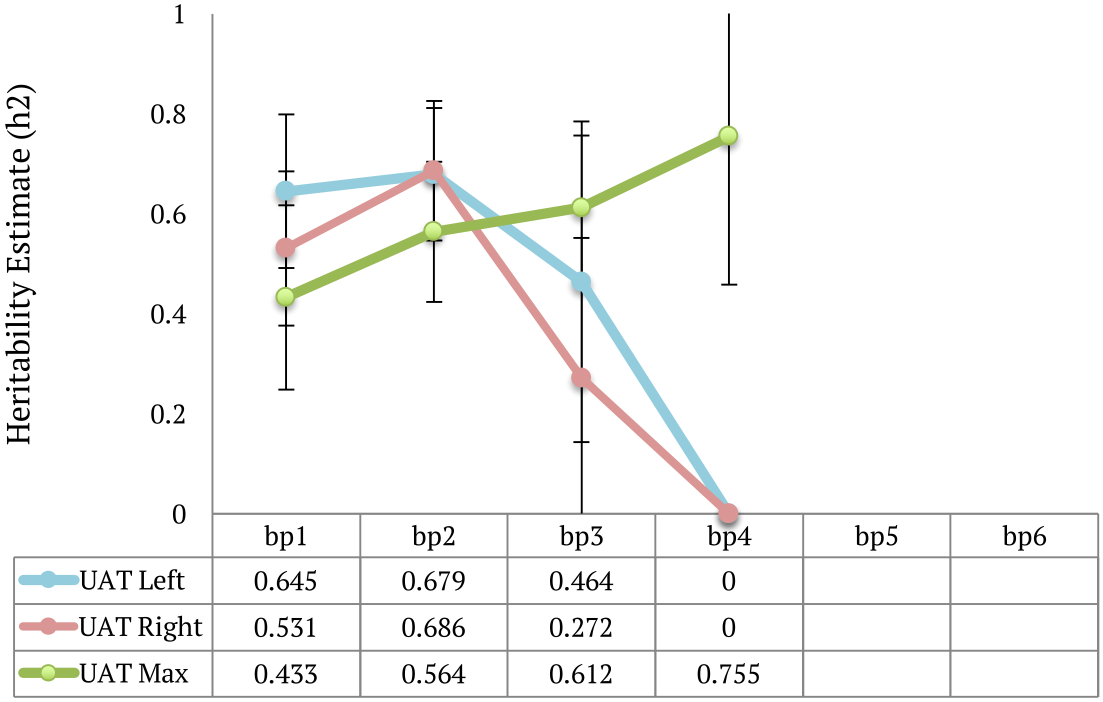
	bp1	bp2	bp3	bp4	bp5	bp6	bp7
UAT Left	0.898	0.636	0.795				
UAT Right	0.658	0.899	0				
UAT Max	0.763	1	0.718				

Figure 31. Breakpoint *h*^{2} estimates: C^1 Shoveling.



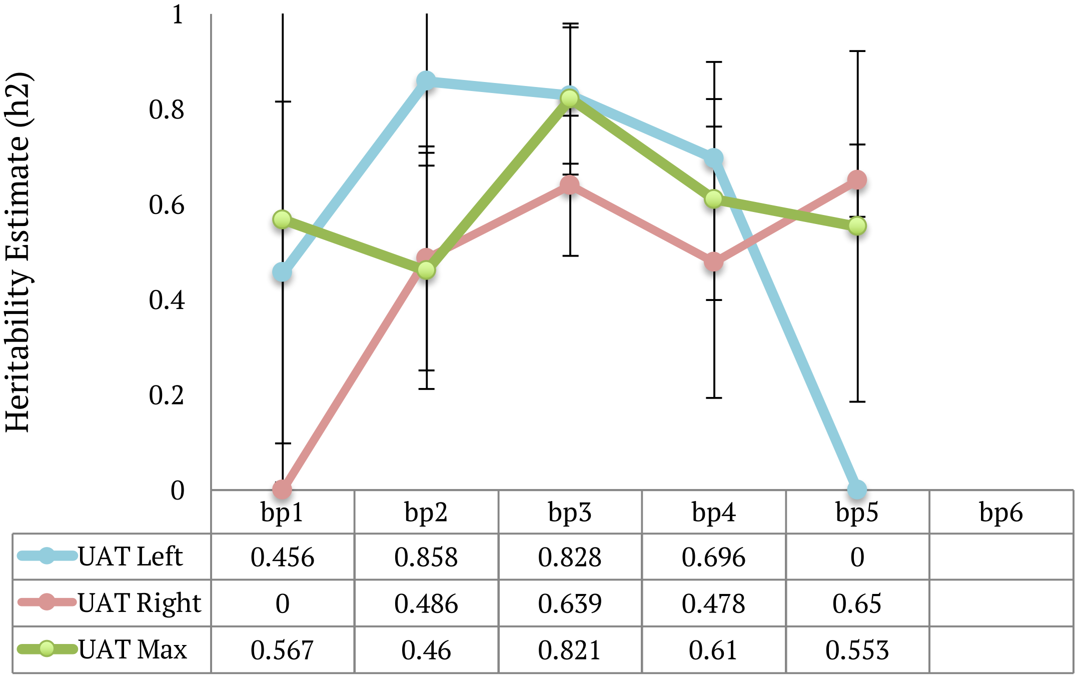
	bp1	bp2	bp3	bp4	bp5	bp6
UAT Left	0.625	0.503	0.676	0.712		
UAT Right	0.533	0.402	0.811	0.838		
UAT Max	1	0.612	0.742	0.827		

Figure 32. Breakpoint h^2 estimates: I^1 Double Shoveling.



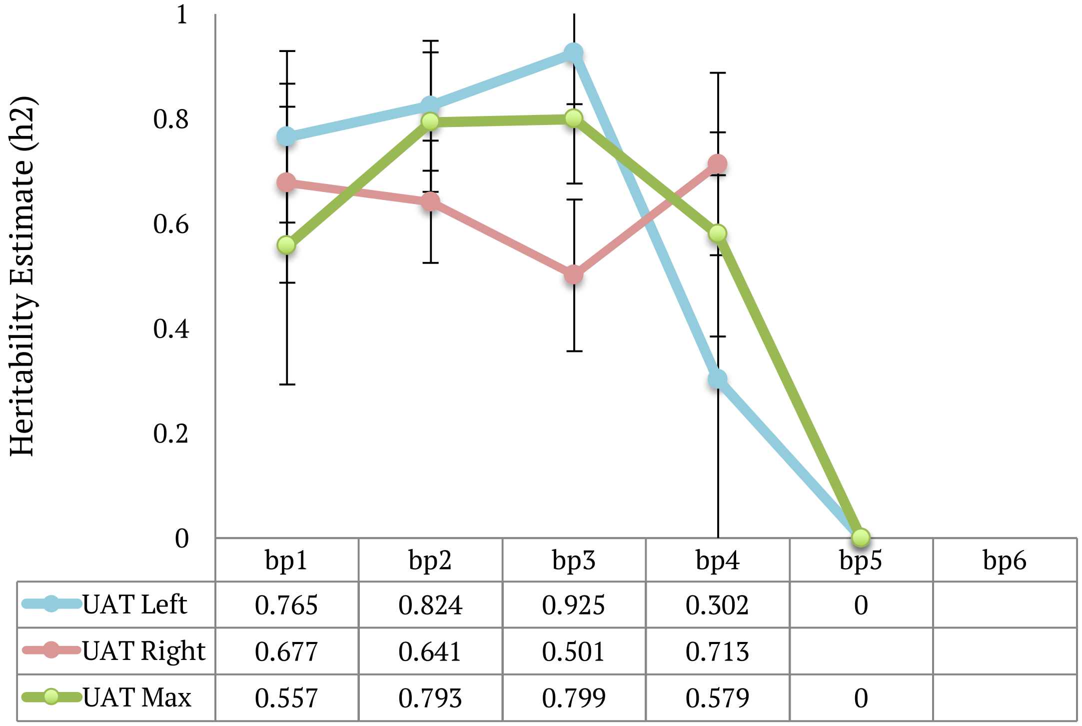
	bp1	bp2	bp3	bp4	bp5	bp6
UAT Left	0.645	0.679	0.464	0		
UAT Right	0.531	0.686	0.272	0		
UAT Max	0.433	0.564	0.612	0.755		

Figure 33. Breakpoint h^2 estimates: I^2 Double Shoveling.



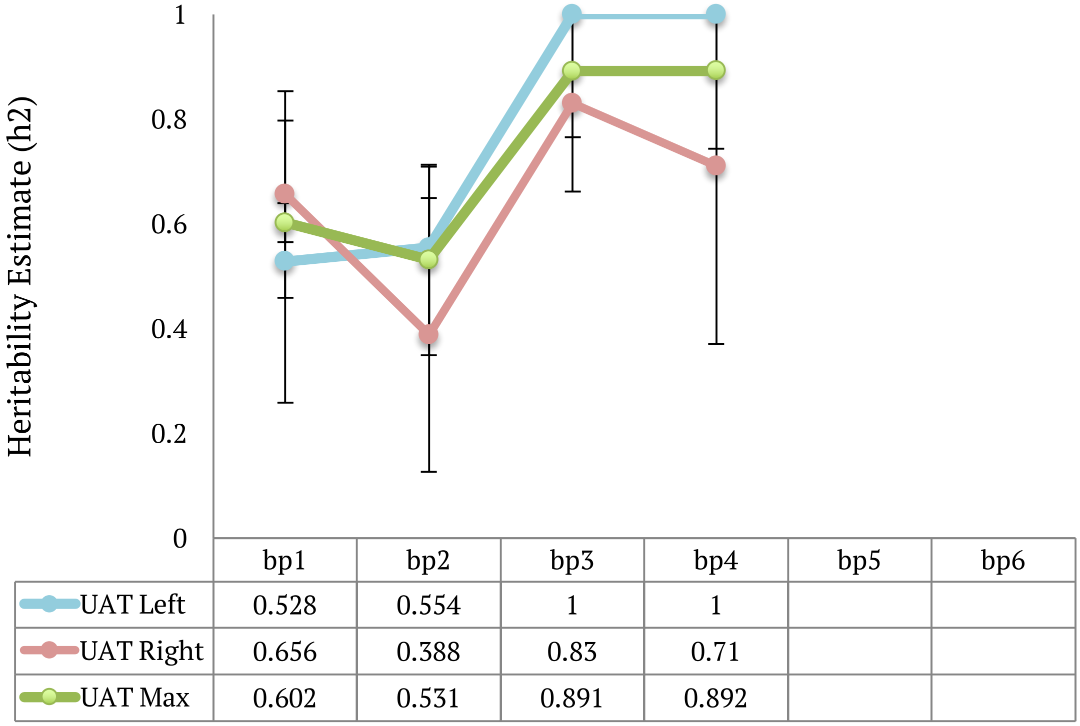
	bp1	bp2	bp3	bp4	bp5	bp6
UAT Left	0.456	0.858	0.828	0.696	0	
UAT Right	0	0.486	0.639	0.478	0.65	
UAT Max	0.567	0.46	0.821	0.61	0.553	

Figure 34. Breakpoint h^2 estimates: C^1 Double Shoveling.



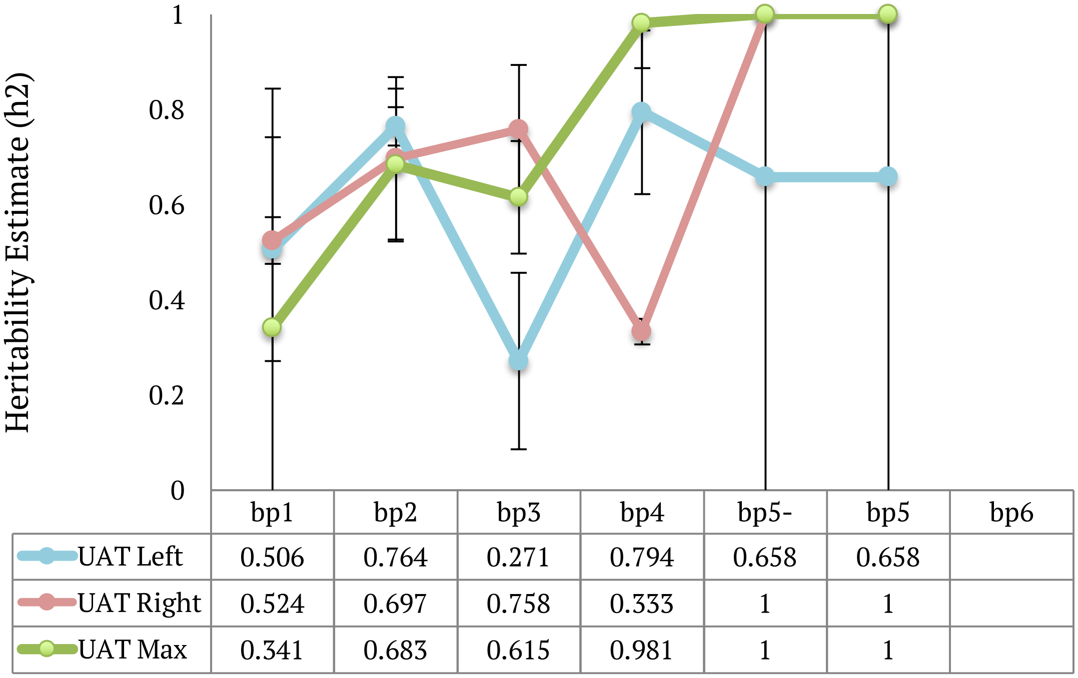
	bp1	bp2	bp3	bp4	bp5	bp6
UAT Left	0.765	0.824	0.925	0.302	0	
UAT Right	0.677	0.641	0.501	0.713		
UAT Max	0.557	0.793	0.799	0.579	0	

Figure 35. Breakpoint h^2 estimates: P^1 Double Shoveling.



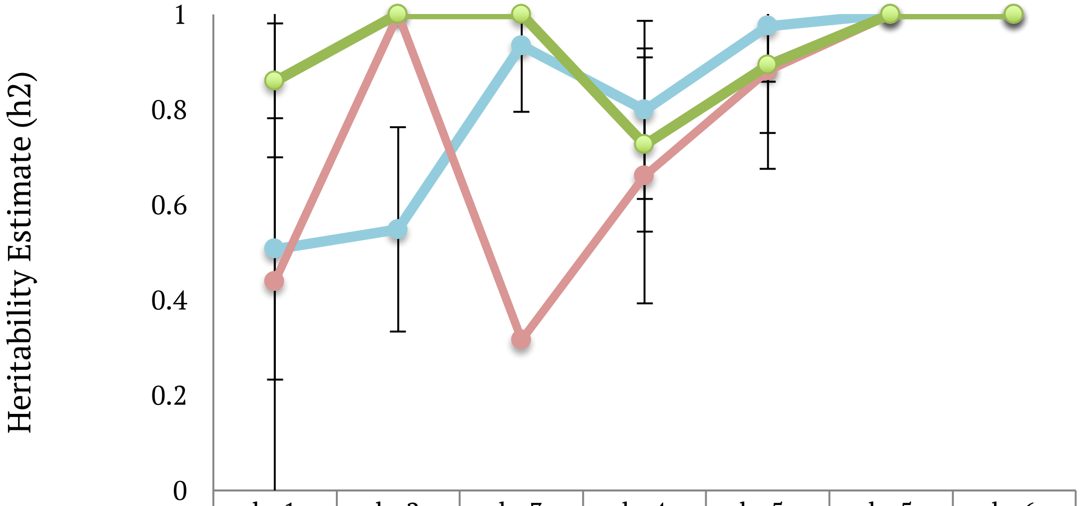
	bp1	bp2	bp3	bp4	bp5	bp6
UAT Left	0.528	0.554	1	1		
UAT Right	0.656	0.388	0.83	0.71		
UAT Max	0.602	0.531	0.891	0.892		

Figure 36. Breakpoint h^2 estimates: P^2 Double Shoveling.



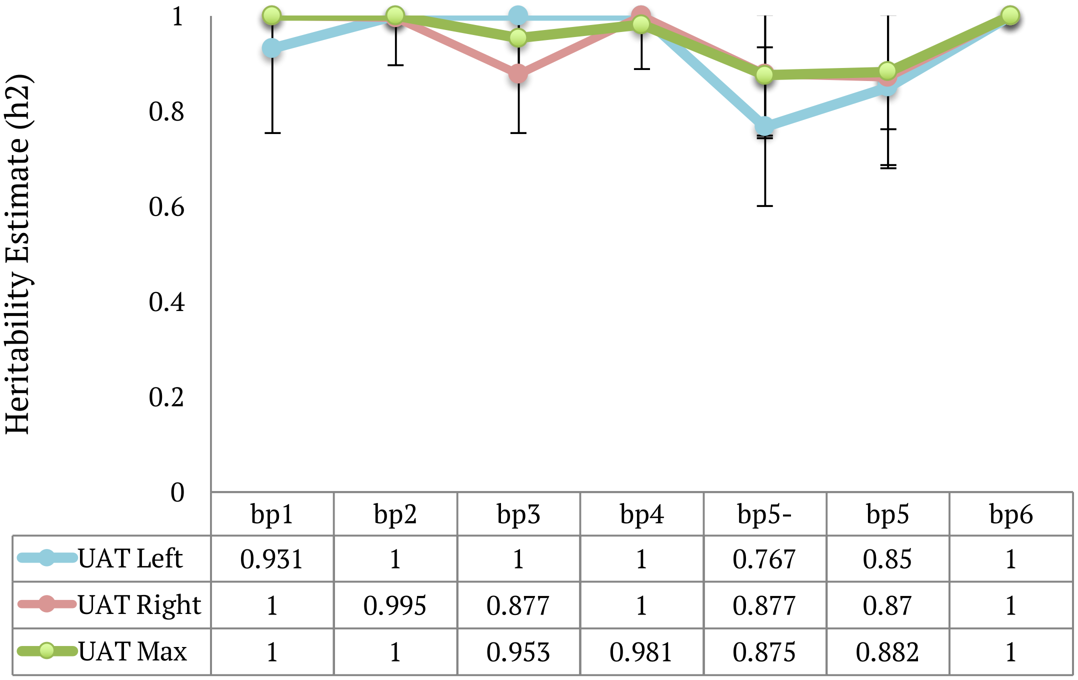
	bp1	bp2	bp3	bp4	bp5-	bp5	bp6
UAT Left	0.506	0.764	0.271	0.794	0.658	0.658	
UAT Right	0.524	0.697	0.758	0.333	1	1	
UAT Max	0.341	0.683	0.615	0.981	1	1	

Figure 37. Breakpoint h^2 estimates: I^1 Tuberculum Dentale.



	bp1	bp2	bp3	bp4	bp5-	bp5	bp6
UAT Left	0.507	0.548	0.934	0.799	0.975	1	1
UAT Right	0.439	1	0.316	0.66	0.881	1	1
UAT Max	0.859	1	1	0.726	0.893	1	1

Figure 38. Breakpoint h^2 estimates: I^2 Tuberculum Dentale.



	bp1	bp2	bp3	bp4	bp5-	bp5	bp6
● UAT Left	0.931	1	1	1	0.767	0.85	1
● UAT Right	1	0.995	0.877	1	0.877	0.87	1
● UAT Max	1	1	0.953	0.981	0.875	0.882	1

Figure 39. Breakpoint h^2 estimates: C^1 Tuberculum Dentale.

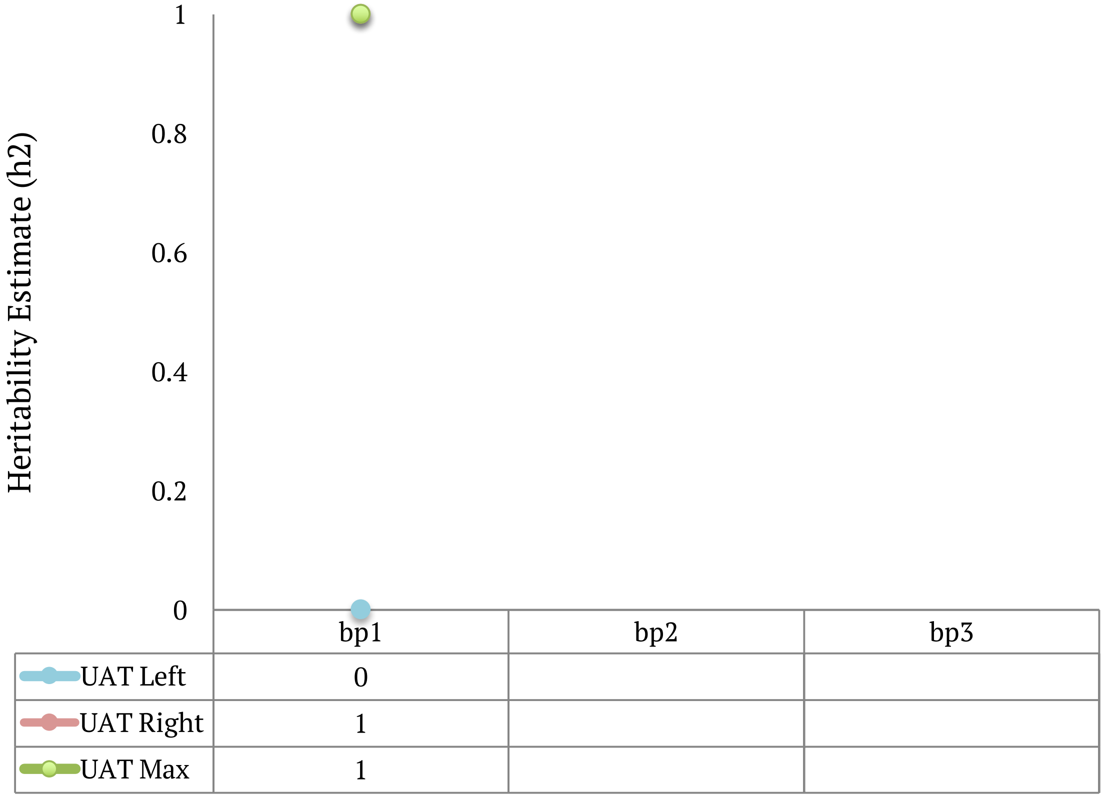
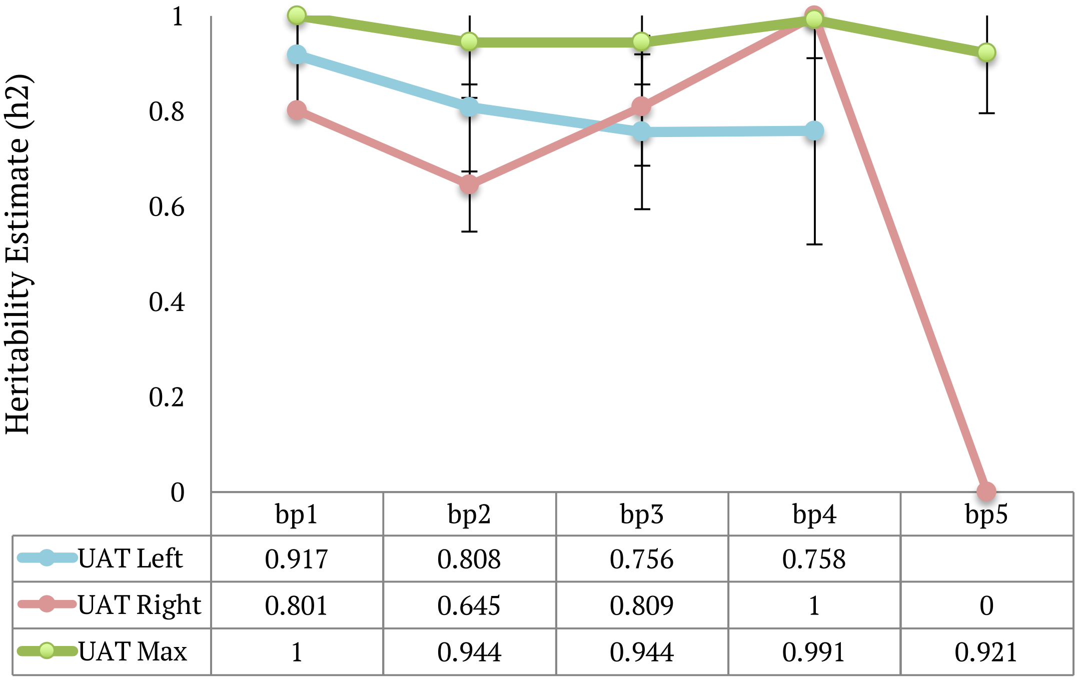
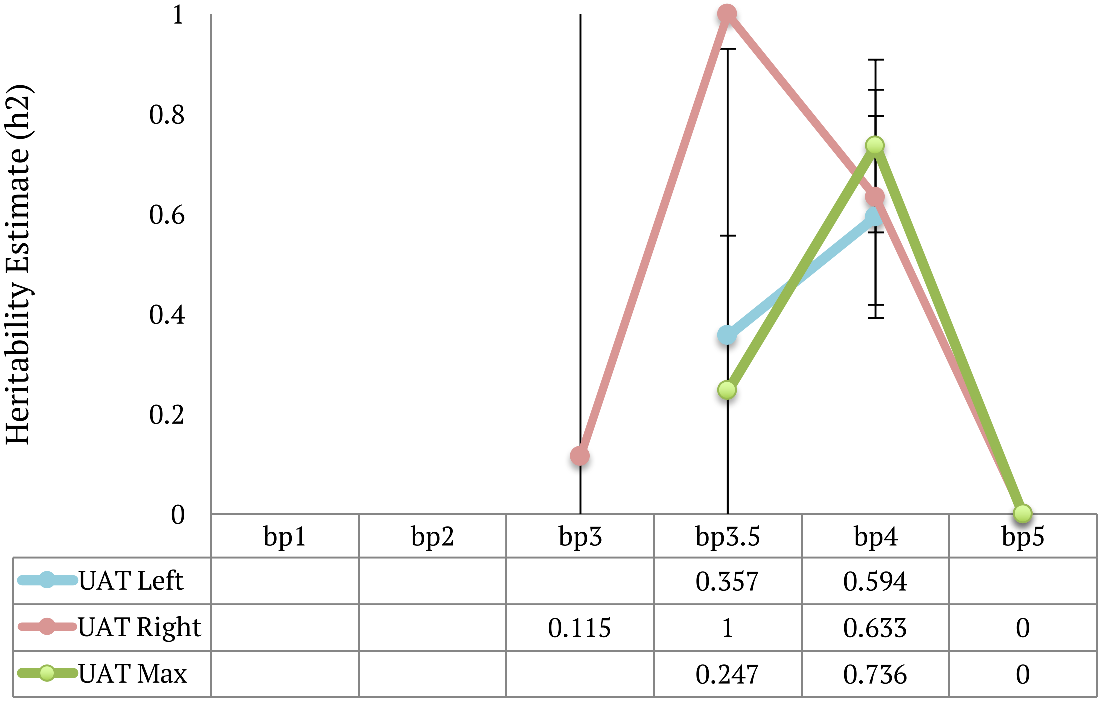


Figure 40. Breakpoint h^2 estimates: C^1 Mesial Ridge.



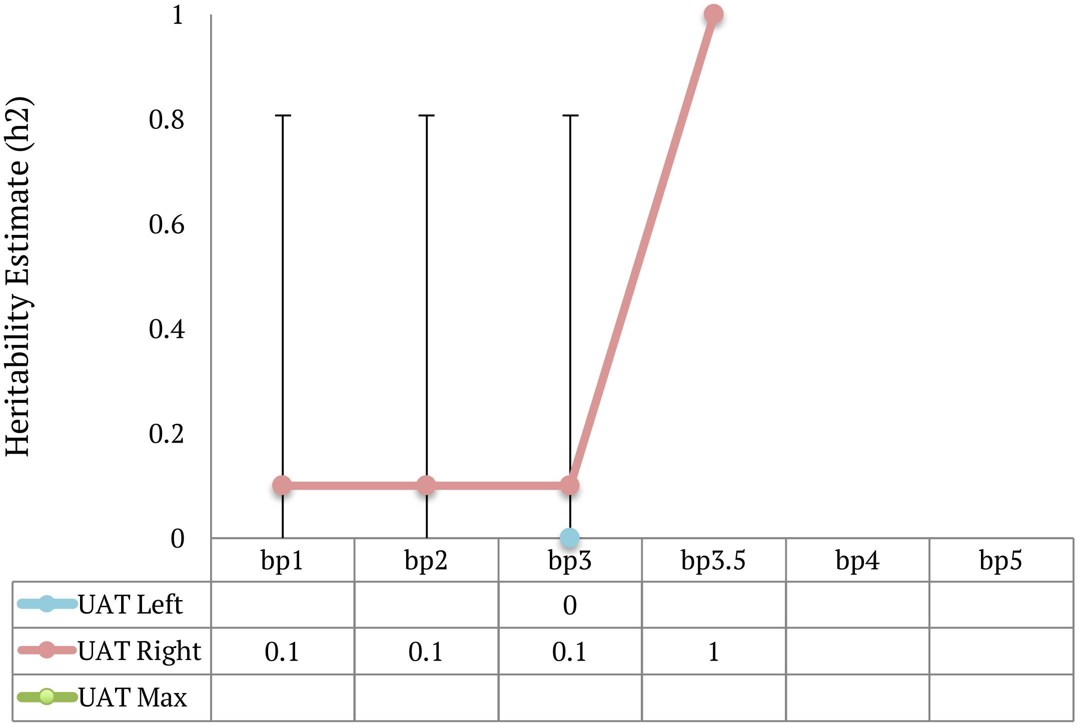
	bp1	bp2	bp3	bp4	bp5
UAT Left	0.917	0.808	0.756	0.758	
UAT Right	0.801	0.645	0.809	1	0
UAT Max	1	0.944	0.944	0.991	0.921

Figure 41. Breakpoint h^2 estimates: C^1 Distal Accessory Ridge.



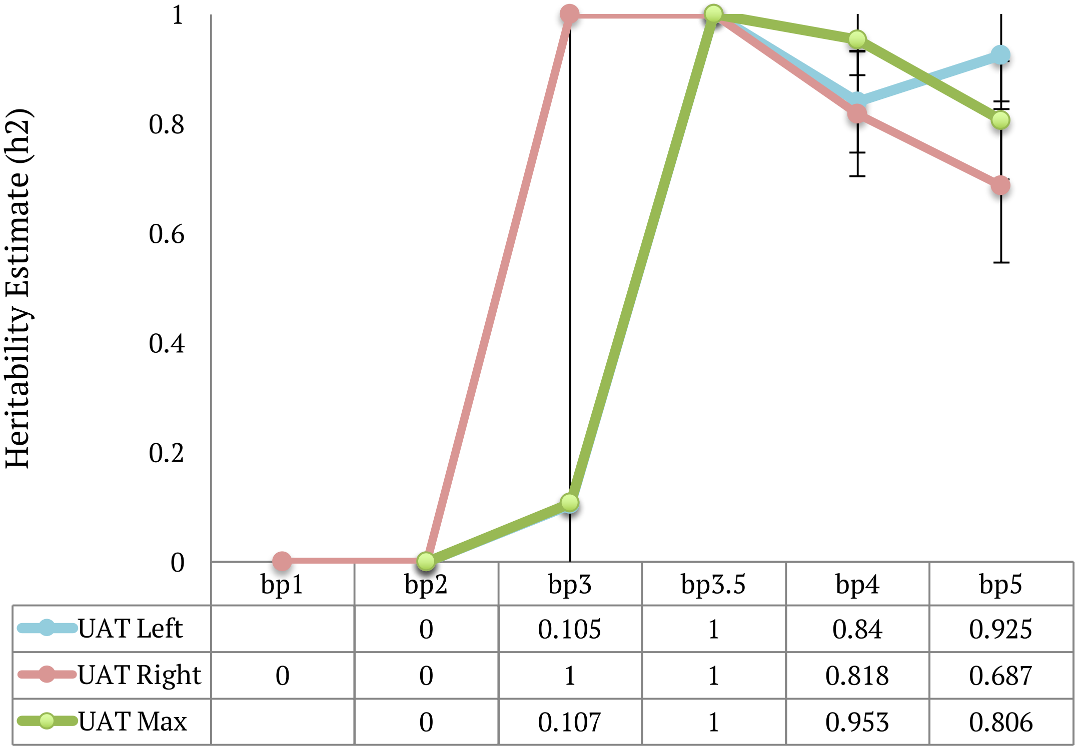
	bp1	bp2	bp3	bp3.5	bp4	bp5
UAT Left				0.357	0.594	
UAT Right			0.115	1	0.633	0
UAT Max				0.247	0.736	0

Figure 42. Breakpoint h^2 estimates: M^2 Metacone.



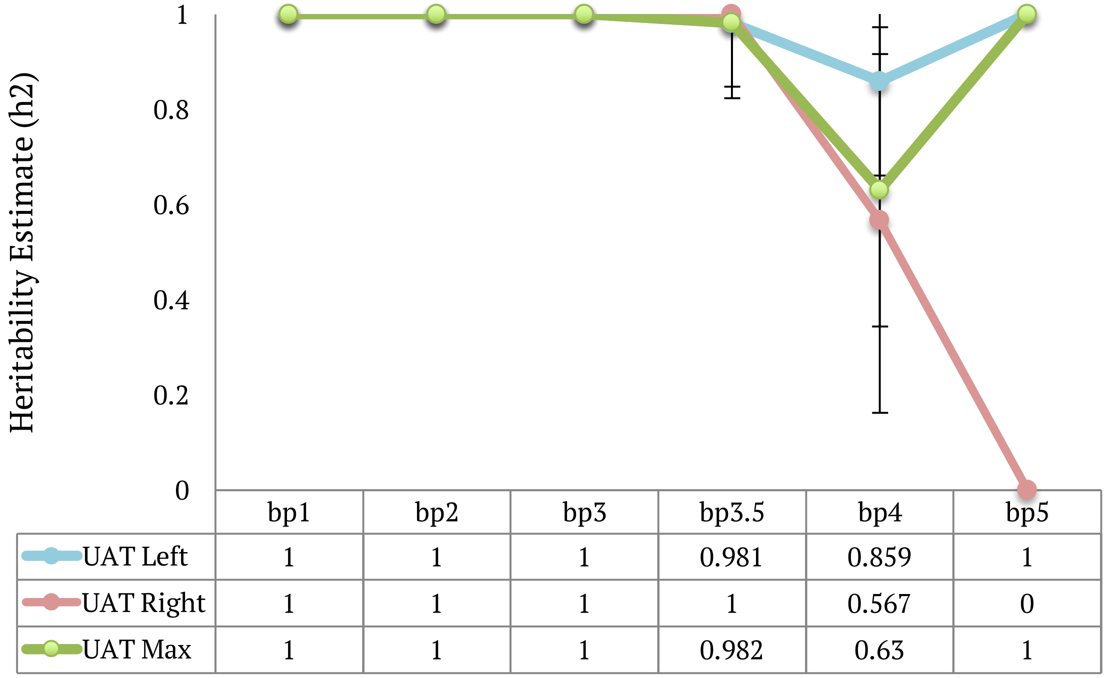
	bp1	bp2	bp3	bp3.5	bp4	bp5
UAT Left			0			
UAT Right	0.1	0.1	0.1	1		
UAT Max						

Figure 43. Breakpoint h^2 estimates: M^3 Metacone.



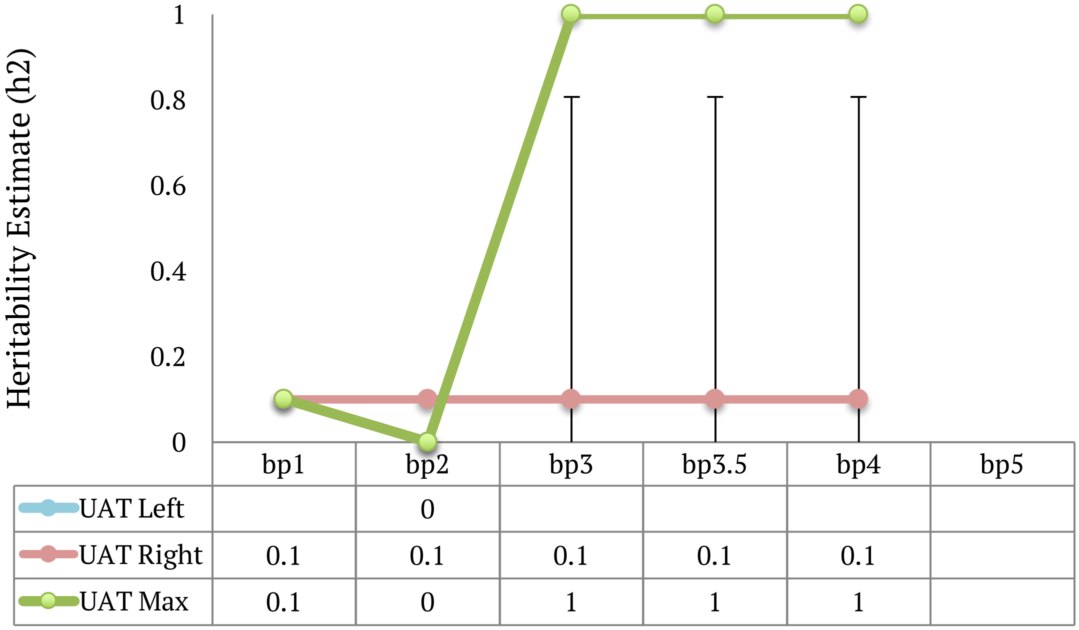
	bp1	bp2	bp3	bp3.5	bp4	bp5
UAT Left		0	0.105	1	0.84	0.925
UAT Right	0	0	1	1	0.818	0.687
UAT Max		0	0.107	1	0.953	0.806

Figure 44. Breakpoint *h*^{2} estimates: M^1 Hypocone.



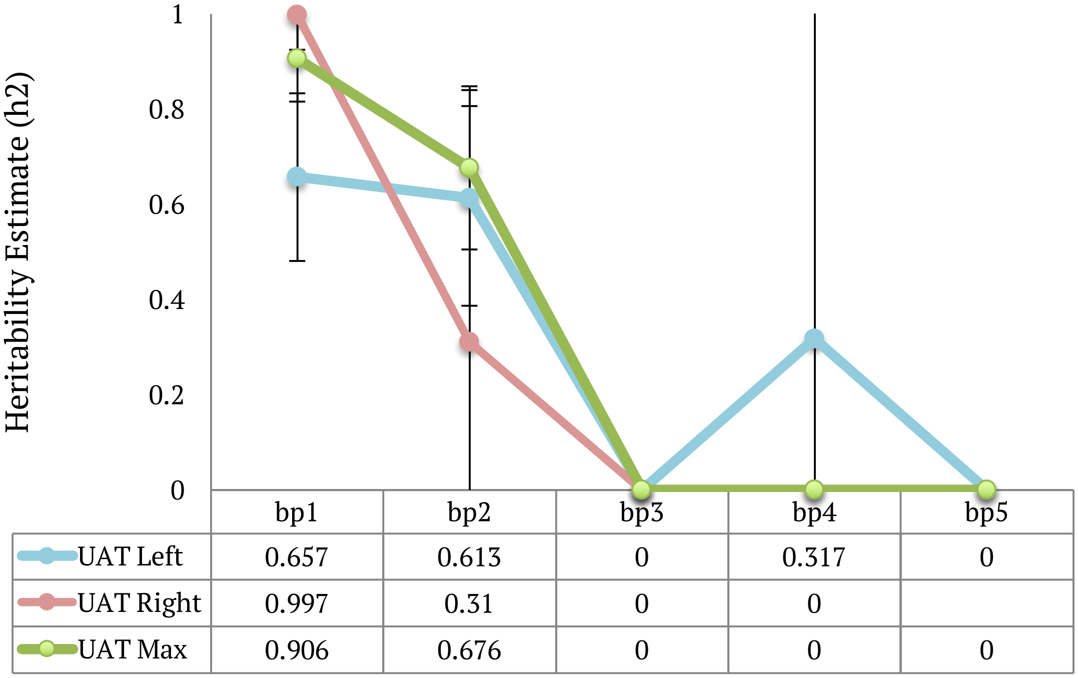
	bp1	bp2	bp3	bp3.5	bp4	bp5
UAT Left	1	1	1	0.981	0.859	1
UAT Right	1	1	1	1	0.567	0
UAT Max	1	1	1	0.982	0.63	1

Figure 45. Breakpoint h^2 estimates: M^2 Hypocone.



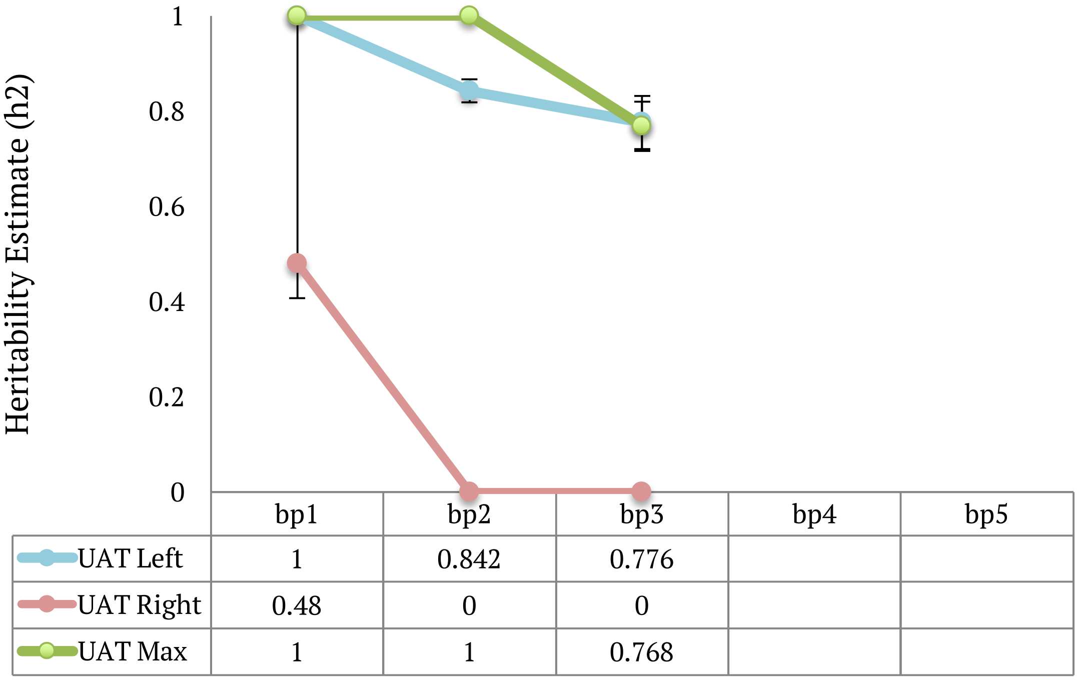
	bp1	bp2	bp3	bp3.5	bp4	bp5
UAT Left		0				
UAT Right	0.1	0.1	0.1	0.1	0.1	
UAT Max	0.1	0	1	1	1	

Figure 46. Breakpoint *h^2* estimates: M^3 Hypocone.



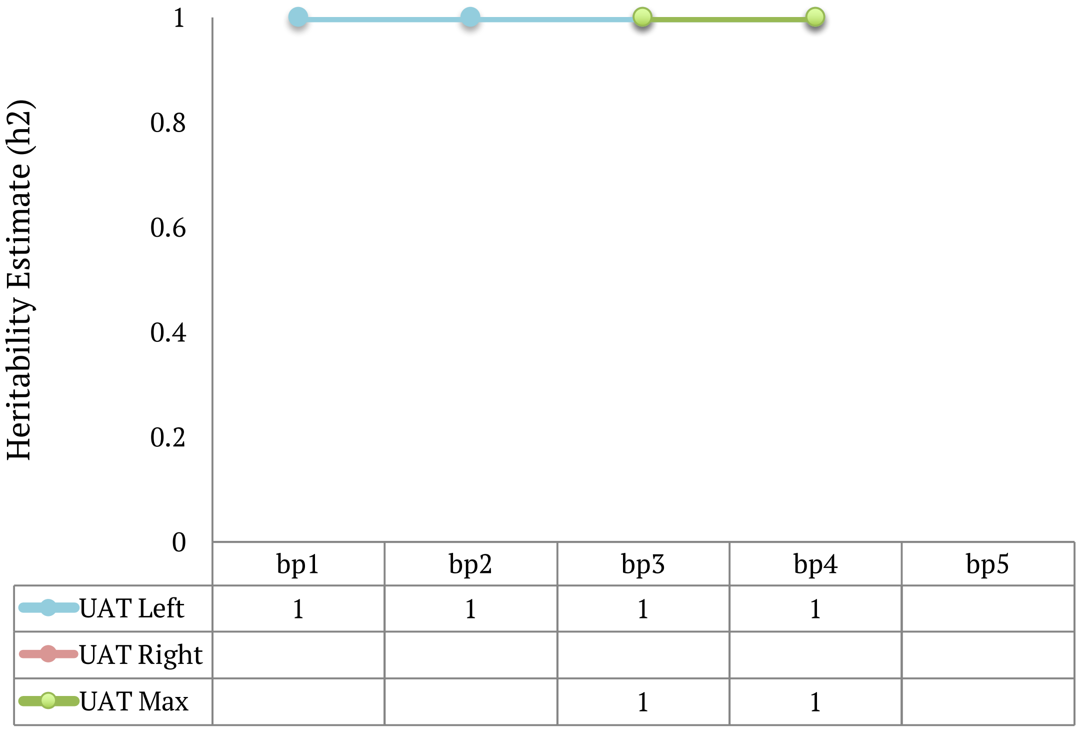
	bp1	bp2	bp3	bp4	bp5
UAT Left	0.657	0.613	0	0.317	0
UAT Right	0.997	0.31	0	0	
UAT Max	0.906	0.676	0	0	0

Figure 47. Breakpoint *h*^{2} estimates: M^1 Cusp 5.



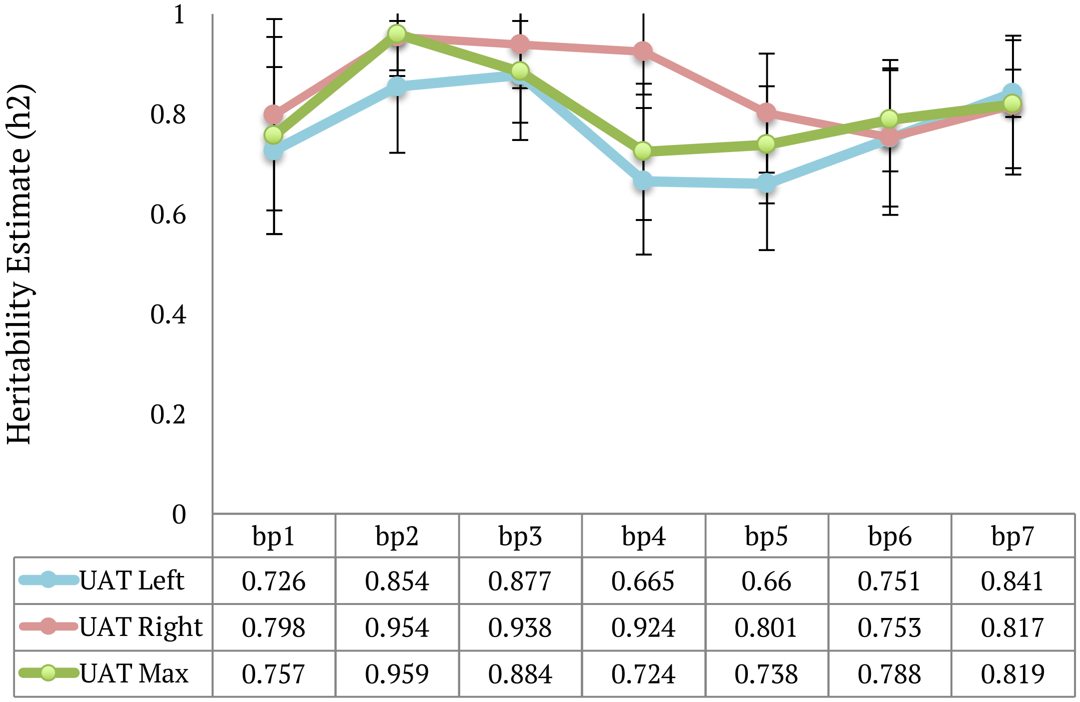
	bp1	bp2	bp3	bp4	bp5
UAT Left	1	0.842	0.776		
UAT Right	0.48	0	0		
UAT Max	1	1	0.768		

Figure 48. Breakpoint *h*^{2} estimates: M^2 Cusp 5.



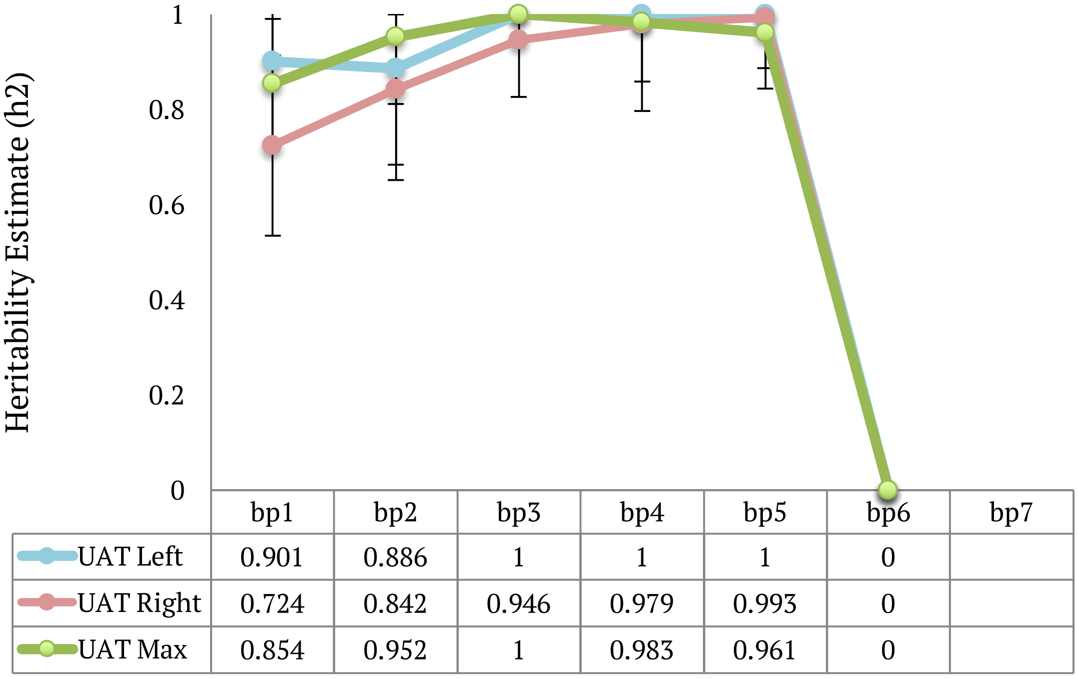
	bp1	bp2	bp3	bp4	bp5
UAT Left	1	1	1	1	
UAT Right					
UAT Max			1	1	

Figure 49. Breakpoint h^2 estimates: M^3 Cusp 5.



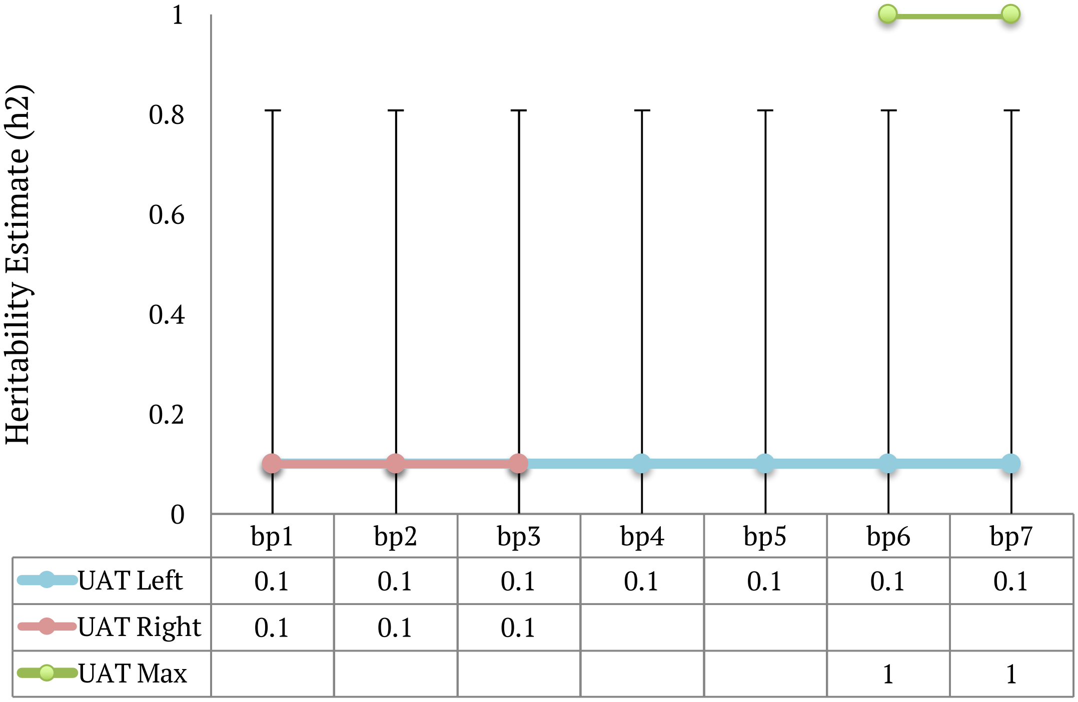
	bp1	bp2	bp3	bp4	bp5	bp6	bp7
UAT Left	0.726	0.854	0.877	0.665	0.66	0.751	0.841
UAT Right	0.798	0.954	0.938	0.924	0.801	0.753	0.817
UAT Max	0.757	0.959	0.884	0.724	0.738	0.788	0.819

Figure 50. Breakpoint h^2 estimates: M^1 Carabelli's Trait.



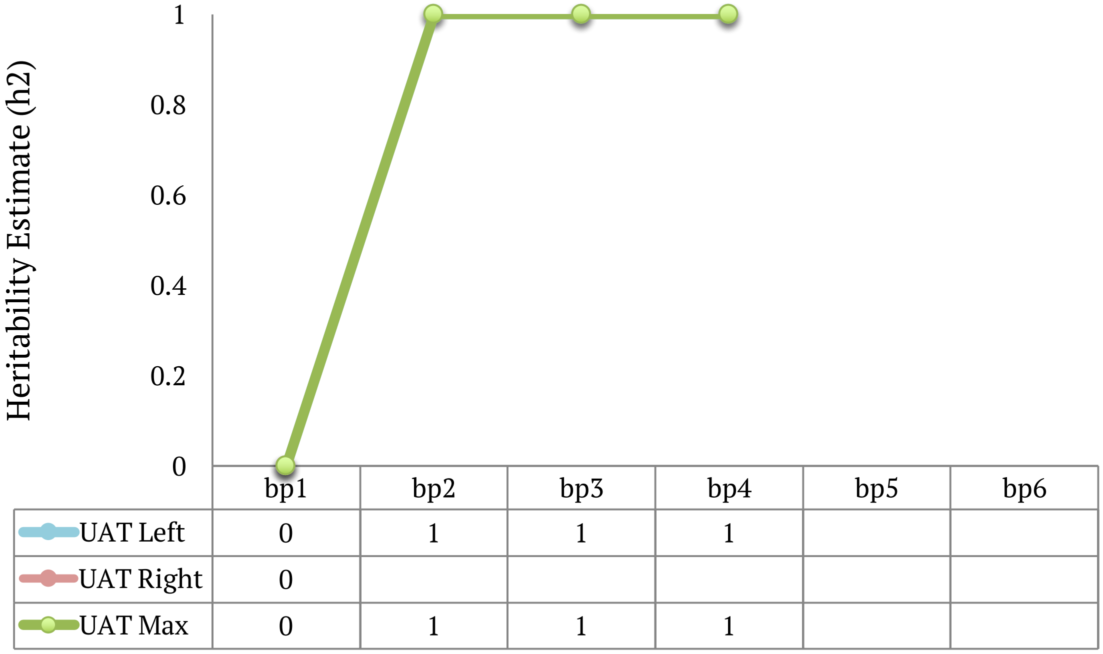
	bp1	bp2	bp3	bp4	bp5	bp6	bp7
UAT Left	0.901	0.886	1	1	1	0	
UAT Right	0.724	0.842	0.946	0.979	0.993	0	
UAT Max	0.854	0.952	1	0.983	0.961	0	

Figure 51. Breakpoint h^2 estimates: M^2 Carabelli's Trait.



	bp1	bp2	bp3	bp4	bp5	bp6	bp7
UAT Left	0.1	0.1	0.1	0.1	0.1	0.1	0.1
UAT Right	0.1	0.1	0.1				
UAT Max						1	1

Figure 52. Breakpoint *h*^{2} estimates: M^3 Carabelli's Trait.



	bp1	bp2	bp3	bp4	bp5	bp6
UAT Left	0	1	1	1		
UAT Right	0					
UAT Max	0	1	1	1		

Figure 53. Breakpoint h^2 estimates: M^2 Parastyle.

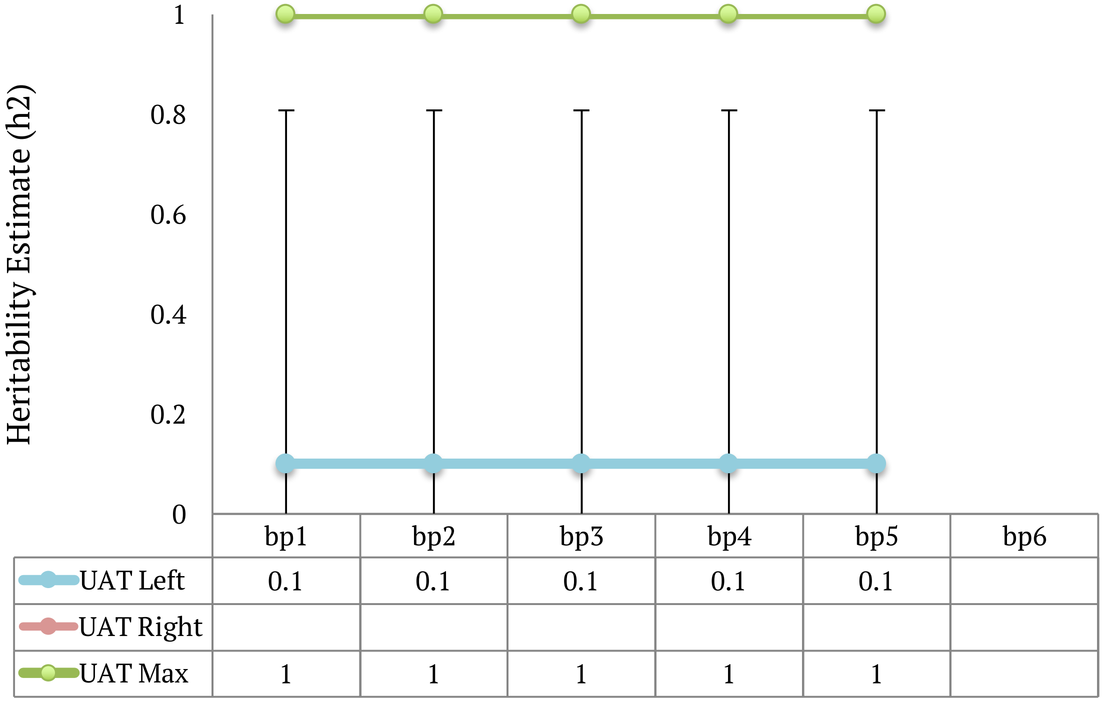
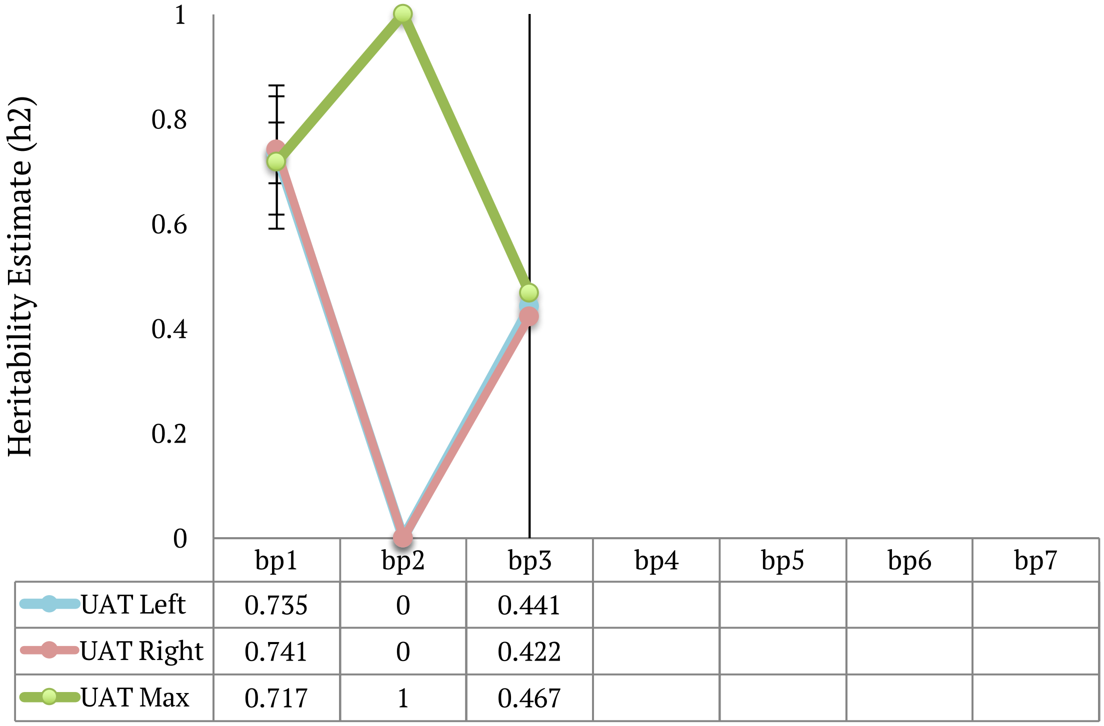
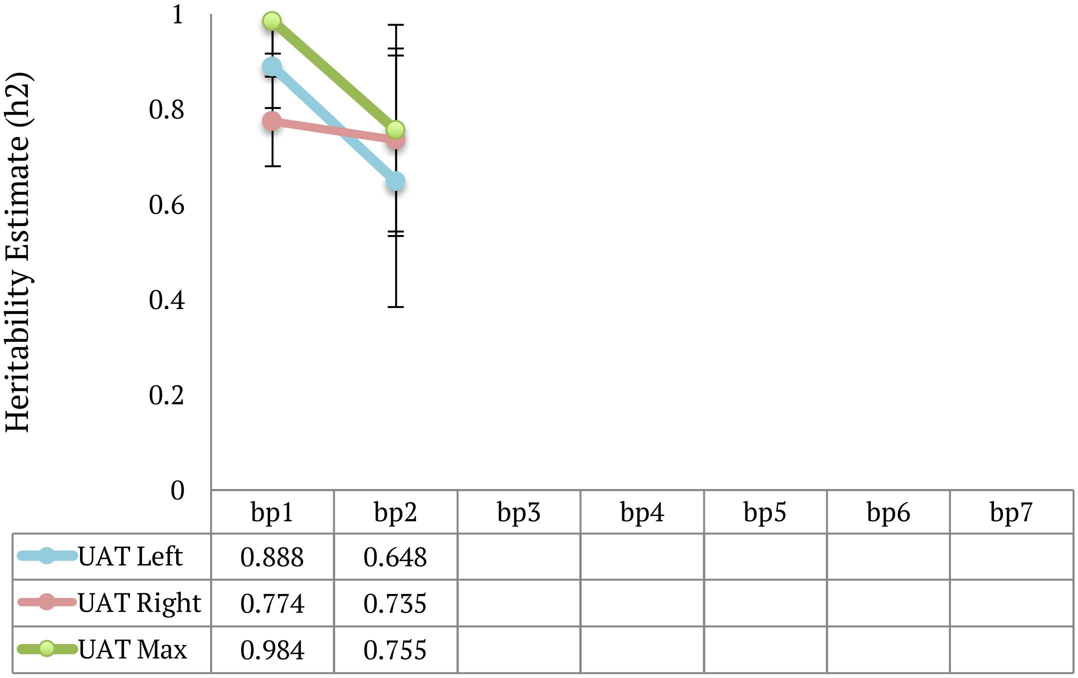


Figure 54. Breakpoint h^2 estimates: M^3 Parastyle.



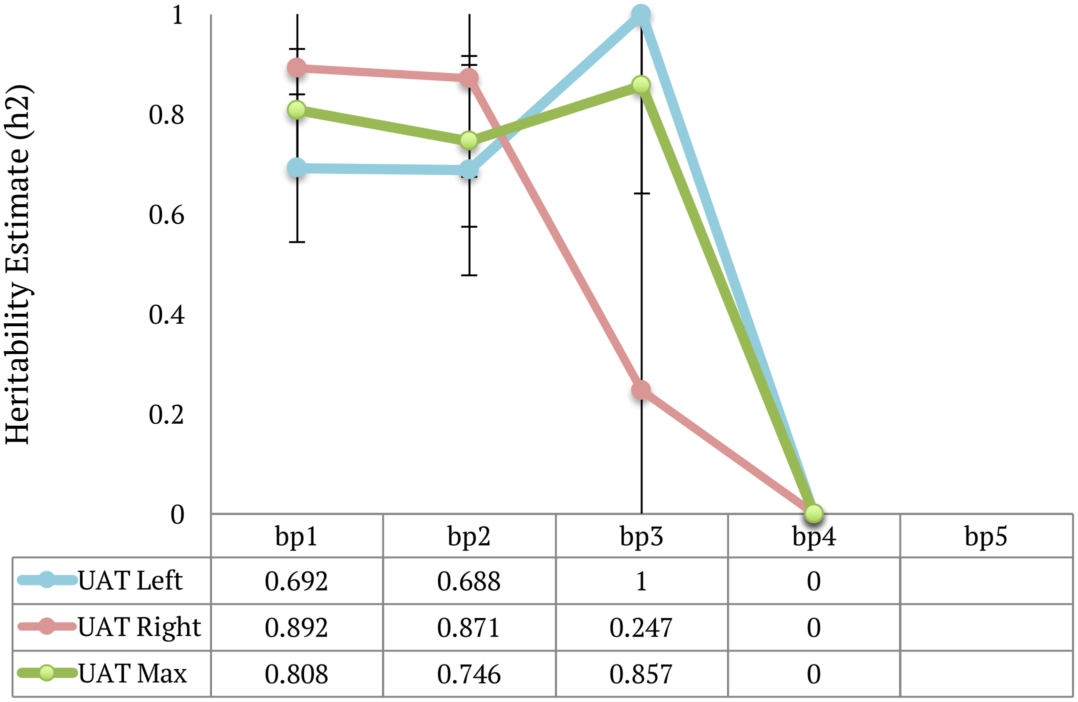
	bp1	bp2	bp3	bp4	bp5	bp6	bp7
UAT Left	0.735	0	0.441				
UAT Right	0.741	0	0.422				
UAT Max	0.717	1	0.467				

Figure 55. Breakpoint h^2 estimates: I_1 Shoveling.



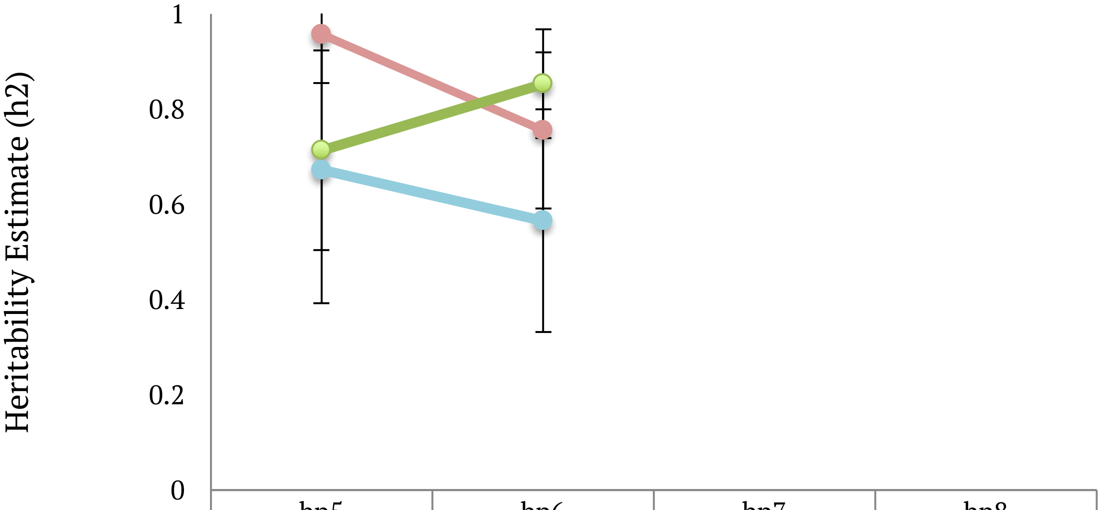
	bp1	bp2	bp3	bp4	bp5	bp6	bp7
● UAT Left	0.888	0.648					
● UAT Right	0.774	0.735					
● UAT Max	0.984	0.755					

Figure 56. Breakpoint h^2 estimates: I_2 Shoveling.



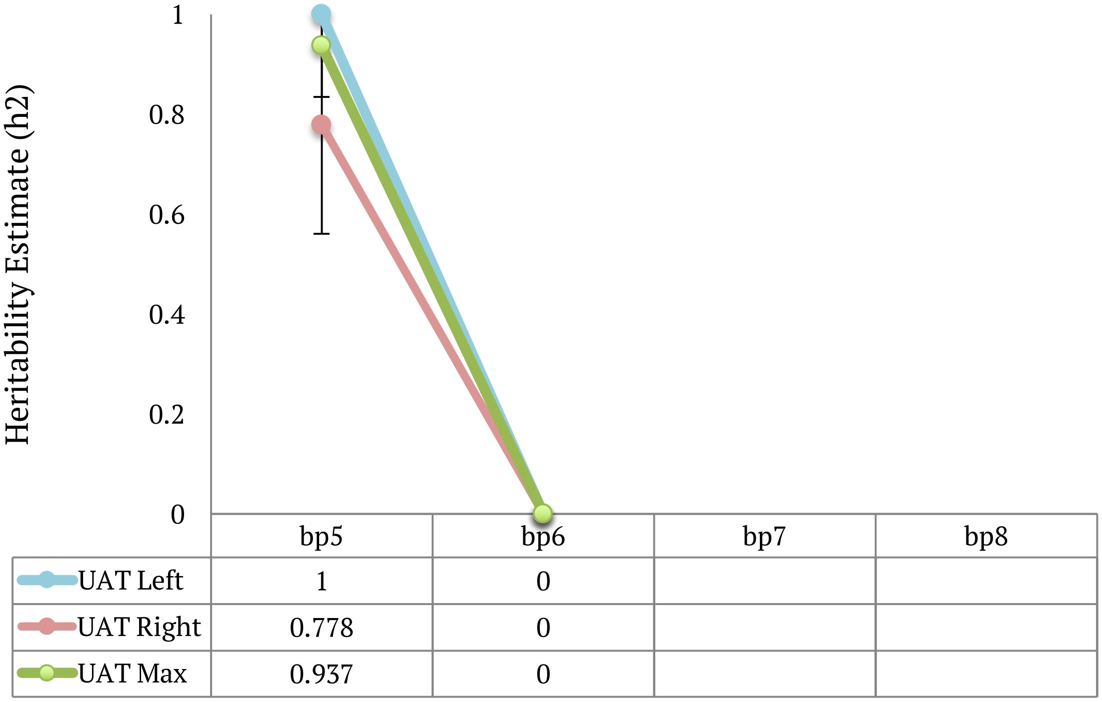
	bp1	bp2	bp3	bp4	bp5
UAT Left	0.692	0.688	1	0	
UAT Right	0.892	0.871	0.247	0	
UAT Max	0.808	0.746	0.857	0	

Figure 57. Breakpoint h^2 estimates: C_1 Distal Accessory Ridge.



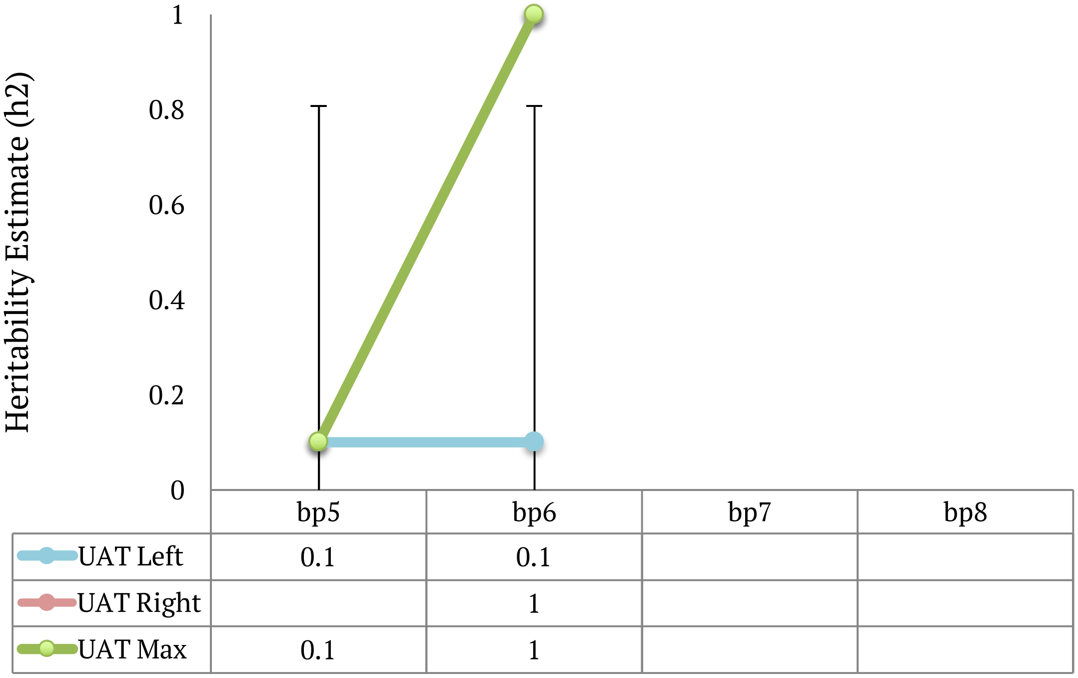
	bp5	bp6	bp7	bp8
UAT Left	0.672	0.565		
UAT Right	0.957	0.755		
UAT Max	0.713	0.853		

Figure 58. Breakpoint h^2 estimates: M_1 Cusp Number.



	bp5	bp6	bp7	bp8
UAT Left	1	0		
UAT Right	0.778	0		
UAT Max	0.937	0		

Figure 59. Breakpoint h^2 estimates: M_2 Cusp Number.



	bp5	bp6	bp7	bp8
UAT Left	0.1	0.1		
UAT Right		1		
UAT Max	0.1	1		

Figure 60. Breakpoint h^2 estimates: M_3 Cusp Number.

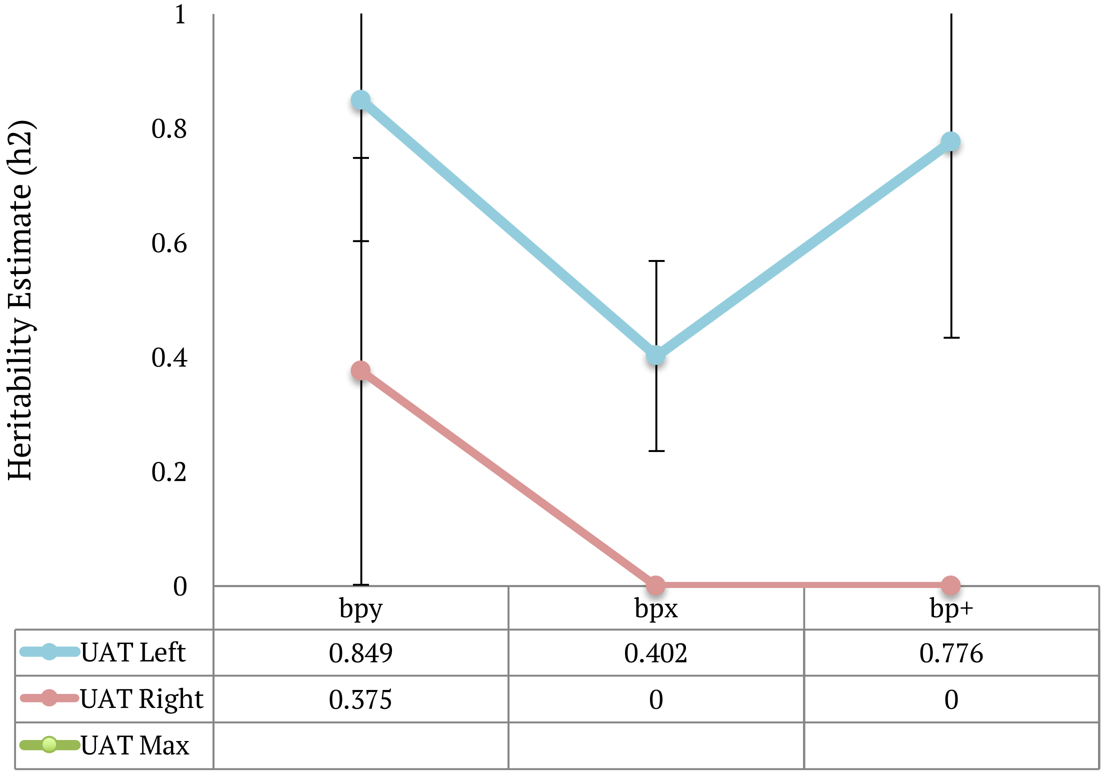
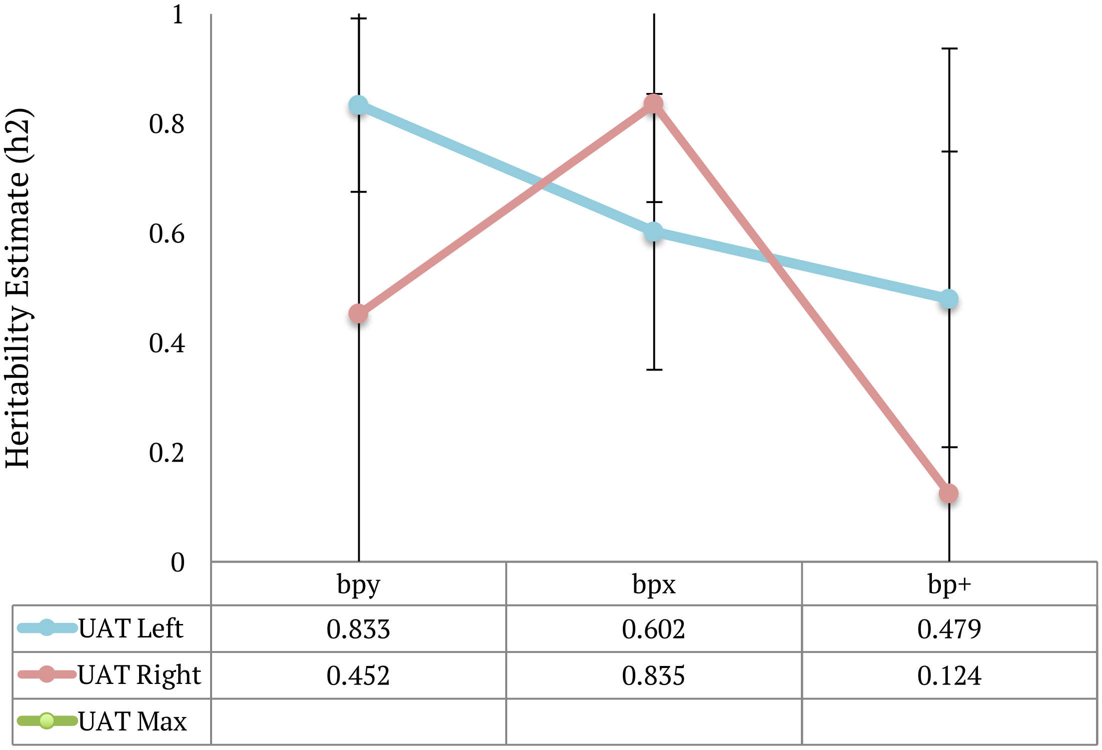
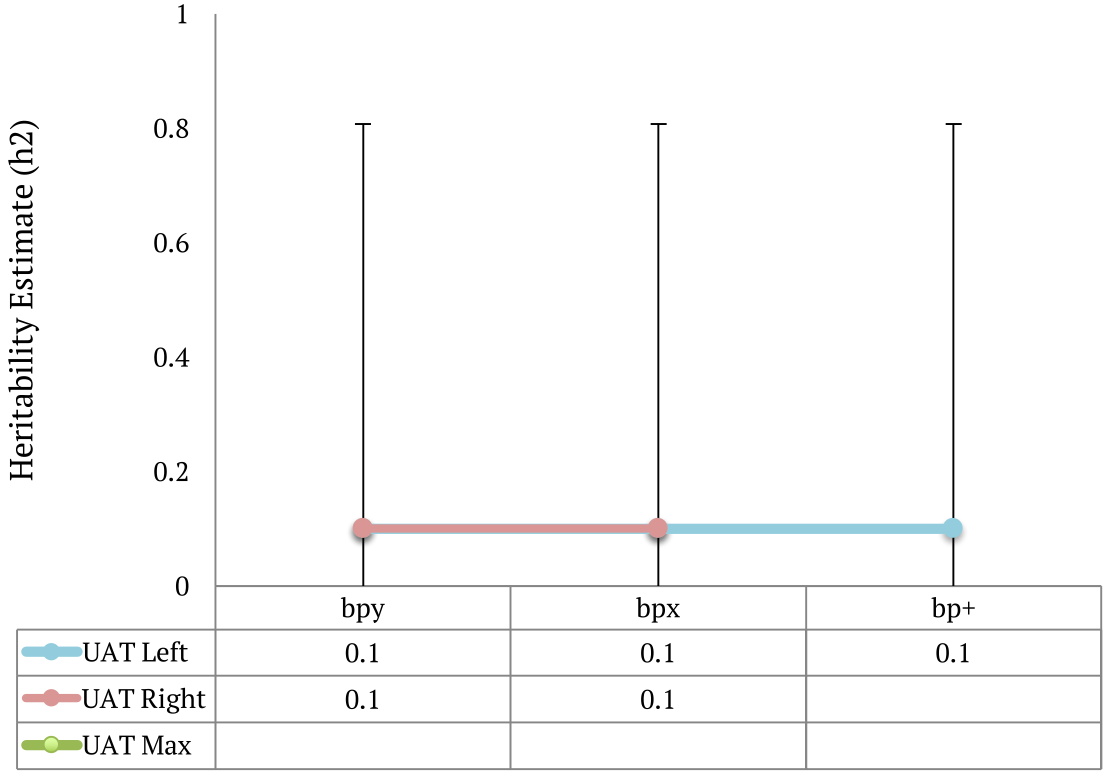


Figure 61. Breakpoint h^2 estimates: M_1 Groove Pattern.



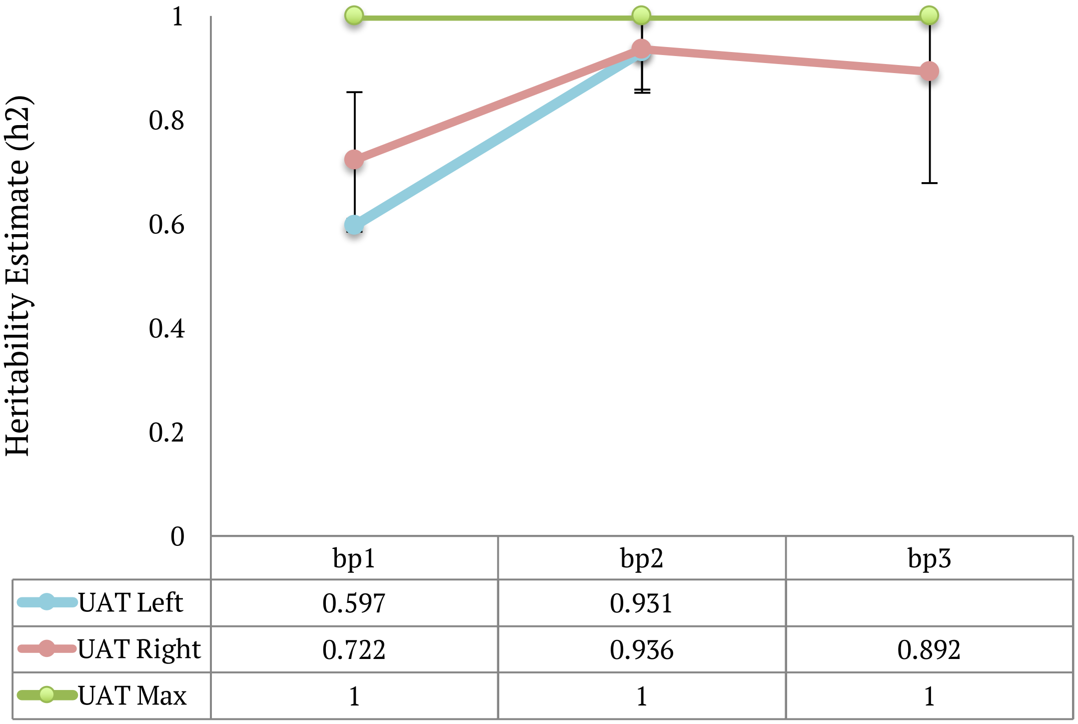
	bpy	bpx	bp+
UAT Left	0.833	0.602	0.479
UAT Right	0.452	0.835	0.124
UAT Max			

Figure 62. Breakpoint h^2 estimates: M_2 Groove Pattern.



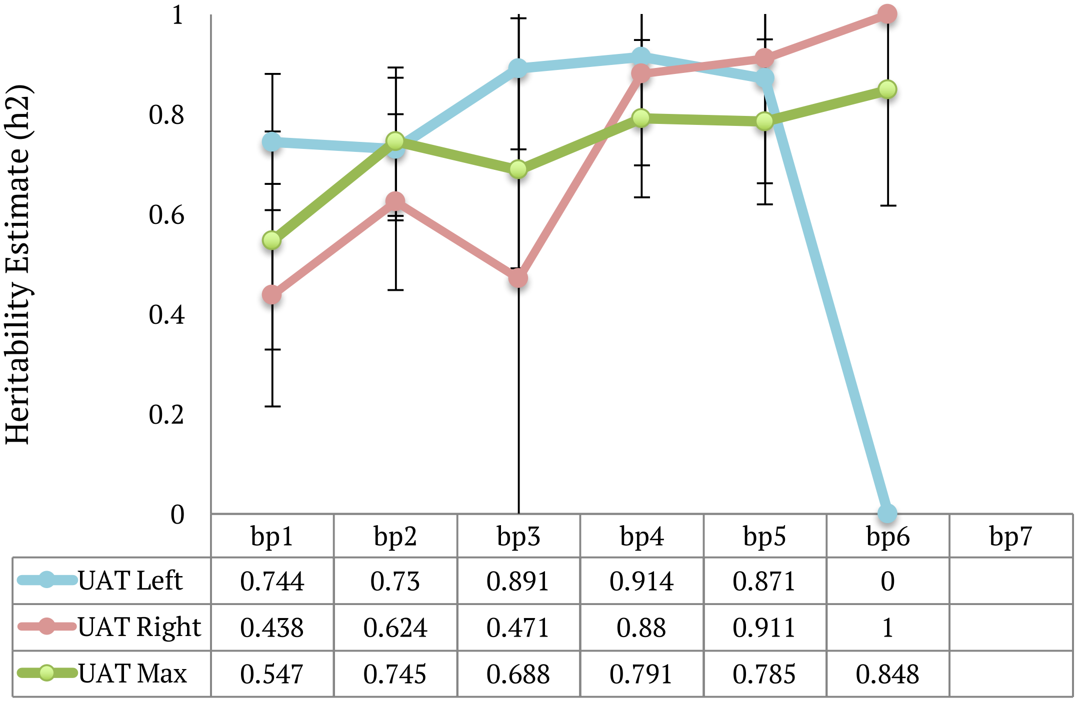
	bpy	bpx	bp+
UAT Left	0.1	0.1	0.1
UAT Right	0.1	0.1	
UAT Max			

Figure 63. Breakpoint h^2 estimates: M_3 Groove Pattern.



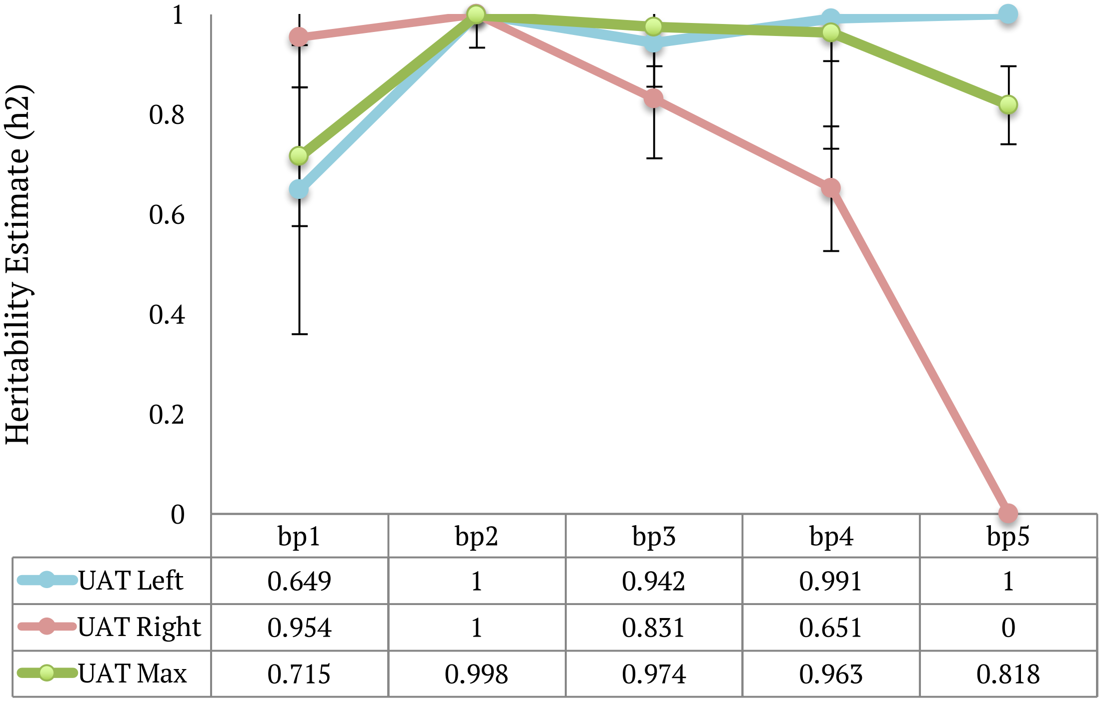
	bp1	bp2	bp3
UAT Left	0.597	0.931	
UAT Right	0.722	0.936	0.892
UAT Max	1	1	1

Figure 64. Breakpoint h^2 estimates: M_1 Deflecting Wrinkle.



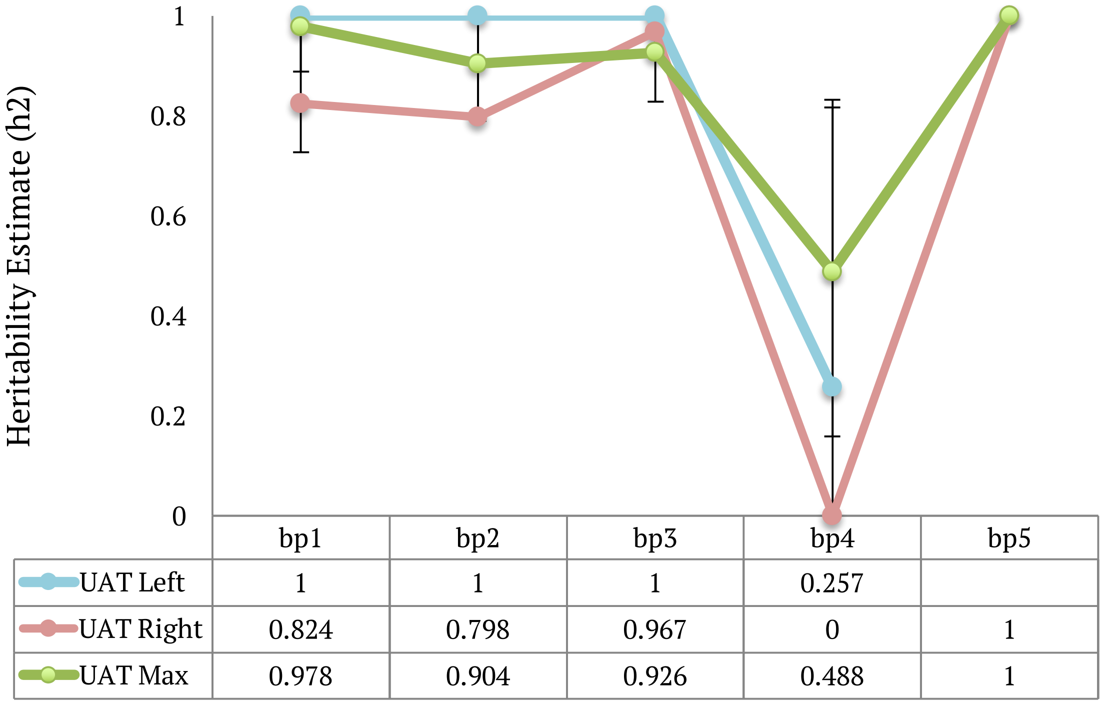
	bp1	bp2	bp3	bp4	bp5	bp6	bp7
UAT Left	0.744	0.73	0.891	0.914	0.871	0	
UAT Right	0.438	0.624	0.471	0.88	0.911	1	
UAT Max	0.547	0.745	0.688	0.791	0.785	0.848	

Figure 65. Breakpoint h^2 estimates: M_1 Protostylid.



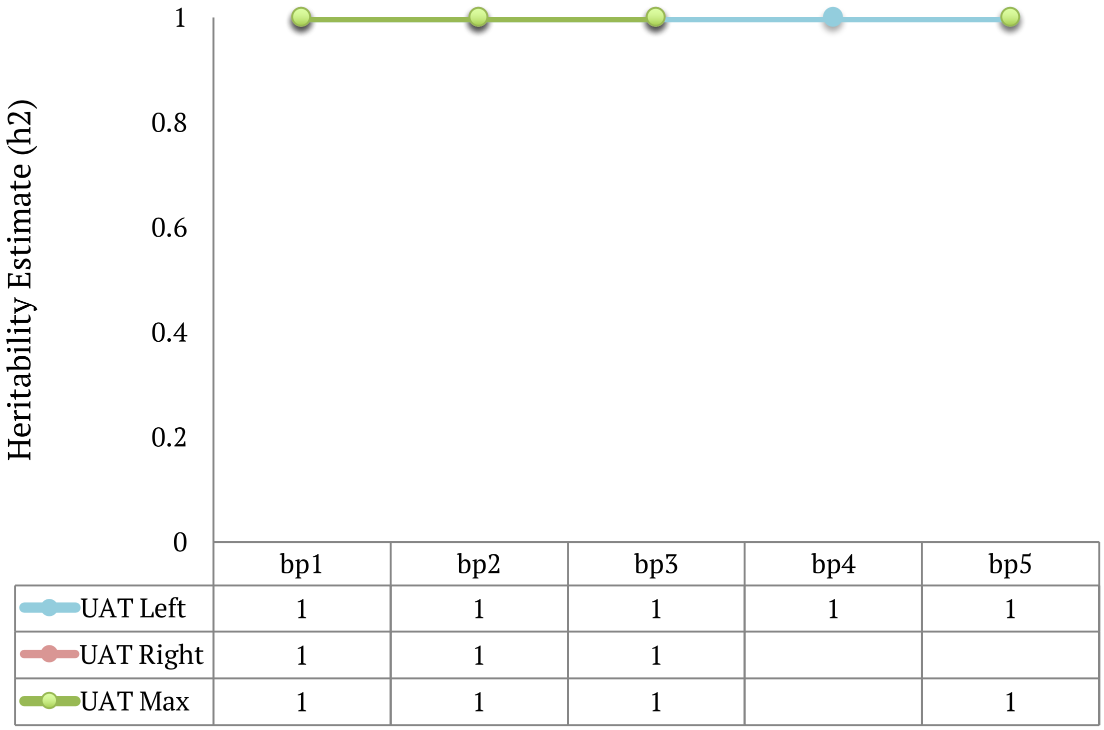
	bp1	bp2	bp3	bp4	bp5
UAT Left	0.649	1	0.942	0.991	1
UAT Right	0.954	1	0.831	0.651	0
UAT Max	0.715	0.998	0.974	0.963	0.818

Figure 66. Breakpoint h^2 estimates: M_1 Cusp 5.



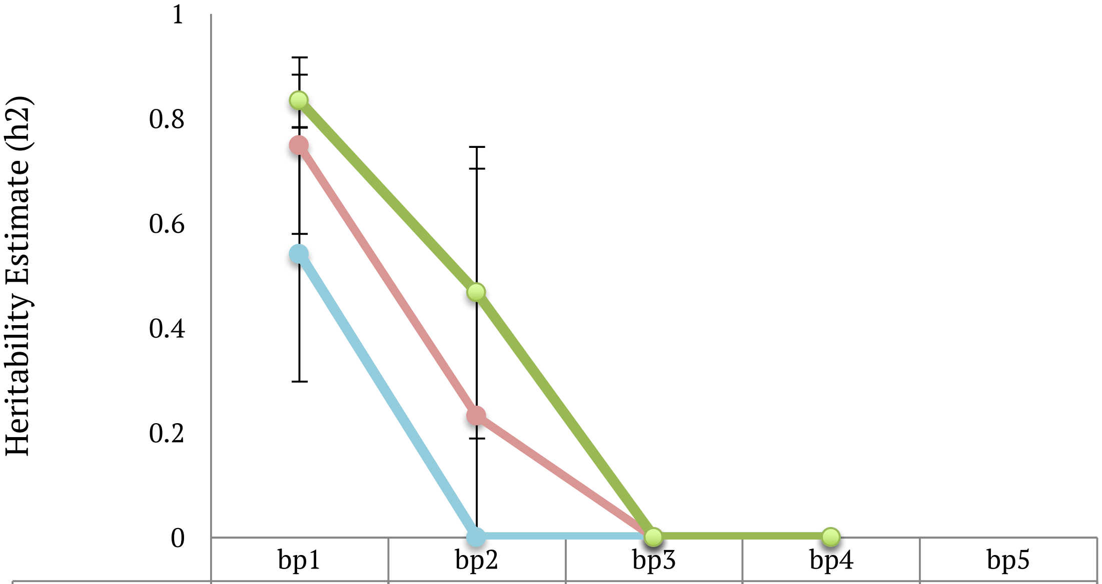
	bp1	bp2	bp3	bp4	bp5
UAT Left	1	1	1	0.257	
UAT Right	0.824	0.798	0.967	0	1
UAT Max	0.978	0.904	0.926	0.488	1

Figure 67. Breakpoint h^2 estimates: M_2 Cusp 5.



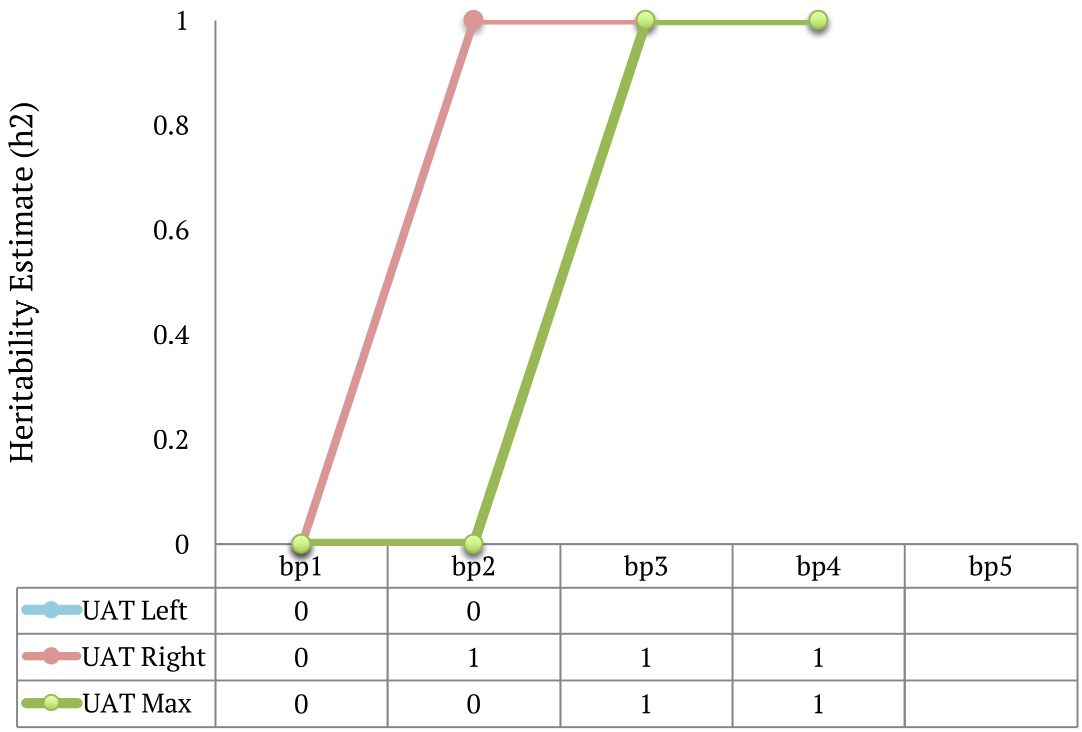
	bp1	bp2	bp3	bp4	bp5
UAT Left	1	1	1	1	1
UAT Right	1	1	1		
UAT Max	1	1	1		1

Figure 68. Breakpoint h^2 estimates: M_3 Cusp 5.



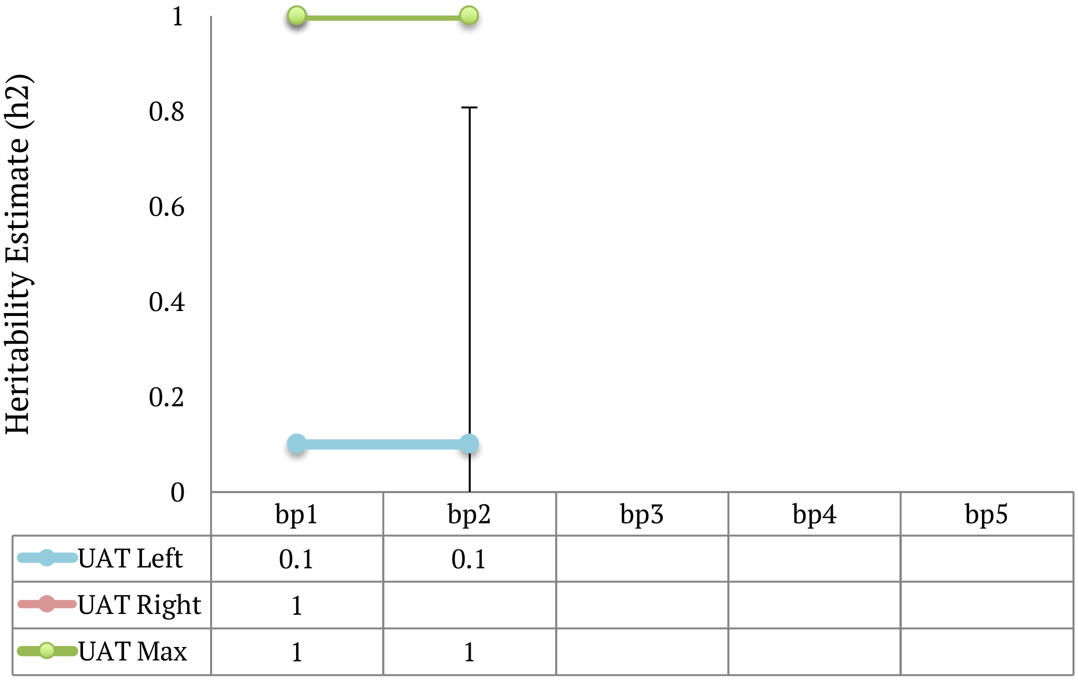
	bp1	bp2	bp3	bp4	bp5
UAT Left	0.541	0	0	0	
UAT Right	0.748	0.231	0		
UAT Max	0.833	0.467	0	0	

Figure 69. Breakpoint h^2 estimates: M_1 Cusp 6.



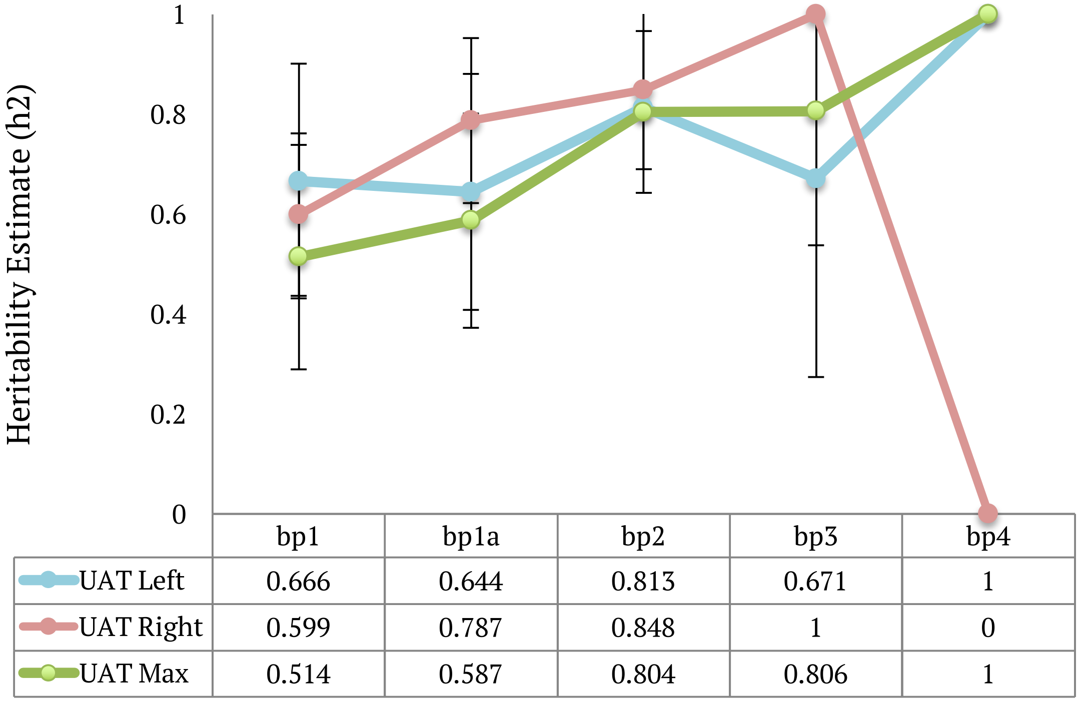
	bp1	bp2	bp3	bp4	bp5
UAT Left	0	0			
UAT Right	0	1	1	1	
UAT Max	0	0	1	1	

Figure 70. Breakpoint h^2 estimates: M_2 Cusp 6.



	bp1	bp2	bp3	bp4	bp5
UAT Left	0.1	0.1			
UAT Right	1				
UAT Max	1	1			

Figure 71. Breakpoint h^2 estimates: M_3 Cusp 6.



	bp1	bp1a	bp2	bp3	bp4
UAT Left	0.666	0.644	0.813	0.671	1
UAT Right	0.599	0.787	0.848	1	0
UAT Max	0.514	0.587	0.804	0.806	1

Figure 72. Breakpoint h^2 estimates: M_1 Cusp 7.

APPENDIX O

UNIVERSITY OF ADELAIDE TWIN STUDY SAMPLE

GENETIC CORRELATION TABLES

Table 1. UAT sample antimeric variance components correlations: deciduous ASUDAS morphology.

Trait [a]	N/Cov [b]	Genetic			Environmental		Phenotypic
		ρ_G [c]	$P(\rho_G=0)$ [d]	$P(\lvert\rho_G\rvert=1)$ [d]	ρ_E [e]	$P(\rho_E=0)$ [d]	ρ_P [f]
i^1 l curve (l-r)[e]	127	1.000±-------**	**<0.001**	-----------	0.005±0.154	0.974	0.576
i^1 shov (l-r)	101/s	1.000±-------**	**0.008**	-----------	-0.043±0.277	0.877	0.527
i^2 shov (l-r)	144	1.000±-------**	**0.002**	-----------	0.091±0.156	0.559	0.407
c^1 shov (l-r)	235/a, s	1.000±-------**	**<0.001**	-----------	-0.275±0.112	**0.025**	0.611
i^1 dshov (l-r)	128	0.982±0.278**	**<0.001**	0.475	-0.151±0.219	0.499	0.399
i^2 dshov (l-r)[w]	157/a*s	---------------	--------	-----------	----------------	-------	-------
c^1 dshov (l-r)	239/a*s	0.998±0.073**	**<0.001**	0.488	-0.017±0.130	0.897	0.599
i^2 td (l-r)	150/a, a*s	1.000±-------**	**<0.001**	-----------	-0.080±0.203	0.694	0.595
c^1 td (l-r)	245/a	1.000±-------**	**<0.001**	-----------	0.109±0.122	0.370	0.670
c^1 dar (l-r)	166	1.000±-------**	**<0.001**	-----------	-0.308±0.196	0.126	0.276
m^1 meta (l-r)[e]	249	0.978±0.077**	**<0.001**	0.387	-0.144±0.131	0.283	0.597
m^2 meta (l-r)	278/a	0.852±0.094**	**<0.001**	0.057	-0.144±0.111	0.208	0.434
m^1 hypo (l-r)	251	1.000±-------**	**<0.001**	-----------	0.114±0.106	0.282	0.642
m^2 hypo (l-r)	279	0.992±0.056**	**<0.001**	0.445	0.005±0.112	0.967	0.648
m^2 c5 (l-r)	272/s	0.868±0.087**	**<0.001**	0.070	0.132±0.140	0.345	0.625
m^2 Carabelli (l-r)	276	1.000±-------**	**<0.001**	-----------	0.227±0.112	**0.046**	0.758
m^2 para (l-r)	278	1.000±-------**	**<0.001**	-----------	0.263±0.117	**0.021**	0.638
i_1 shov (l-r)	94	0.590±0.144*	**0.008**	**0.003**	0.678±0.129	<**0.001**	0.623
i_2 shov (l-r)	150/a, a*s	1.000±-------**	**<0.001**	-----------	0.153±0.149	0.305	0.610
c_1 dar (l-r)	166	1.000±-------**	**0.006**	-----------	0.031±0.169	0.856	0.351
m_2 ant fovea (l-r)	268	0.753±0.139*	**<0.001**	**0.053**	0.182±0.120	0.134	0.446
m_1 cno (l-r)	239/s	1.000±-------**	**<0.001**	-----------	0.020±0.126	0.871	0.591
m_2 cno (l-r)[cf]	------	---------------	--------	-----------	----------------	-------	-------
m_2 dwrink (l-r)	261	1.000±-------**	**<0.001**	-----------	-0.152±0.118	0.228	0.607

m_2 pstylid (l-r)	269/s, a*s	0.912±0.055**	**<0.001**	0.055	0.096±0.131	0.463	0.662
m_1 c5 (l-r)	239/s	1.000±-------**	**<0.001**	-----------	-0.085±0.125	0.501	0.578
m_2 c5 (l-r)	281/a, a*s	0.875±0.176**	**0.001**	0.249	0.173±0.120	0.161	0.412
m_1 c6 (l-r)[cf]	------	---------------	--------	-----------	---------------	-------	-------
m_2 c6 (l-r)[cf]	------	---------------	--------	-----------	---------------	-------	-------
m_2 c7 (l-r)	283	0.938±0.054**	**<0.001**	0.120	0.107±0.121	0.374	0.687
m_2 dtcrest (l-r)[w]	------	---------------	--------	-----------	---------------	-------	-------

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[a] l=left; r=right; i=incisor; c=canine; m=molar. Maxillary and mandibular traits indicated by superscript and subscript, respectively. For a list of morphological trait abbreviations, see Appendix C. "e" superscript indicates a trait that was originally flagged for intra-observer error because the error range exceeded a single grade, but whose mean error does not exceed 0.300. Traits with mean error exceeding 0.300 were omitted from the correlation analyses. "w" superscript indicates models that are suspect due to standard deviation ranges for certain estimates. "cf" superscript indicates model convergence failure. [b] Covariates fixed in the genetic correlation models if significant in associated univariate models. "a"=age; "s"=sex; "a*s"=age/sex interaction. [c] Maximum-likelihood estimate of genetic correlation. Cases of incomplete pleiotropy indicated by a single asterisks. Cases of complete pleiotropy indicated by two asterisks. Dashes are associated with incalculable parameter estimates. [d] Probability of hypothesis (as indicated in parentheses) being true given pedigree structure with values p<0.050 bolded. Dashes are associated with incalculable parameter estimates. [e] Maximum-likelihood estimate of environmental correlation. Dashes are associated with incalculable parameter estimates. [f] Maximum-likelihood estimate of derived phenotypic correlation. Dashes are associated with incalculable parameter estimates.

Table 2. UAT sample antimeric variance components correlations: permanent ASUDAS morphology.

Trait[a]	N/Cov[b]	Genetic			Environmental		Phenotypic
		ρ_G[c]	$P(\rho_G=0)$[d]	$P(\lvert\rho_G\rvert=1)$[d]	ρ_E[e]	$P(\rho_E=0)$[d]	ρ_P[f]
I^1 L CURVE (L-R)^E	298/A*S	0.903±0.064**	**<0.001**	0.054	0.185±0.110	0.098	0.590
I^1 SHOV (L-R)	284/A	0.917±0.041*	**<0.001**	**0.009**	0.385±0.122	**0.002**	0.793
I^2 SHOV (L-R)	235/ALL	0.981±0.053**	<**0.001**	0.358	-0.130±0.138	0.361	0.662
C^1 SHOV (L-R)	165	0.904±0.111**	**<0.001**	0.196	0.076±0.196	0.699	0.611
I^1 DSHOV (L-R)	311	0.873±0.079*	**<0.001**	**0.036**	-0.234±0.108	**0.039**	0.546
I^2 DSHOV (L-R)	262/A*S	0.816±0.103*	**<0.001**	**0.044**	0.125±0.132	0.347	0.520
C^1 DSHOV (L-R)	189/A, S	1.000±-------**	**<0.001**	-----------	-0.028±0.176	0.872	0.664
P^1 DSHOV (L-R)	234	0.978±0.055**	**<0.001**	0.338	0.262±0.134	0.055	0.693
P^2 DSHOV (L-R)	180/S, A*S	1.000±-------**	**<0.001**	-----------	-0.301±0.135	0.055	0.610
I^1 TD (L-R)	274/S	1.000±-------**	**<0.001**	-----------	0.122±0.132	0.361	0.715
I^2 TD (L-R)	151/S	1.000±-------**	**<0.001**	-----------	-0.047±0.207	0.822	0.812
C^1 TD (L-R)	135/ALL	0.999±0.031**	**<0.001**	0.485	-0.344±0.228	0.190	0.872
C^1 MRIDGE (L-R)^W	-------	----------------	-------	-----------	--------------	-------	-------
C^1 DAR (L-R)	200/S	0.901±0.070**	**<0.001**	0.081	-0.023±0.176	0.896	0.676
M^1 META (L-R)^E	327	1.000±-------**	**<0.001**	-----------	0.221±0.095	**0.028**	0.555
M^2 META (L-R)	151/S, A*S	0.990±0.232**	**0.002**	0.483	0.544±0.127	**<0.001**	0.668
M^1 HYPO (L-R)	319/S	1.000±-------**	**<0.001**	-----------	-0.206±0.108	0.073	0.620
M^2 HYPO (L-R)	112	1.000±-------**	**<0.001**	-----------	-0.523±0.312	0.276	0.878
M^1 C5 (L-R)	292/A, A*S	0.968±0.051**	**<0.001**	0.263	-0.085±0.143	0.558	0.675
M^2 C5 (L-R)	117	1.000±-------**	**<0.001**	-----------	-0.498±0.220	0.095	0.596
M^1 CARAB (L-R)	302/A, A*S	0.965±0.032**	**<0.001**	0.119	0.438±0.100	**<0.001**	0.801
M^2 CARAB (L-R)	135/A, A*S	0.792±0.100*	**<0.001**	**0.023**	0.056±0.257	0.828	0.641
M^1 PARA (L-R)	314	0.886±0.110**	**<0.001**	0.148	-0.429±0.118	**0.001**	0.306
M^2 PARA (L-R)^W	-------	----------------	-------	-----------	--------------	-------	-------

I^2 PEG (L-R)^{W}	-------	----------------	-------	-----------	---------------	-------	-------
I^2 CONG ABS (L-R)^{W}	-------	----------------	-------	-----------	---------------	-------	-------
I_1 SHOV (L-R)	308/S	1.000±-------**	**<0.001**	-----------	0.420±0.085	<**0.001**	0.744
I_2 SHOV (L-R)	278/A	0.990±0.054**	**<0.001**	0.423	-0.067±0.112	0.552	0.618
C_1 DAR (L-R)	226/S	1.000±0.121**	**<0.001**	0.499	0.008±0.177	0.962	0.578
M_1 CNO (L-R)	293	1.000±-------**	**<0.001**	-----------	0.223±0.111	**0.039**	0.588
M_2 CNO (L-R)^{E}	140	0.991±0.092**	**<0.001**	0.462	-0.144±0.308	0.653	0.695
M_1 ANT FOVEA (L-R)	294	1.000±-------**	**<0.001**	-----------	-0.098±0.155	0.528	0.655
M_1 DWRINK (L-R)	301	0.973±0.059**	**<0.001**	0.324	-0.278±0.112	**0.023**	0.580
M_1 PSTYLID (L-R)	293	0.916±0.100**	**<0.001**	0.207	0.282±0.158	0.103	0.605
M_1 C5 (L-R)	280/ALL	0.935±0.046**	**<0.001**	0.062	-0.149±0.131	0.275	0.696
M_2 C5 (L-R)	145/S	1.000±-------**	**<0.001**	-----------	0.290±0.249	0.283	0.784
M_1 C6 (L-R)	281/A*S	1.000±-------**	**<0.001**	-----------	0.152±0.114	0.183	0.512
M_2 C6 (L-R)^{W}	-------	----------------	-------	-----------	---------------	-------	-------
M_1 C7 (L-R)	330/S	1.000±-------**	**<0.001**	-----------	0.144±0.134	0.263	0.694
M_2 C7 (L-R)^{E}	187	1.000±-------**	**0.047**	-----------	0.182±0.152	0.269	0.368
M_1 DTCREST (L-R)^{W}	-------	----------------	-------	-----------	---------------	-------	-------
M_2 DTCREST (L-R)^{W}	-------	----------------	-------	-----------	---------------	-------	-------
I_1 CONG ABS (L-R)^{CF}	-------	----------------	-------	-----------	---------------	-------	-------
P_2 CONG ABS (L-R)^{CF}	-------	----------------	-------	-----------	---------------	-------	-------
M_3 CONG ABS (L-R)^{CF}	-------	----------------	-------	-----------	---------------	-------	-------

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[a] L=left; R=right; I=incisor; C=canine; P=premolar; M=molar. Maxillary and mandibular traits indicated by superscript and subscript, respectively. For a list of morphological trait abbreviations, see Appendix C. “E” superscript indicates a trait that was originally flagged for intra-observer error because the error range exceeded a single grade, but whose mean error does not exceed 0.300. Traits with mean error exceeding 0.300 were omitted from the correlation analyses. All third molar traits were omitted from the correlation analyses due to sample size limitations. “W” superscript indicates models that are suspect due to standard deviation ranges for certain estimates. “CF” superscript indicates model convergence failure. [b] Covariates fixed in the genetic correlation models if significant in associated univariate models. “A”=age; “S”=sex; “A*S”=age/sex interaction; ALL=all covariates. [c] Maximum-likelihood estimate of genetic correlation. Cases of incomplete pleiotropy indicated by a single asterisks. Cases of complete pleiotropy indicated by

two asterisks. Dashes are associated with incalculable parameter estimates. [d]Probability of hypothesis (as indicated in parentheses) being true given pedigree structure with values $p<0.050$ bolded. Dashes are associated with incalculable parameter estimates. [e]Maximum-likelihood estimate of environmental correlation. Dashes are associated with incalculable parameter estimates. [f]Maximum-likelihood estimate of derived phenotypic correlation. Dashes are associated with incalculable parameter estimates.

Table 3. UAT sample variance components within-class correlations: deciduous ASUDAS morphology.

		Genetic			Environmental		Phenotypic
Trait [a]	N/Cov[b]	ρ_G[c]	$P(\rho_G=0)$[d]	$P(\lvert\rho_G\rvert=1)$[d]	ρ_E[e]	$P(\rho_E=0)$[d]	ρ_P[f]
Anterior Dentition							
i^1 l curve[e]							
i^1 shov	129/s	0.267±0.188	0.178	**0.028**	0.268±0.224	0.257	0.254
i^2 shov	156	-0.078±0.181	0.666	**<0.001**	0.288±0.183	0.143	0.050
c^1shov	242/all	0.034±0.150	0.819	**<0.001**	0.084±0.186	0.655	0.045
i^1 dshov	135	-0.252±0.162	0.128	**<0.001**	-0.033±0.199	0.867	-0.179
i^2 dshov[e]	160/a*s	0.146±0.201	0.461	**0.018**	-0.408±0.153	**0.018**	-0.088
c^1 dshov	241/s	0.099±0.140	0.476	**<0.001**	-0.280±0.175	0.136	0.006
i^2 td	164	0.095±0.151	0.531	**<0.001**	-0.118±0.231	0.614	0.038
c^1 td	254/a	0.255±0.149	0.105	**<0.001**	0.207±0.192	0.299	0.237
c^1 dar	189	-0.414±0.198*	**0.025**	**0.010**	0.569±0.140	**0.004**	-0.036
i_1 shov	137	-0.213±0.257	0.394	**0.029**	0.440±0.227	0.106	0.051
i_2 shov	157/a, s	-0.184±0.192	0.330	**0.002**	0.082±0.189	0.667	-0.083
c_1 dar	189	0.095±0.233	0.681	**0.009**	-0.190±0.225	0.418	-0.022
i^1 shov							
i^2 shov	146/s	0.173±0.250	0.497	**0.032**	0.299±0.185	0.128	0.235
c^1 shov	241/all	-0.386±0.201	0.059	**0.032**	0.189±0.168	0.275	-0.178
i^1 dshov	133/s	-0.436±0.276	0.105	0.070	0.090±0.243	0.712	-0.181
i^2 dshov[e]	159/s, a*s	0.442±0.449	0.296	0.164	-0.215±0.212	0.335	0.006
c^1 dshov	241/s	-0.230±0.210	0.284	**0.038**	-0.078±0.214	0.717	-0.162
i^2 td	155/s	0.171±0.238	0.473	**0.027**	-0.014±0.250	0.995	0.092
c^1 td	250/a, s	0.260±0.237	0.257	**0.041**	0.056±0.203	0.783	0.163
c^1 dar	183/s	0.112±0.242	0.654	**0.008**	0.414±0.203	0.079	0.264

i_1 shov	123/s	0.089±0.364	0.811	**0.021**	0.479±0.272	0.146	0.301
i_2 shov	155/a, s	0.379±0.249	0.139	**0.027**	-0.049±0.191	0.796	0.166
c_1 dar	181/s	0.348±0.334	0.276	0.080	-0.111±0.252	0.666	0.090
i^2 shov							
c^1 shov	243/all	0.090±0.162	0.580	**<0.001**	0.115±0.171	0.504	0.095
i^1 dshov	159	-0.191±0.212	0.364	**0.001**	0.245±0.175	0.182	-0.004
i^2 dshov^e	164/a*s	0.169±0.269	0.538	**0.042**	-0.060±0.151	0.693	0.026
c^1 dshov	244/s	0.087±0.165	0.605	**<0.001**	0.100±0.195	0.611	0.089
i^2 td	159	0.236±0.176	0.195	**<0.001**	0.083±0.172	0.630	0.176
c^1 td	252/a	0.098±0.189	0.614	**<0.001**	0.349±0.153	**0.038**	0.205
c^1 dar	203	-0.093±0.230	0.686	**0.001**	0.152±0.188	0.427	0.025
i_1 shov	158	0.407±0.367	0.233	0.106	0.198±0.236	0.401	0.288
i_2 shov	171/a, s	0.518±0.203*	**0.026**	**0.012**	0.104±0.180	0.563	0.321
c_1 dar	196	-0.097±0.254	0.700	**0.006**	0.205±0.194	0.307	0.064
c^1 shov							
i^1 dshov	243/all	0.103±0.174	0.556	**<0.001**	-0.036±0.159	0.821	0.060
i^2 dshov^e	247/all	-0.212±0.236	0.367	0.065	-0.062±0.147	0.675	-0.114
c^1 dshov	251/all	0.375±0.094*	**<0.001**	**<0.001**	0.061±0.141	0.665	0.303
i^2 td	244/all	-0.127±0.137	0.357	**<0.001**	0.226±0.176	0.223	-0.041
c^1 td	257/all	0.185±0.115	0.115	**<0.001**	0.117±0.138	0.401	0.161
c^1 dar	239/all	-0.390±0.155*	**0.011**	**0.002**	0.095±0.146	0.520	-0.203
i_1 shov	240/all	-0.254±0.268	0.332	**0.032**	0.192±0.155	0.227	-0.072
i_2 shov	245/all	-0.043±0.166	0.798	**0.001**	0.205±0.163	0.224	0.037
c_1 dar	248/all	-0.257±0.169	0.129	**0.004**	0.103±0.150	0.495	-0.114
i^1 dshov							
i^2 dshov^e	161/a*s	-0.172±0.307	0.560	0.064	0.316±0.163	0.070	0.107
c^1 dshov	242/s	-0.066±0.173	0.700	**<0.001**	0.294±0.193	0.160	0.052
i^2 td	166	-0.008±0.185	0.965	**0.001**	0.114±0.212	0.594	0.035
c^1 td	255/a	-0.107±0.193	0.577	**<0.001**	0.137±0.186	0.466	-0.009
c^1 dar	192	0.013±0.213	0.952	**<0.001**	-0.162±0.180	0.374	-0.065
i_1 shov	137	-0.184±0.302	0.529	**0.037**	0.076±0.247	0.758	-0.050

i_2 shov	158/a, s	-0.041±0.205	0.840	**0.001**	0.422±0.158	**0.023**	0.153
c_1 dar	188	-0.267±0.263	0.305	**0.020**	0.029±0.200	0.885	-0.114
i^2 dshov^e							
c^1 dshov	246/s, a*s	0.228±0.237	0.336	**0.055**	0.073±0.155	0.637	0.127
i^2 td	171/a*s	0.053±0.255	0.837	**0.044**	-0.030±0.161	0.851	0.007
c^1 td	256/a, a*s	-0.108±0.276	0.693	**0.041**	-0.158±0.151	0.306	-0.045
c^1 dar	206/a*s	0.451±0.361	0.152	0.143	-0.197±0.148	0.198	0.023
i_1 shov	162/a*s	-0.260±0.570	0.662	0.104	-0.138±0.247	0.585	-0.174
i_2 shov	175/all	-0.178±0.393	0.620	0.110	0.316±0.130	**0.025**	0.149
c_1 dar	197/a*s	-0.744±0.449	0.079	0.303	0.075±0.178	0.676	-0.177
c^1 dshov							
i^2 td	247/s	0.104±0.144	0.470	**<0.001**	-0.004±0.203	0.985	0.075
c^1 td	260/a, s	-0.184±0.119	0.138	**<0.001**	-0.032±0.145	0.824	0.117
c^1 dar	242/s	0.405±0.163*	**0.013**	**0.002**	0.182±0.138	0.202	-0.177
i_1 shov	245/s	-0.013±0.232	0.954	**0.020**	-0.414±0.169	**0.034**	-0.164
i_2 shov	247/a, s	0.017±0.171	0.921	**0.001**	0.157±0.156	0.322	0.065
c_1 dar	248/s	-0.008±0.180	0.967	**0.003**	-0.229±0.157	0.159	-0.089
i^2 td							
c^1 td	250/a	-0.171±0.176	0.331	**<0.001**	0.102±0.207	0.625	0.146
c^1 dar	211	0.217±0.197	0.276	**<0.001**	-0.113±0.214	0.601	0.084
i_1 shov	168	-0.451±0.211	0.083	**0.012**	0.340±0.229	0.185	0.390
i_2 shov	178/a, s	0.216±0.186	0.258	**0.001**	0.091±0.183	0.622	0.164
c_1 dar	202	0.175±0.233	0.472	**0.009**	0.200±0.215	0.374	0.178
c^1 td							
c^1 dar	255	0.336±0.171*	**0.050**	**<0.001**	-0.126±0.160	0.439	0.131
i_1 shov	253/a	0.030±0.278	0.915	**0.015**	0.268±0.209	0.223	0.143
i_2 shov	257/a, s	0.149±0.211	0.481	**0.001**	0.044±0.176	0.805	0.101
c_1 dar	257/a	0.019±0.209	0.928	**0.005**	0.191±0.154	0.227	0.100
c^1 dar							
i_1 shov	179	-0.180±0.300	0.538	**0.029**	0.423±0.181	**0.041**	0.144
i_2 shov	202/a, s	0.062±0.219	0.779	**0.001**	0.122±0.168	0.473	0.092

c_1 dar	198	0.658±0.263**	**0.016**	0.121	0.079±0.173	0.645	0.323
i_1 shov							
i_2 shov	150/a, s	0.496±0.293	0.120	0.067	0.139±0.195	0.480	0.298
c_1 dar	177	-0.261±0.390	0.457	0.095	0.526±0.151	**0.007**	0.213
i_2 shov							
c_1 dar	195/a, s	0.057±0.262	0.827	**0.005**	0.126±0.180	0.490	0.094
Postcanine Dentition							
m^1 meta^e							
m^2 meta	280/s	0.080±0.122	0.515	**<0.001**	-0.072±0.139	0.605	0.031
m^1 hypo	252	0.384±0.133*	**0.005**	**<0.001**	-0.113±0.123	0.262	0.186
m^2 hypo	281	0.041±0.116	0.726	**<0.001**	0.027±0.142	0.851	0.037
m^2 c5	278/s	-0.030±0.141	0.832	**<0.001**	-0.027±0.138	0.842	-0.029
m^2 Carabelli	279	0.056±0.106	0.594	**<0.001**	-0.204±0.136	0.148	<0.001
m^2 para	281	-0.036±0.125	0.777	**<0.001**	-0.150±0.132	0.267	-0.074
m_2 ant fovea	276	0.315±0.161	0.060	**0.001**	-0.092±0.134	0.496	0.129
m_1 cno	261/s	0.033±0.124	0.788	**<0.001**	-0.068±0.133	0.609	0.001
m_2 cno^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 dwrink	274	-0.001±0.118	0.996	**<0.001**	0.051±0.138	0.714	0.013
m_1 c5	260/s	0.116±0.117	0.326	**<0.001**	-0.029±0.131	0.822	0.071
m_2 c5	284/a, a*s	-0.047±0.201	0.814	**0.009**	0.081±0.133	0.545	0.019
m_1 c6^{cf}	-----------	---------------	-------	---------	---------------	-------	---------
m_2 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c7	284	-0.106±0.111	0.339	**<0.001**	0.021±0.134	0.874	-0.072
m_2 dtcrest	276	0.224±0.113	0.055	**<0.001**	0.009±0.139	0.949	0.156
m^2 meta							
m^1 hypo	280/s	0.136±0.140	0.324	**<0.001**	-0.070±0.126	0.579	0.053
m^2 hypo	279/s	0.134±0.108	0.218	**<0.001**	-0.059±0.121	0.628	0.075
m^2 c5	279/s	-0.287±0.139*	**0.045**	**<0.001**	-0.050±0.133	0.708	-0.190
m^2 Carabelli	279/s	0.064±0.101	0.527	**<0.001**	-0.241±0.126	0.069	-0.004
m^2 para	281/s	-0.046±0.118	0.699	**<0.001**	0.087±0.121	0.475	0.001

m_2 ant fovea	285/a, s	0.193±0.175	0.268	**0.001**	-0.096±0.137	0.486	0.055
m_1 cno	281/s	0.061±0.129	0.641	**<0.001**	0.195±0.134	0.156	0.106
m_2 cno^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 dwrink	284/s	-0.041±0.121	0.732	**<0.001**	0.156±0.143	0.285	0.014
m_1 c5	281/s	0.114±0.121	0.350	**<0.001**	0.060±0.132	0.649	0.096
m_2 c5	286/all	0.359±0.203	0.066	**0.021**	-0.052±0.125	0.676	0.127
m_1 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c7	286/s	-0.124±0.106	0.245	**<0.001**	0.059±0.124	0.636	-0.073
m_2 dtcrest	285/s	0.010±0.123	0.935	**<0.001**	-0.062±0.141	0.662	-0.014
m^1 hypo							
m^2 hypo	281	0.490±0.123*	**<0.001**	**<0.001**	-0.075±0.126	0.556	0.272
m^2 c5	279/s	0.019±0.159	0.904	**<0.001**	0.161±0.127	0.213	0.084
m^2 Carabelli	280	0.346±0.111*	**0.004**	**<0.001**	0.127±0.134	0.347	0.267
m^2 para	281	-0.063±0.144	0.663	**<0.001**	0.160±0.125	0.210	0.030
m_2 ant fovea	276/a	0.011±0.191	0.956	**<0.001**	-0.064±0.129	0.619	-0.029
m_1 cno	262/s	0.321±0.149*	**0.031**	**<0.001**	-0.140±0.124	0.268	0.135
m_2 cno^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 dwrink	275	0.324±0.126*	**0.013**	**<0.001**	-0.086±0.134	0.522	0.181
m_1 c5	261/s	0.459±0.127*	**0.001**	**<0.001**	-0.135±0.121	0.272	0.231
m_2 c5	284/a, a*s	-0.108±0.219	0.621	**0.008**	0.028±0.124	0.823	-0.026
m_1 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c7	284	0.147±0.123	0.240	**<0.001**	0.031±0.127	0.807	0.105
m_2 dtcrest	277	0.309±0.134*	**0.020**	**<0.001**	-0.186±0.130	0.165	0.109
m^2 hypo							
m^2 c5	279/s	0.380±0.116*	**0.002**	**<0.001**	-0.249±0.121	0.055	0.165
m^2 Carabelli	280	0.306±0.092*	**0.001**	**<0.001**	-0.108±0.129	0.407	0.219
m^2 para	281	0.278±0.108*	**0.012**	**<0.001**	-0.097±0.120	0.425	0.155
m_2 ant fovea	286/a	-0.323±0.157*	**0.033**	**0.001**	0.328±0.121	**0.014**	-0.044
m_1 cno	282/s	0.258±0.137	0.055	**<0.001**	-0.220±0.139	0.129	0.104

m_2 cno^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 dwrink	285	0.158±0.108	0.145	**<0.001**	-0.029±0.141	0.837	0.111
m_1 c5	282/s	0.288±0.117*	**0.017**	**<0.001**	-0.001±0.139	0.992	0.200
m_2 c5	287/a, a*s	0.344±0.174*	**0.050**	**0.009**	-0.062±0.130	0.639	0.132
m_1 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_1 c7^{e}	283	0.106±0.115	0.357	**<0.001**	-0.020±0.156	0.899	0.073
m_2 dtcrest	286	-0.023±0.112	0.838	**<0.001**	-0.027±0.132	0.839	-0.024
m^2 c5							
m^2 Carabelli	279/s	0.251±0.113*	**0.050**	**<0.001**	-0.111±0.150	0.449	0.137
m^2 para	281/s	0.118±0.148	0.422	**<0.001**	0.080±0.126	0.524	0.102
m_2 ant fovea	285/a, s	0.326±0.207	0.116	**0.003**	-0.146±0.139	0.304	0.075
m_1 cno	277/s	-0.033±0.149	0.827	**<0.001**	0.095±0.142	0.508	0.017
m_2 cno^{w}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 dwrink	283/s	0.129±0.142	0.368	**<0.001**	0.241±0.163	0.154	0.160
m_1 c5	277/s	-0.021±0.138	0.878	**<0.001**	0.097±0.134	0.475	0.024
m_2 c5	287/all	0.056±0.232	0.808	**0.006**	0.003±0.130	0.980	0.024
m_1 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c7	287/s	0.054±0.128	0.678	**<0.001**	0.068±0.135	0.616	0.057
m_2 dtcrest	285/s	0.162±0.139	0.249	**<0.001**	0.020±0.166	0.903	0.106
m^2 Carabelli							
m^2 para	281	0.378±0.107*	**0.001**	**<0.001**	-0.202±0.122	0.111	0.221
m_2 ant fovea	285/a	-0.060±0.144	0.675	**<0.001**	<-0.001±0.145	0.997	-0.035
m_1 cno	279/s	-0.060±0.114	0.599	**<0.001**	0.166±0.141	0.248	-0.008
m_2 cno^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 dwrink	284	-0.016±0.100	0.870	**<0.001**	-0.074±0.149	0.620	-0.027
m_1 c5	279/s	0.072±0.105	0.497	**<0.001**	0.101±0.134	0.454	0.077
m_2 c5	286/a, a*s	-0.099±0.170	0.556	**0.007**	0.057±0.150	0.706	-0.031
m_1 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------

m_2 c7	286	0.075±0.093	0.421	**<0.001**	0.196±0.132	0.153	0.096
m_2 dtcrest	285	-0.020±0.104	0.849	**<0.001**	0.232±0.153	0.149	0.034
m^2 para							
m_2 ant fovea	286/a	0.005±0.171	0.976	**<0.001**	0.127±0.123	0.313	0.064
m_1 cno	282/s	-0.109±0.132	0.415	**<0.001**	0.126±0.133	0.351	-0.028
m_2 cno^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 dwrink	286	0.348±0.112*	**0.003**	**<0.001**	-0.203±0.124	0.115	0.183
m_1 c5	283/s	-0.025±0.127	0.847	**<0.001**	0.050±0.130	0.699	0.001
m_2 c5	288/a, a*s	-0.012±0.198	0.952	**0.005**	0.064±0.612	0.612	0.028
m_1 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c7	287	0.181±0.109	0.099	**<0.001**	0.013±0.122	0.912	0.129
m_2 dtcrest	287	0.031±0.116	0.791	**<0.001**	-0.105±0.124	0.402	-0.016
m_2 ant fovea							
m_1 cno	276/a, s	0.099±0.183	0.591	**<0.001**	-0.075±0.156	0.633	0.018
m_2 cno^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 dwrink	274/a	0.082±0.173	0.649	**<0.001**	0.373±0.121	**0.005**	0.189
m_1 c5	275/a, s	0.127±0.169	0.455	**<0.001**	-0.048±0.146	0.743	0.045
m_2 c5	284/a, a*s	-0.110±0.326	0.727	**0.029**	-0.138±0.122	0.276	-0.058
m_1 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c6^{w}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c7	284/a	0.030±0.150	0.840	**<0.001**	0.109±0.129	0.403	0.057
m_2 dtcrest	277/a	0.366±0.161*	**0.019**	**<0.001**	-0.140±0.128	0.282	0.123
m_1 cno							
m_2 cno^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 dwrink	272/s	0.244±0.133	0.059	**<0.001**	-0.368±0.132	**0.014**	0.067
m_1 c5	240/s	0.940±0.041**	**<0.001**	0.078	0.624±0.081	**<0.001**	0.826
m_2 c5	283/all	-0.167±0.213	0.451	**0.005**	0.007±0.160	0.967	-0.073
m_1 c6^{cf}	-----------	---------------	-------	---------	---------------	-------	---------
m_2 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c7	284/s	0.058±0.113	0.061	**<0.001**	0.157±0.130	0.240	0.084

m_2 dtcrest^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 cno^{cf}							
all traits^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 dwrink							
m_1 c5	271/s	0.124±0.124	0.308	**<0.001**	-0.140±0.143	0.335	0.051
m_2 c5	283/a, a*s	-0.001±0.199	0.994	**0.006**	-0.039±0.144	0.787	-0.016
m_1 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c6^{cf}	-----------	---------------	-------	---------	---------------	-------	---------
m_2 c7	284	0.321±0.099*	**0.002**	**<0.001**	-0.011±0.139	0.935	0.246
m_2 dtcrest	268	0.082±0.115	0.472	**<0.001**	-0.181±0.131	0.178	0.010
m_1 c5							
m_2 c5	283/all	0.090±0.202	0.655	**0.006**	0.001±0.148	0.993	0.041
m_1 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c7	284/s	0.088±0.108	0.414	**<0.001**	0.106±0.126	0.401	0.093
m_2 dtcrest	271/s	-0.041±0.118	0.731	**<0.001**	0.221±0.133	0.111	0.042
m_2 c5							
m_1 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c6^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c7	285/a, a*s	0.246±0.169	0.141	**0.006**	-0.261±0.127	0.055	0.019
m_2 dtcrest	283/a, a*s	-0.453±0.174*	**0.009**	**0.016**	0.150±0.124	0.238	-0.138
m_1 c6^{cf}							
all traits^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c6^{cf}							
all traits^{cf}	-----------	---------------	-------	---------	----------------	-------	---------
m_2 c7							
m_2 dtcrest	284	0.120±0.104	0.253	**<0.001**	0.009±0.126	0.941	0.090

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[a] i=incisor; c=canine; m=molar. Maxillary and mandibular traits indicated by superscript and subscript, respectively. All traits represented by their maximum antimeric expression score. For a list of morphological trait abbreviations, see Appendix C. “e” superscript indicates a trait that was originally flagged for intra-observer error because the error range

exceeded a single grade, but whose mean error does not exceed 0.300. Traits with mean error exceeding 0.300 were omitted from the correlation analyses. "w" superscript indicates models that are suspect due to standard deviation ranges for certain estimates. "cf" superscript indicates model convergence failure. [b] Covariates fixed in the genetic correlation models if significant in associated univariate models. "a"=age; "s"=sex; "a*s"=age/sex interaction; "all"=all covariates. [c] Maximum-likelihood estimate of genetic correlation. Cases of incomplete pleiotropy indicated by a single asterisks. Cases of complete pleiotropy indicated by two asterisks. Dashes are associated with incalculable parameter estimates. [d] Probability of hypothesis (as indicated in parentheses) being true given pedigree structure with values $p<0.050$ bolded. Dashes are associated with incalculable parameter estimates. [e] Maximum-likelihood estimate of environmental correlation. Dashes are associated with incalculable parameter estimates. [f] Maximum-likelihood estimate of derived phenotypic correlation. Dashes are associated with incalculable parameter estimates.

Table 4. UAT sample variance components within-class correlations: permanent ASUDAS morphology.

		Genetic			Environmental		Phenotypic
Trait [a]	N/Cov[b]	ρ_G[c]	$P(\rho_G=0)$[d]	$P(\lvert\rho_G\rvert=1)$[d]	ρ_E[e]	$P(\rho_E=0)$[d]	ρ_P[f]
Anterior Dentition+							
I^1 L CURVE^E							
I^1 SHOV	298/A, A*S	0.136±0.104	0.200	**<0.001**	0.141±0.127	0.272	0.134
I^2 SHOV	298/A	-0.120±0.110	0.274	**<0.001**	0.205±0.133	0.137	-0.030
C^1SHOV	298/A*S	-0.565±0.129*	**<0.001**	**<0.001**	0.119±0.173	0.500	-0.330
I^1 DSHOV	298/A*S	-0.071±0.144	0.621	**<0.001**	0.050±0.127	0.696	-0.021
I^2 DSHOV	298/A, A*S	0.028±0.130	0.829	**<0.001**	0.021±0.125	0.869	0.025
C^1 DSHOV	298/ALL	-0.134±0.161	0.404	**<0.001**	-0.134±0.157	0.398	-0.134
P^1 DSHOV	298/A*S	-0.370±0.127*	**0.005**	**<0.001**	0.032±0.139	0.820	-0.230
P^2 DSHOV	298/S, A*S	-0.095±0.185	0.599	**<0.001**	0.052±0.154	0.737	-0.034
I^1 TD	298/A*S	-0.168±0.129	0.191	**<0.001**	-0.044±0.144	0.761	-0.125
I^2 TD	298/A*S	-0.099±0.137	0.476	**<0.001**	-0.174±0.208	0.416	-0.108
C^1 TD	298/A*S	-0.101±0.131	0.445	**<0.001**	-0.096±0.234	0.684	-0.092
C^1 DAR	298/A*S	-0.328±0.121*	**0.007**	**<0.001**	0.438±0.121	**0.002**	-0.151
I_1 SHOV	308/A*S	0.118±0.138	0.402	**<0.001**	0.030±0.131	0.822	0.082
I_2 SHOV	298/A*S	-0.283±0.115*	**0.014**	**0.001**	0.117±0.122	0.345	-0.148
C_1 DAR	298/S, A*S	-0.038±0.146	0.792	**<0.001**	0.122±0.144	0.404	0.022
I^1 SHOV							
I^2 SHOV	284/ALL	0.632±0.070*	**<0.001**	**<0.001**	-0.146±0.152	0.350	0.489
C^1SHOV	286/A	0.317±0.133*	**0.027**	**<0.001**	0.172±0.287	0.558	0.278
I^1 DSHOV	292/A	-0.044±0.126	0.725	**<0.001**	0.024±0.146	0.869	-0.022
I^2 DSHOV	291/A	0.089±0.113	0.433	**<0.001**	0.071±0.142	0.617	0.082
C^1 DSHOV	288/A, S	0.071±0.151	0.641	**<0.001**	-0.058±0.232	0.803	0.032

P^1 DSHOV	287/A	0.029±0.120	0.810	**<0.001**	-0.351±0.183	0.090	-0.062
P^2 DSHOV	288/A, S	0.027±0.165	0.869	**<0.001**	0.154±0.272	0.580	0.062
I^1 TD	284/A	0.421±0.123*	**<0.001**	**<0.001**	-0.125±0.171	0.475	0.276
I^2 TD	285/A	0.205±0.114	0.078	**<0.001**	-0.225±0.244	0.381	0.144
C^1 TD	285/A	0.221±0.112	0.062	**<0.001**	0.519±0.288	0.180	0.256
C^1 DAR	286/A, S	0.091±0.110	0.407	**<0.001**	0.034±0.269	0.900	0.082
I_1 SHOV	305/A	0.615±0.087*	**<0.001**	**<0.001**	-0.120±0.137	0.392	0.399
I_2 SHOV	291/A	0.308±0.093*	**0.002**	**<0.001**	0.112±0.134	0.405	0.261
C_1 DAR	287/A, S	0.246±0.142	0.086	**<0.001**	-0.102±0.230	0.662	0.147
I^2 SHOV							
C^1SHOV	242/ALL	0.522±0.110*	**<0.001**	**<0.001**	-0.017±0.219	0.940	0.386
I^1 DSHOV	291/ALL	0.134±0.124	0.295	**<0.001**	-0.050±0.173	0.772	0.079
I^2 DSHOV	265/ALL	0.274±0.103*	**0.012**	**<0.001**	-0.183±0.141	0.210	0.151
C^1 DSHOV	254/ALL	0.199±0.132	0.131	**<0.001**	-0.312±0.155	0.063	0.054
P^1 DSHOV	258/ALL	0.018±0.117	0.880	**<0.001**	-0.043±0.156	0.784	0.003
P^2 DSHOV	254/ALL	0.136±0.141	0.331	**<0.001**	-0.115±0.166	0.495	0.061
I^1 TD	266/ALL	0.577±0.090*	**<0.001**	**<0.001**	-0.318±0.170	0.097	0.380
I^2 TD	237/ALL	0.066±0.112	0.558	**<0.001**	0.272±0.230	0.269	0.095
C^1 TD	243/ALL	0.304±0.105*	**0.007**	**<0.001**	0.030±0.253	0.907	0.269
C^1 DAR	249/ALL	0.080±0.103	0.438	**<0.001**	0.187±0.154	0.240	0.096
I_1 SHOV	302/ALL	0.463±0.116*	**<0.001**	**<0.001**	0.021±0.151	0.890	0.311
I_2 SHOV	284/ALL	0.517±0.084*	**<0.001**	**<0.001**	-0.174±0.138	0.225	0.365
C_1 DAR	257/ALL	0.153±0.121	0.213	**<0.001**	0.056±0.159	0.727	0.126
C^1 SHOV							
I^1 DSHOV	312	0.110±0.186	0.558	**<0.001**	-0.154±0.231	0.511	0.108
I^2 DSHOV	266/A	0.386±0.148*	**0.013**	**<0.001**	-0.250±0.170	0.164	0.168
C^1 DSHOV	190/A, S	0.628±0.187*	**<0.001**	**0.034**	-0.171±0.171	0.334	0.304
P^1 DSHOV	236	0.620±0.179*	**<0.001**	**0.028**	-0.389±0.160	**0.036**	0.255
P^2 DSHOV	218/S	0.469±0.195*	**0.010**	**0.009**	-0.460±0.147	**0.010**	0.114
I^1 TD	282	0.626±0.128*	**<0.001**	**0.001**	-0.220±0.198	0.292	0.385
I^2 TD	208	0.345±0.125*	**0.006**	**<0.001**	-0.864±0.064	**<0.001**	0.133

C^1 TD	171	0.426±0.099*	**<0.001**	**<0.001**	-0.237±0.203	0.271	0.319
C^1 DAR	207/S	0.171±0.124	0.178	**<0.001**	0.201±0.203	0.340	0.173
I_1 SHOV	316	0.190±0.167	0.250	**<0.001**	-0.244±0.164	0.165	0.031
I_2 SHOV	303	0.399±0.123*	**0.003**	**<0.001**	-0.259±0.188	0.200	0.219
C_1 DAR	236/S	0.147±0.178	0.396	**<0.001**	-0.135±0.195	0.495	0.047
I^1 DSHOV							
I^2 DSHOV	293/A	0.313±0.146*	**0.037**	**<0.001**	0.276±0.130	**0.040**	0.297
C^1 DSHOV	293/A, S	0.278±0.188	0.150	**<0.001**	-0.002±0.185	0.991	0.158
P^1 DSHOV	315	0.320±0.158	0.057	**<0.001**	-0.176±0.175	0.324	0.128
P^2 DSHOV	315/S	0.322±0.156	0.055	**<0.001**	-0.173±0.176	0.335	0.133
I^1 TD	312	-0.105±0.150	0.492	**<0.001**	0.185±0.155	0.248	-0.003
I^2 TD	313	-0.015±0.165	0.927	**<0.001**	0.110±0.311	0.728	0.012
C^1 TD	312	0.068±0.159	0.664	**<0.001**	-0.246±0.324	0.473	0.004
C^1 DAR	313/S	0.079±0.144	0.583	**<0.001**	-0.035±0.217	0.873	0.046
I_1 SHOV	329	-0.066±0.164	0.681	**<0.001**	0.195±0.132	0.155	0.048
I_2 SHOV	316	-0.083±0.159	0.592	**<0.001**	0.431±0.112	**0.001**	0.122
C_1 DAR	314/S	0.066±0.178	0.712	**<0.001**	0.043±0.169	0.802	0.056
I^2 DSHOV							
C^1 DSHOV	270/A, S	0.469±0.180*	**0.011**	**0.003**	0.078±0.155	0.617	0.290
P^1 DSHOV	273/A	0.123±0.147	0.402	**<0.001**	0.084±0.158	0.598	0.108
P^2 DSHOV	271/A, S	0.228±0.177	0.208	**<0.001**	-0.095±0.167	0.576	0.094
I^1 TD	279/A	0.048±0.136	0.725	**<0.001**	0.195±0.147	0.198	0.097
I^2 TD	262/A	0.106±0.139	0.455	**<0.001**	0.065±0.263	0.805	0.090
C^1 TD	266/A	0.147±0.132	0.269	**<0.001**	0.036±0.237	0.880	0.116
C^1 DAR	271/A, S	0.196±0.128	0.132	**<0.001**	-0.051±0.177	0.772	0.129
I_1 SHOV	303/A	0.047±0.150	0.754	**<0.001**	0.123±0.132	0.356	0.079
I_2 SHOV	289/A	-0.001±0.123	0.996	**<0.001**	0.330±0.122	**0.013**	0.111
C_1 DAR	275/A, S	0.351±0.160*	**0.032**	**<0.001**	-0.114±0.165	0.495	0.169
C^1 DSHOV							
P^1 DSHOV	216/A, S	0.756±0.162**	**<0.001**	0.072	0.194±0.171	0.255	0.517
P^2 DSHOV	205/A, S	0.647±0.157*	**<0.001**	**0.011**	-0.145±0.167	0.396	0.322

I^1 TD	267/A, S	0.341±0.175	0.058	**<0.001**	-0.111±0.189	0.564	0.179
I^2 TD	219/A, S	0.197±0.167	0.247	**<0.001**	-0.266±0.300	0.416	0.090
C^1 TD	189/A, S	-0.015±0.132	0.909	**<0.001**	0.243±0.193	0.234	0.028
C^1 DAR	197/A, S	0.355±0.133*	**0.007**	**<0.001**	-0.599±0.128	**0.002**	0.121
I_1 SHOV	298/A, S	-0.217±0.179	0.226	**<0.001**	0.090±0.160	0.578	-0.085
I_2 SHOV	285/A, S	-0.118±0.143	0.406	**<0.001**	0.125±0.144	0.391	-0.033
C_1 DAR	218/A, S	0.228±0.197	0.226	**0.001**	-0.423±0.156	**0.022**	-0.041
P^1 DSHOV							
P^2 DSHOV	238/S	0.713±0.117*	**<0.001**	**0.003**	0.138±0.171	0.421	0.489
I^1 TD	290	-0.150±0.156	0.370	**<0.001**	0.049±0.221	0.824	-0.091
I^2 TD	254	-0.015±0.140	0.914	**<0.001**	0.014±0.224	0.949	-0.009
C^1 TD	236	-0.040±0.126	0.751	**<0.001**	0.068±0.225	0.762	-0.021
C^1 DAR	237/S	0.369±0.115*	**0.003**	**<0.001**	-0.154±0.187	0.421	0.253
I_1 SHOV	322	-0.294±0.144*	**0.048**	**<0.001**	0.136±0.153	0.382	-0.136
I_2 SHOV	307	0.024±0.127	0.853	**<0.001**	0.058±0.138	0.674	0.034
C_1 DAR	247/S	0.240±0.164	0.147	**<0.001**	-0.057±0.177	0.747	0.131
P^2 DSHOV							
I^1 TD	286/S	-0.068±0.177	0.701	**<0.001**	0.338±0.175	0.088	0.070
I^2 TD	237/S	0.084±0.166	0.616	**<0.001**	0.389±0.240	0.162	0.139
C^1 TD	218/S	0.141±0.142	0.325	**<0.001**	0.163±0.208	0.445	0.130
C^1 DAR	225/S	0.168±0.137	0.226	**<0.001**	-0.177±0.183	0.349	0.080
I_1 SHOV	319/S	-0.195±0.176	0.287	**<0.001**	0.077±0.188	0.682	-0.086
I_2 SHOV	305/S	-0.072±0.143	0.618	**<0.001**	0.162±0.144	0.271	0.008
C_1 DAR	240/S	0.073±0.199	0.710	**<0.001**	-0.103±0.168	0.547	-0.001
I^1 TD							
I^2 TD	280	0.327±0.125*	**0.017**	**<0.001**	-0.029±0.309	0.926	0.260
C^1 TD	280	0.459±0.109*	**<0.001**	**<0.001**	-0.038±0.242	0.876	0.371
C^1 DAR	284/S	0.101±0.128	0.434	**<0.001**	-0.201±0.208	0.353	0.041
I_1 SHOV	322	0.301±0.161*	**0.049**	**<0.001**	-0.122±0.148	0.426	0.140
I_2 SHOV	307	0.383±0.120*	**0.002**	**<0.001**	-0.088±0.162	0.591	0.243
C_1 DAR	288/S	-0.052±0.161	0.747	**<0.001**	0.113±0.188	0.551	0.001

I^2 TD							
C^1 TD	204	0.281±0.113*	**0.020**	**<0.001**	0.068±0.295	0.818	0.264
C^1 DAR	231/S	0.233±0.106*	**0.035**	**<0.001**	-0.465±0.189	**0.050**	0.164
I_1 SHOV	317	-0.067±0.130	0.613	**<0.001**	0.035±0.197	0.859	-0.043
I_2 SHOV	301	0.044±0.135	0.747	**<0.001**	0.210±0.270	0.455	0.071
C_1 DAR	251/S	0.107±0.164	0.526	**<0.001**	0.305±0.290	0.335	0.142
C^1 TD							
C^1 DAR	208/S	-0.004±0.105	0.972	**<0.001**	-0.101±0.216	0.644	-0.013
I_1 SHOV	315	0.204±0.135	0.132	**<0.001**	0.116±0.235	0.626	0.171
I_2 SHOV	303	0.098±0.112	0.386	**<0.001**	0.563±0.152	**0.009**	0.159
C_1 DAR	236/S	0.136±0.124	0.282	**<0.001**	0.359±0.209	0.128	0.162
C^1 DAR							
I_1 SHOV	317/S	-0.036±0.122	0.768	**<0.001**	0.035±0.167	0.833	-0.018
I_2 SHOV	303/S	0.102±0.107	0.343	**<0.001**	0.062±0.147	0.674	0.093
C_1 DAR	236/S	0.524±0.157*	**0.001**	**<0.002**	-0.313±0.210	0.181	0.283
I_1 SHOV							
I_2 SHOV	318	0.811±0.091*	**<0.001**	**<0.001**	-0.048±0.131	0.717	0.488
C_1 DAR	318/S	0.084±0.157	0.593	**<0.001**	-0.029±0.152	0.848	0.040
I_2 SHOV							
C_1 DAR	304/S	0.075±0.134	0.577	**<0.001**	0.068±0.146	0.643	0.072
Postcanine Dentition							
M^1 META^E							
M^2 META	330	0.470±0.178*	**0.030**	**<0.001**	0.385±0.133	**0.013**	0.424
M^1 HYPO	308/A	0.264±0.125*	**0.050**	**<0.001**	-0.059±0.133	0.657	0.136
M^2 HYPO	330	0.009±0.210	0.964	**<0.001**	0.548±0.173	**0.022**	0.135
M^1 C5	308/A, A*S	0.027±0.159	0.864	**<0.001**	0.123±0.143	0.395	0.062
M^2 C5	329	0.361±0.171*	**0.033**	**<0.001**	-0.750±0.139	**0.013**	0.140
M^1 CTRAIT	308/A, A*S	-0.020±0.145	0.891	**<0.001**	0.093±0.119	0.441	0.030
M^2 CTRAIT	330	0.215±0.207	0.300	**<0.001**	-0.194±0.229	0.414	0.071
M^1 PARA^E	330	0.052±0.139	0.708	**<0.001**	-0.079±0.122	0.518	-0.002

M^2 PARA^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 CNO	330	0.063±0.184	0.733	**<0.001**	-0.070±0.124	0.574	-0.007
M_2 CNO	338	0.019±0.218	0.931	**<0.001**	-0.215±0.205	0.302	-0.075
M_1 AFOVEA^E	314/A, A*S	-0.071±0.139	0.611	**<0.001**	0.143±0.138	0.310	0.007
M_1 DWRINK	335	0.234±0.117*	**0.050**	**<0.001**	-0.005±0.178	0.979	0.150
M_1 PSTYLID	330/S	0.187±0.181	0.312	**<0.001**	0.004±0.127	0.974	0.093
M_1 C5	310/A*S	0.020±0.133	0.883	**<0.001**	0.330±0.121	**0.012**	0.111
M_2 C5	328	0.195±0.195	0.335	**<0.001**	-0.182±0.208	0.381	0.044
M_1 C6	330	0.272±0.190	0.154	**<0.001**	-0.141±0.121	0.251	0.047
M_2 C6^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	335/S	-0.067±0.205	0.745	**<0.001**	-0.013±0.127	0.918	-0.037
M_2 C7^E	329	0.067±0.355	0.848	**0.045**	-0.043±0.165	0.796	-0.003
M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^W	---------------	----------------	-------	---------	----------------	-------	--------
M^2 META							
M^1 HYPO	303/A	0.160±0.194	0.420	**0.001**	0.309±0.191	0.136	0.213
M^2 HYPO	171	0.339±0.161	0.061	**<0.001**	0.130±0.277	0.643	0.252
M^1 C5	294/A, A*S	0.210±0.188	0.282	**<0.001**	-0.111±0.186	0.557	0.090
M^2 C5	171	-0.019±0.155	0.903	**<0.001**	0.369±0.250	0.195	0.031
M^1 CTRAIT	306/A, A*S	0.230 ±0.188	0.223	**<0.001**	-0.200±0.172	0.257	0.049
M^2 CTRAIT	177	-0.012±0.199	0.952	**<0.001**	0.384±0.222	0.124	0.100
M^1 PARA^E	316	0.427±0.184*	**0.022**	**0.005**	-0.125±0.193	0.521	0.198
M^2 PARA^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 CNO	303	0.269±0.238	0.242	**0.005**	-0.070±0.142	0.625	0.088
M_2 CNO	183	-0.026±0.201	0.896	**<0.001**	-0.020±0.194	0.920	-0.023
M_1 AFOVEA^E	304/A, A*S	0.010±0.212	0.964	**<0.001**	0.298±0.231	0.229	0.108
M_1 DWRINK	324	0.422±0.164*	**0.010**	**0.003**	-0.541±0.171	**0.038**	0.151
M_1 PSTYLID	312/S	0.261±0.200	0.206	**<0.001**	-0.268±0.159	0.102	0.009
M_1 C5	284/A*S	0.186±0.136	0.187	**<0.001**	-0.060±0.160	0.709	0.107
M_2 C5	183	-0.001±0.186	0.997	**<0.001**	0.029±0.185	0.876	0.011
M_1 C6	304	0.420±0.276	0.112	**0.028**	-0.082±0.142	0.564	0.136

M_2 C6^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	333/S	0.614±0.221*	**0.011**	**0.042**	-0.305±0.178	0.100	0.130
M_2 C7^{E}	197	0.081±0.358	0.820	**0.049**	0.090±0.184	0.629	0.085
M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M^1 HYPO							
M^2 HYPO	302/A	0.515±0.139*	**0.001**	**<0.001**	-0.101±0.296	0.735	0.404
M^1 C5	304/A, A*S	0.237±0.116*	**0.037**	**<0.001**	-0.118±0.138	0.399	0.136
M^2 C5	302/A	-0.009±0.151	0.951	**<0.001**	-0.153±0.386	0.699	-0.021
M^1 CTRAIT	307/A, A*S	0.379 ±0.093*	**<0.001**	**<0.001**	0.029±0.122	0.813	0.273
M^2 CTRAIT	303/A	0.414±0.129*	**0.004**	**<0.001**	0.110±0.229	0.633	0.345
M^1 PARA^{E}	308/A	0.137±0.103	0.186	**<0.001**	-0.220±0.120	0.078	0.038
M^2 PARA^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_1 CNO	305/A	0.327±0.141*	**0.022**	**<0.001**	-0.056±0.133	0.678	0.164
M_2 CNO	301/A	0.052±0.152	0.732	**<0.001**	0.261±0.200	0.218	0.107
M_1 AFOVEA^{E}	311/A, A*S	0.086±0.104	0.416	**<0.001**	0.134±0.142	0.348	0.098
M_1 DWRINK	312/A	0.141±0.096	0.144	**<0.001**	-0.021±0.238	0.930	0.111
M_1 PSTYLID	308/A, S	0.150±0.135	0.261	**<0.001**	0.061±0.139	0.659	0.116
M_1 C5	305/A*S	0.292±0.087*	**0.002**	**<0.001**	-0.054±0.134	0.692	0.218
M_2 C5	301/A	0.175±0.142	0.224	**<0.001**	0.182±0.199	0.373	0.177
M_1 C6	306/A	0.254±0.147	0.080	**<0.001**	-0.052±0.133	0.697	0.122
M_2 C6^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	312/A, S	0.273±0.156	0.080	**0.001**	-0.121±0.132	0.369	0.096
M_2 C7^{E}	301/A	0.232±0.276	0.413	**0.048**	-0.075±0.225	0.741	0.073
M_1 DTCREST^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M^2 HYPO							
M^1 C5	293/A, A*S	0.474±0.116*	**0.001**	**<0.001**	0.214±0.188	0.270	0.425
M^2 C5	131	0.106±0.112	0.346	**<0.001**	-0.053±0.332	0.873	0.098
M^1 CTRAIT	304/A, A*S	0.504 ±0.134*	**0.003**	**<0.001**	0.145±0.422	0.736	0.418
M^2 CTRAIT	161	0.463±0.112*	**<0.001**	**<0.001**	-0.254±0.262	0.362	0.377

M^1 PARA^E	315	0.218±0.117	0.079	**<0.001**	0.108±0.225	0.635	0.195
M^2 PARA^W	---------------	----------------	-------	---------	----------------	-------	--------
M$_1$ CNO	303	0.375±0.158*	**0.030**	**<0.001**	-0.415±0.274	0.209	0.186
M$_2$ CNO	160	0.266±0.158	0.077	**0.001**	-0.228±0.249	0.379	0.170
M$_1$ AFOVEA^E	302/A, A*S	-0.198±0.186	0.291	**<0.001**	0.580±0.312	0.222	-0.080
M$_1$ DWRINK	321	0.348±0.111*	**0.003**	**<0.001**	-0.552±0.194	**0.045**	0.277
M$_1$ PSTYLID	310/S	0.367±0.146*	**0.023**	**<0.001**	0.040±0.216	0.853	0.265
M$_1$ C5	284/A*S	0.397±0.123*	**0.005**	**<0.001**	0.111±0.197	0.575	0.363
M$_2$ C5	162	0.389±0.131*	**0.003**	**<0.001**	-0.211±0.220	0.357	0.271
M$_1$ C6	304	0.314±0.164	0.070	**<0.001**	-0.453±0.207	0.079	0.129
M$_2$ C6^W	---------------	----------------	-------	---------	----------------	-------	--------
M$_1$ C7	333/S	0.388±0.168*	**0.028**	**0.001**	-0.470±0.215	0.086	0.159
M$_2$ C7^E	190	-0.006±0.236	0.979	**0.037**	-0.043±0.308	0.888	-0.013
M$_1$ DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M$_2$ DTCREST^W	---------------	----------------	-------	---------	----------------	-------	--------
M^1 C5							
M^2 C5	293/A, A*S	0.196±0.137	0.158	**<0.001**	-0.025±0.240	0.917	0.164
M^1 CTRAIT	307/A, A*S	0.390 ±0.108*	**0.001**	**<0.001**	-0.009±0.135	0.947	0.268
M^2 CTRAIT	293/A, A*S	0.438±0.126*	**0.002**	**<0.001**	-0.086±0.193	0.660	0.325
M^1 PARA^E	306/A, A*S	0.088±0.109	0.429	**<0.001**	0.231±0.131	0.089	0.127
M^2 PARA^W	---------------	----------------	-------	---------	----------------	-------	--------
M$_1$ CNO	304/A, A*S	0.324±0.145*	**0.037**	**<0.001**	0.004±0.142	0.978	0.193
M$_2$ CNO	293/A, A*S	0.334±0.158*	**0.036**	**<0.001**	-0.090±0.180	0.618	0.219
M$_1$ AFOVEA^E	312/A, A*S	0.143±0.119	0.223	**<0.001**	-0.310±0.157	0.071	0.031
M$_1$ DWRINK	314/A, A*S	0.384±0.105*	**<0.001**	**<0.001**	-0.562±0.162	**0.023**	0.217
M$_1$ PSTYLID	306/ALL	0.377±0.132*	**0.009**	**<0.001**	0.104±0.144	0.470	0.274
M$_1$ C5	303/A, A*S	0.121±0.096	0.215	**<0.001**	0.216±0.139	0.133	0.139
M$_2$ C5	293/A, A*S	0.456±0.142*	**0.002**	**<0.001**	-0.143±0.169	0.406	0.292
M$_1$ C6	303/A, A*S	0.285±0.151	0.068	**<0.001**	-0.024±0.140	0.865	0.175
M$_2$ C6^W	---------------	----------------	-------	---------	----------------	-------	--------
M$_1$ C7	314/ALL	0.300±0.167	0.112	**<0.001**	0.076±0.174	0.664	0.199

M_2 C7^{E}	294/ALL	-0.085±0.269	0.753	**0.046**	0.166±0.205	0.421	0.029
M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M^2 C5							
M^1 CTRAIT	304/A, A*S	0.153 ±0.158	0.328	**<0.001**	-0.243±0.428	0.590	0.096
M^2 CTRAIT	163	0.100±0.111	0.374	**<0.001**	0.433±0.239	0.132	0.119
M^1 PARA^{E}	314	0.081±0.117	0.488	**<0.001**	-0.059±0.235	0.803	0.063
M^2 PARA^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_1 CNO	302	0.189±0.176	0.276	**<0.001**	-0.224±0.430	0.621	0.103
M_2 CNO	162	-0.158±0.122	0.202	**<0.001**	0.599±0.171	**0.018**	-0.086
M_1 AFOVEA^{E}	302/A, A*S	-0.185±0.160	0.259	**<0.001**	0.020±0.437	0.964	0.159
M_1 DWRINK	321	0.099±0.110	0.374	**<0.001**	-0.030±0.304	0.922	0.092
M_1 PSTYLID	310/S	0.352±0.160*	**0.026**	**<0.001**	-0.915±0.040	**<0.001**	0.156
M_1 C5	283/A*S	-0.086±0.120	0.478	**<0.001**	0.084±0.362	0.818	-0.073
M_2 C5	165	-0.110±0.121	0.365	**<0.001**	0.949±0.026	**<0.001**	-0.030
M_1 C6	303	0.302±0.170	0.077	**<0.001**	-0.141±0.301	0.646	0.181
M_2 C6^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	333/S	-0.071±0.184	0.698	**<0.001**	0.014±0.296	0.963	-0.043
M_2 C7^{E}	189	0.017±0.233	0.942	**0.040**	-0.092±0.445	0.838	-0.004
M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M^1 CTRAIT							
M^2 CTRAIT	306/A, A*S	0.769±0.106*	**<0.001**	**0.011**	-0.308±0.177	0.115	0.482
M^1 PARA^{E}	309/A, A*S	0.110±0.110	0.323	**<0.001**	0.047±0.122	0.702	0.089
M^2 PARA^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_1 CNO	309/A, A*S	0.019±0.151	0.903	**<0.001**	0.159±0.129	0.182	0.079
M_2 CNO	305/A, A*S	0.123±0.155	0.430	**<0.001**	0.279±0.182	0.149	0.168
M_1 AFOVEA^{E}	314/A, A*S	0.114±0.109	0.307	**<0.001**	0.039±0.141	0.779	0.092
M_1 DWRINK	315/A, A*S	0.143±0.110	0.198	**<0.001**	-0.144±0.292	0.639	0.086
M_1 PSTYLID	309/ALL	0.350±0.134*	**0.010**	**<0.001**	-0.113±0.121	0.356	0.160
M_1 C5	308/A, A*S	0.160±0.097	0.105	**<0.001**	0.035±0.132	0.790	0.127

M_2 C5	305/A, A*S	0.259±0.148	0.089	**<0.001**	0.084±0.184	0.648	0.205
M_1 C6	309/A, A*S	0.037±0.149	0.806	**<0.001**	0.185±0.123	0.140	0.100
M_2 C6^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	314/ALL	0.055±0.162	0.737	**<0.001**	0.126±0.125	0.319	0.086
M_2 C7^E	304/A, A*S	-0.118±0.274	0.665	**0.050**	0.087±0.185	0.639	-0.007
M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M^2 CTRAIT							
M^1 PARA^E	316	0.324±0.127*	**0.013**	**<0.001**	-0.321±0.192	0.135	0.182
M^2 PARA^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 CNO	305	0.364±0.152*	**0.021**	**<0.001**	-0.137±0.159	0.398	0.197
M_2 CNO	173	0.204±0.145	0.188	**<0.001**	0.252±0.185	0.192	0.212
M_1 AFOVEA^E	303/A, A*S	-0.068±0.189	0.715	**<0.001**	0.492±0.224	0.098	0.061
M_1 DWRINK	323	0.213±0.122	0.083	**<0.001**	-0.333±0.287	0.317	0.147
M_1 PSTYLID	310/S	0.534±0.148*	**0.001**	**0.001**	-0.360±0.174	0.070	0.270
M_1 C5	285/A*S	0.268±0.111	**0.020**	**<0.001**	0.016±0.182	0.930	0.225
M_2 C5	174	0.235±0.132	0.096	**<0.001**	0.277±0.175	0.133	0.242
M_1 C6	306	0.258±0.171	0.146	**<0.001**	-0.043±0.161	0.789	0.148
M_2 C6^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	335/S	0.432±0.195*	**0.037**	**0.002**	-0.312±0.209	0.181	0.166
M_2 C7^E	194	-0.015±0.280	0.958	**0.038**	0.028±0.274	0.920	0.002
M_1 DTCREST^W	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^W	---------------	----------------	-------	---------	----------------	-------	--------
M^1 PARA^E							
M^2 PARA^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 CNO	326	0.263±0.131*	**0.046**	**<0.001**	-0.050±0.124	0.687	0.137
M_2 CNO	315	0.115±0.155	0.456	**<0.001**	-0.131±0.190	0.500	0.043
M_1 AFOVEA^E	313/A, A*S	0.063±0.104	0.546	**<0.001**	-0.128±0.132	0.338	0.015
M_1 DWRINK	337	0.094±0.089	0.290	**<0.001**	-0.048±0.148	0.746	0.069
M_1 PSTYLID	325/S	0.565±0.146*	**<0.001**	**0.004**	-0.317±0.138	**0.039**	0.215
M_1 C5	305/A*S	-0.028±0.094	0.764	**<0.001**	0.148±0.129	0.260	0.009

M_2 C5	315	0.087±0.140	0.534	**<0.001**	-0.097±0.182	0.599	0.034
M_1 C6	326	0.259±0.133	0.055	**<0.001**	-0.023±0.123	0.852	0.140
M_2 C6^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	336/S	0.286±0.152	0.061	**<0.001**	0.001±0.131	0.993	0.153
M_2 C7^E	316	0.769±0.248**	**0.002**	0.210	-0.270±0.177	0.160	0.227
M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^W	---------------	----------------	-------	---------	----------------	-------	--------
M^2 PARA^W							
ALL TRAITS^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 CNO							
M_2 CNO	300	0.124±0.188	0.511	**<0.001**	-0.047±0.159	0.770	0.055
M_1 AFOVEA^E	309/A*S	0.052±0.146	0.720	**<0.001**	-0.184±0.132	0.175	-0.033
M_1 DWRINK	324	0.211±0.154	0.217	**<0.001**	-0.469±0.211	0.221	0.031
M_1 PSTYLID	320/S	0.261±0.195	0.173	**0.001**	-0.061±0.133	0.651	0.097
M_1 C5	284/A*S	0.166±0.127	0.194	**<0.001**	0.048±0.143	0.736	0.117
M_2 C5	300	0.037±0.179	0.835	**<0.001**	-0.015±0.156	0.924	0.016
M_1 C6	296	0.818±0.058*	**<0.001**	**<0.001**	0.857±0.034	**<0.001**	0.838
M_2 C6^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	330/S	0.091±0.219	0.676	**<0.001**	-0.072±0.141	0.612	0.002
M_2 C7^E	304	0.607±0.434	0.088	0.248	-0.043±0.133	0.745	0.161
M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^W	---------------	----------------	-------	---------	----------------	-------	--------
M_2 CNO							
M_1 AFOVEA^E	300/A, A*S	0.234±0.154	0.148	**<0.001**	0.258±0.253	0.336	0.240
M_1 DWRINK	318	0.383±0.136*	**0.007**	**<0.001**	-0.065±0.375	0.864	0.295
M_1 PSTYLID	306/S	0.241±0.182	0.205	**0.001**	-0.206±0.191	0.295	0.079
M_1 C5	283/A*S	0.298±0.129*	**0.025**	**<0.001**	-0.048±0.174	0.782	0.224
M_2 C5	145	0.963±0.021*	**<0.001**	**0.028**	0.797±0.061	**<0.001**	0.911
M_1 C6	300	-0.052±0.195	0.791	**<0.001**	-0.011±0.159	0.943	-0.034
M_2 C6^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	332/S	0.115±0.217	0.597	**<0.001**	-0.180±0.199	0.373	-0.012

M_2 C7^E	187	-0.292±0.273	0.279	0.055	0.241±0.211	0.270	-0.024
M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 A FOVEA^E							
M_1 DWRINK	302/A*S	0.258±0.079*	**0.002**	**<0.001**	0.042±0.141	0.766	0.224
M_1 PSTYLID	312/ALL	0.053±0.136	0.698	**<0.001**	0.135±0.150	0.374	0.078
M_1 C5	308/A, A*S	0.092±0.095	0.338	**<0.001**	0.033±0.135	0.807	0.081
M_2 C5	301/A, A*S	0.163±0.152	0.292	**<0.001**	0.220±0.240	0.381	0.177
M_1 C6	309/A, A*S	0.091±0.146	0.529	**<0.001**	-0.222±0.128	0.096	-0.023
M_2 C6^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	312/ALL	-0.019±0.154	0.900	**<0.001**	-0.013±0.147	0.929	-0.016
M_2 C7^E	303/A, A*S	0.358±0.341	0.317	0.088	-0.300±0.286	0.375	0.042
M_1 DTCREST^W	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 DWRINK							
M_1 PSTYLID	325/S	0.049±0.129	0.707	**<0.001**	0.246±0.196	0.247	0.083
M_1 C5	308/A*S	-0.116±0.088	0.187	**<0.001**	0.010±0.256	0.967	-0.101
M_2 C5	320	0.236±0.125	0.070	**<0.001**	0.308±0.254	0.285	0.236
M_1 C6	325	0.354±0.169	0.062	**0.004**	-0.469±0.199	0.164	0.099
M_2 C6^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	331/S	-0.115±0.129	0.356	**<0.001**	0.680±0.086	**<0.001**	0.086
M_2 C7^E	325	0.150±0.279	0.617	0.055	-0.191±0.456	0.716	0.032
M_1 DTCREST^W	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 PSTYLID							
M_1 C5	302/S, A*S	0.190±0.130	0.136	**<0.001**	-0.252±0.138	0.085	0.057
M_2 C5	307/S	0.396±0.151*	**0.016**	**<0.001**	-0.327±0.184	0.100	0.150
M_1 C6	320/S	0.088±0.195	0.650	**<0.001**	0.076±0.134	0.572	0.082
M_2 C6^W	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	331/S	0.350±0.228	0.121	**0.005**	-0.067±0.134	0.619	0.114
M_2 C7^E	313/S	0.849±0.262**	**0.003**	0.290	-0.097±0.140	0.491	0.270

M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C5							
M_2 C5	283/A*S	0.434±0.114*	**0.001**	**<0.001**	-0.033±0.169	0.843	0.335
M_1 C6	283/A*S	-0.272±0.123*	**0.035**	**<0.001**	-0.107±0.141	0.449	-0.200
M_2 C6^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	311/S, A*S	-0.006±0.151	0.966	**<0.001**	0.020±0.184	0.912	0.002
M_2 C7^{E}	283/A*S	-0.040±0.214	0.852	0.055	0.040±0.184	0.828	-0.006
M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 C5							
M_1 C6	300	-0.135±0.187	0.470	**<0.001**	0.028±0.156	0.855	-0.064
M_2 C6^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	332/S	0.121±0.196	0.537	**<0.001**	-0.097±0.182	0.594	0.024
M_2 C7^{E}	188/A*S	-0.016±0.247	0.948	**0.039**	-0.027±0.205	0.895	-0.020
M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C6							
M_2 C6^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_1 C7	330/S	0.067±0.227	0.767	**<0.001**	-0.005±0.140	0.969	0.026
M_2 C7^{E}	304	0.730±0.502	0.064	0.324	-0.085±0.129	0.516	0.152
M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 C6^{W}							
ALL TRAITS^{W}	---------------	----------------	-------	---------	----------------	-------	--------

M_1 C7							
M_2 C7^{E}	332/S	0.856±0.345**	**0.020**	0.344	-0.206±0.163	0.211	0.152
M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 C7^{E}							
M_1 DTCREST^{CF}	---------------	----------------	-------	---------	----------------	-------	--------
M_2 DTCREST^{W}	---------------	----------------	-------	---------	----------------	-------	--------
M_1 DTCREST^{CF}							
ALL TRAITS^{CF}	---------------	----------------	-------	---------	----------------	-------	--------

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[a] I=incisor; C=canine; PM=premolar; M=molar. Maxillary and mandibular traits indicated by superscript and subscript, respectively. All traits represented by their maximum antimeric expression score. For a list of morphological trait abbreviations, see Appendix C. "E" superscript indicates a trait that was originally flagged for intra-observer error because the error range exceeded a single grade, but whose mean error does not exceed 0.300. Traits with mean error exceeding 0.300 were omitted from the correlation analyses. All third molar traits were omitted from the correlation analyses due to sample size limitations. "W" superscript indicates models that are suspect due to standard deviation ranges for certain estimates. "CF" superscript indicates model convergence failure. [b] Covariates fixed in the genetic correlation models if significant in associated univariate models. "A"=age; "S"=sex; "A*S"=age/sex interaction; "ALL"=all covariates. +Note that premolar double shoveling was included in the anterior dentition as this trait is homologous to traits that occur in anterior elements. [c] Maximum-likelihood estimate of genetic correlation. Cases of incomplete pleiotropy indicated by a single asterisks. Cases of complete pleiotropy indicated by two asterisks. Dashes are associated with incalculable parameter estimates. [d] Probability of hypothesis (as indicated in parentheses) being true given pedigree structure with values p<0.050 bolded. Dashes are associated with incalculable parameter estimates. [e] Maximum-likelihood estimate of environmental correlation. Dashes are associated with incalculable parameter estimates. [f] Maximum-likelihood estimate of derived phenotypic correlation. Dashes are associated with incalculable parameter estimates.

Table 5. UAT sample variance components correlations: deciduous and permanent morphological homologues (ASUDAS).

Trait [a]	N/Cov[b]	Genetic			Environmental		Phenotypic
		ρ_G[c]	$P(\rho_G=0)$[d]	$P(\|\rho_G\|=1)$[d]	ρ_E[e]	$P(\rho_E=0)$[d]	ρ_P[f]
L Curve (i^1-I^1)^E	348/Y	0.330±0.161*	**0.049**	**<0.001**	0.119±0.207	0.568	0.262
Shov (i^1-I^1)	324/Y	0.467±0.167*	**0.020**	**0.024**	0.221±0.195	0.278	0.361
Shov (i^2-I^2)	305/Y	0.420±0.165*	**0.024**	**0.001**	0.333±0.210	0.148	0.370
Shov (c^1-C^1)	313/Y	0.475±0.137*	**0.002**	**<0.001**	-0.310±0.222	0.194	0.279
DShov (i^1-I^1)	333/N	-0.212±0.178	0.254	**<0.001**	-0.274±0.206	0.208	-0.223
DShov (i^2-I^2)	331/N	-0.334±0.306	0.248	0.073	0.354±0.165	**0.054**	0.106
DShov (c^1-C^1)	335/Y	0.524±0.143*	**0.001**	**<0.001**	-0.242±0.174	0.188	0.255
TD (i^2-I^2)	245/N	0.068±0.218	0.074	**<0.001**	-0.253±0.252	0.342	0.011
TD (c^1-C^1)	317/N	0.413±0.160*	**0.016**	**<0.001**	0.118±0.295	0.692	0.323
DAR (c^1-C^1)	282/Y	0.272±0.162	0.105	**<0.001**	0.249±0.156	0.127	0.241
Meta (m^2-M^1)^E	355/Y	0.189±0.158	0.230	**<0.001**	0.099±0.148	0.502	0.147
Meta (m^2-M^2)	344/Y	0.183±0.186	0.315	**<0.001**	-0.239±0.155	0.142	0.003
Hypo (m^2-M^1)	352/N	0.597±0.089*	**<0.001**	**<0.001**	0.126±0.140	0.370	0.460
Hypo (m^2-M^2)	332/N	0.445±0.143*	**0.006**	**<0.001**	-0.128±0.441	0.776	0.346
C5 (m^2-M^1)	349/Y	0.547±0.132*	**<0.001**	**<0.001**	-0.323±0.133	**0.032**	0.234
C5 (m^2-M^2)	326/Y	-0.157±0.175	0.372	**<0.001**	0.483±0.181	**0.034**	-0.062
Carabelli (m^2-M^1)	354/Y	0.635±0.075*	**<0.001**	**<0.001**	0.040±0.131	0.760	0.491

Carabelli (m^2-M^2)	337/N	0.368±0.147*	**0.019**	**<0.001**	-0.340±0.186	0.099	0.253
Para (m^2-M^1)	356/Y	0.239±0.122	0.057	**<0.001**	0.265±0.124	**0.043**	0.243
Para (m^2-M^2)^{W}	-------	---------------	--------	-----------	----------------	-------	-------
Shov (i_1-I_1)	323/N	0.617±0.328**	**0.043**	0.170	-0.368±0.194	0.092	0.110
Shov (i_2-I_2)	333/Y	0.414±0.164*	**0.012**	**0.001**	0.519±0.209	**0.037**	0.445
DAR (c_1-C_1)	301/Y	0.649±0.202**	**0.006**	0.064	0.003±0.194	0.988	0.338
AFovea (m_2-M_1)^{E}	329/Y	0.691±0.139*	**<0.001**	**0.032**	-0.077±0.138	0.583	0.353
CNo (m_2-M_1)^{CF}	-------	---------------	--------	-----------	----------------	-------	-------
CNo (m_2-M_2)^{CF}	-------	---------------	--------	-----------	----------------	-------	-------
DWrink (m_2-M_1)	332/N	0.520±0.078*	**<0.001**	**<0.001**	-0.016±0.158	0.920	0.440
Pstylid (m_2-M_1)^{E}	340/Y	0.659±0.128*	**<0.001**	**0.009**	-0.300±0.132	**0.038**	0.300
C5 (m_2-M_1)	343/Y	0.168±0.165	0.329	**0.008**	-0.195±0.138	0.170	0.146
C5 (m_2-M_2)	335/Y	-0.391±0.249	0.109	**0.018**	0.502±0.202	**0.050**	0.042
C6 (m_2-M_1)^{CF}	-------	---------------	--------	-----------	----------------	-------	-------
C6 (m_2-M_2)^{CF}	-------	---------------	--------	-----------	----------------	-------	-------
C7 (m_2-M_1)	352	0.649±0.154*	**<0.001**	**0.027**	-0.234±0.136	0.107	0.265
C7 (m_2-M_2)^{E}	345	0.455±0.240	0.056	0.071	-0.096±0.214	0.657	0.180
DTCrest (m_2-M_1)^{CF}	-------	---------------	--------	-----------	----------------	-------	-------
DTCrest (m_2-M_2)^{W}	-------	---------------	--------	-----------	----------------	-------	-------

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[a] i/I=incisor; c/C=canine; m/M=molar. Maxillary and mandibular traits indicated by superscript and subscript, respectively. Deciduous and permanent traits indicated by lowercase and uppercase script, respectively. All traits represented by their maximum antimeric expression score. For a list of morphological trait abbreviations, see Appendix C. "E" superscript indicates a trait that was originally flagged for intra-observer error because the error range exceeded a single grade, but whose mean error does not exceed 0.300. Traits with mean error exceeding 0.300 were omitted from the correlation analyses. "W" superscript indicates models that are suspect due to standard deviation ranges for certain estimates. "CF" superscript indicates model convergence failure. [b] Covariates fixed in the genetic correlation models if significant in associated univariate models. Only sex was fixed for deciduous-permanent homologue correlations due to the structure of the "age" dataset. "N"=sex covariate not fixed; "Y"=sex covariate fixed.
[c] Maximum-likelihood estimate of genetic correlation. Cases of incomplete pleiotropy indicated by a single asterisks. Cases of complete pleiotropy indicated by two asterisks. Dashes are associated with incalculable parameter estimates.

[d] Probability of hypothesis (as indicated in parentheses) being true given pedigree structure with values $p<0.050$ bolded. Dashes are associated with incalculable parameter estimates. [e] Maximum-likelihood estimate of environmental correlation. Dashes are associated with incalculable parameter estimates. [f] Maximum-likelihood estimate of derived phenotypic correlation. Dashes are associated with incalculable parameter estimates.