

THESIS

NONMETRIC DENTAL TRAIT CORRESPONDENCE IN THE STUCKLEN COLLECTION:
INTRA-INDIVIDUAL CORRELATIONS BETWEEN THE DECIDUOUS AND
PERMANENT DENTITIONS

Submitted by

Katherine T. Brown

Department of Anthropology and Geography

In partial fulfillment of the requirements

For the Degree of Master of Arts

Colorado State University

Fort Collins, Colorado

Summer 2026

Master's Committee:

Advisor: Michelle M. Glantz

Andrew Du
Ellie McNutt

Copyright by Katherine T. Brown 2026

All Rights Reserved

ABSTRACT

NONMETRIC DENTAL TRAIT CORRESPONDENCE IN THE STUCKLEN COLLECTION: INTRA-INDIVIDUAL CORRELATIONS BETWEEN THE DECIDUOUS AND PERMANENT DENTITIONS

A foundational assumption in dental anthropology is that the deciduous and permanent dentitions share an underlying developmental architecture, so that trait expression in one dentition should predict expression in the other within the same individual. Butler's morphogenetic field theory and the Patterning Cascade Model both generate specific, testable predictions about which trait pairs should show the strongest cross-dentition correspondence, and the quantitative genetic literature provides independent evidence of shared heritability across diphyodont homologues. The empirical literature directly testing within-individual correspondence is small and methodologically inconsistent, with most studies relying on incompatible scoring systems that make direct ordinal comparison analytically unfeasible. This study examines 22 deciduous-permanent trait pairs in 46 individuals from the Stucklen Collection, a longitudinal dental cast series from Wilmington, Delaware, using the Arizona State University Dental Anthropology System to score both dentitions. Three correlation methods are applied to each trait pair: Goodman-Kruskal's gamma, tetrachoric correlation, and Spearman's rank correlation. Cross-dentition correspondence is trait-specific and limited in overall extent. Four trait pairs produced robust signals on two or more tests: canine mesial ridge, Carabelli's cusp, hypocone, and incisor shoveling. The pattern of significant results partially confirms the predictions of field theory and the Patterning Cascade Model, with early-forming primary cusp complex traits outperforming late-

forming accessory cusps. Methodological comparison across tests reveals that Spearman's rank correlation captures co-absence correspondence that gamma systematically excludes. These findings extend the cross-dentition correspondence literature to a third longitudinal North American collection and underscore the importance of unified scoring and multi-method assessment for evaluating the developmental integration of the human diphyodont dental complex.

ACKNOWLEDGEMENTS

I want to thank Dr. Rachel Watkins & the Penn Museum for allowing me to access the Stucklen Collection and for the support I have received for my research project. Dr. Richard Stucklen, thank you for amassing this collection over the course of your career and for donating your life's work to Penn in order for other researchers to benefit from it.

I would like to give a big thank you to my advisor, Dr. Mica Glantz. Thank you for taking me on as your student, for supporting me throughout my Master's, and for traveling with me to Philadelphia for my data collection.

Thank you to my committee members Dr. Andrew Du & Dr. Ellie McNutt, your support and expertise throughout the last two years has been invaluable to this project. I would also like to thank the faculty and staff in the Anthropology & Geography department here at CSU who have supported me over the last two years: Dr. Michael Pante, Dr. Connie Fellmann, Valeria Meza Alba, & Josh Zaffos.

The experiences and opportunities I got at the University of Tennessee, Knoxville have allowed me to become the professional I am today. Dr. Amy Mundorff, thank you for introducing me to dental anthropology and for encouraging me on my journey to graduate school. I thank Dr. Sierra Bow for taking on an unprepared undergraduate with big plans for a thesis and for teaching me how to be a researcher.

I have been incredibly lucky to work with so many incredible archaeologists during my CRM career (too many to name here!), but I would specifically like to thank Christopher Goodmaster, Alex Younger, & Pritam Chowdry. From accepting a newbie who was still green

behind the ears, to allowing me to participate in multiple once-in-a-lifetime projects, I cannot thank you all enough.

My time in graduate school would have been astronomically more difficult (& way less fun) without the incredibly supportive cohort I was a part of. I want to specifically thank Jenna Dagher, Lily Gregson, Isabel Heslin, & Elaine Henson. I cannot wait to see where we all end up at the end of our grad school journeys.

My friends and family have been so supportive of me throughout my graduate school journey. Thank you to my best friend, Gray Bagci, thanks for all the late-night discord calls, and my partner Gage Moorehead, for always being just a phone call away. I also want to thank Emma Kelly, Lia Sams, and the rest of the Insensitivity Trainers. Our Thursday night D&D sessions have kept me sane (for the most part) the last two years. To my mom & dad, thank you for taking me to museums when I was little, encouraging me to be curious about the world around me, and inspiring me to follow my dreams no matter what. I love you both & I hope I've made you proud!

TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS	iv
LIST OF TABLES	ix
LIST OF FIGURES	x
CHAPTER I: INTRODUCTION.....	1
1.1 Nonmetric Dental Morphological Traits in Biological Anthropology	1
1.2 The Cross-Dentition Correspondence Problem	1
1.3 Edgar and Lease (2007) as the Direct Predecessor	3
1.4 Advances Since 2007	4
1.5 The Present Study: Significance of the Stucklen Collection	5
1.6 Organization of the Thesis	6
CHAPTER II: BACKGROUND	7
2.1 The Biological and Methodological Basis of Nonmetric Dental Morphology	7
2.2 Field Theory, the Patterning Cascade Model, and Cross-Dentition Correspondence	9
2.3 The Genetic Architecture of Deciduous and Permanent Dental Traits.....	13
2.4 Methodological Issues in Comparing the Two Dentitions	15
2.5 This Study in Context	17
CHAPTER III: MATERIALS AND METHODS	18

3.1 The Stucklen Collection.....	18
3.2 Data Collection	19
3.3 Final Sample Composition.....	20
3.4 Trait Scoring Procedure	21
3.5 Pre-Analysis Data Treatment.....	24
3.6 Statistical Analysis.....	25
3.7 Null and Alternative Results in Context	27
CHAPTER IV: RESULTS.....	30
4.1 Sample and Trait Frequency Descriptions.....	30
4.2 Goodman-Kruskal's Gamma Results	33
4.2.1 Molar Traits	36
4.2.2 Anterior Traits.....	37
4.3 Tetrachoric Correlation Results	38
4.4 Spearman's Rank Correlation Results	40
4.4.1 Molar Traits	42
4.4.2 Anterior Traits.....	43
4.5 Cross-Method Comparison	43
4.6 Research Questions	49
CHAPTER V: DISCUSSION.....	52
5.1 Research Questions.....	52

5.2 Comparison to Other Cross-Dentition Correspondence Studies	61
5.3 Developmental Mechanisms: The Patterning Cascade Model and Activator-Inhibitor Dynamics	64
5.4 What Does Correspondence Mean at the Individual Level?	67
5.5 Non-Significant Traits and Limitations	69
CHAPTER VI: CONCLUSION	73
6. 1 Future Directions	75
REFERENCES	77

LIST OF TABLES

Table 1. Nonmetric dental traits scored in this study.....	21
Table 2. Score frequencies for each trait by dentition.....	30
Table 3. Goodman-Kruskal's Gamma (γ) results.....	34
Table 4. Tetrachoric correlation (r_{Tet}) results.....	39
Table 5. Spearman rank correlation (r_s) results.....	41
Table 6. Cross-method summary for all trait pairs.....	45
Table 7. Summary of deciduous–permanent correlation results for all 22 trait pairs analyzed in the Stucklen Collection, with a priori predictions and hypothesis conformance.....	53
Table 8. γ and tetrachoric results for original data from Edgar & Lease.....	62
Table 9. Sample sizes and estimability status for all 22 deciduous–permanent trait pairs.....	70

LIST OF FIGURES

Figure 1. Application of morphogenetic field theory to human dentition, adapted from Butler (1939) and Dahlberg (1945).....	10
Figure 2. Age distributions of the Stucklen Collection analytical sample ($N = 46$).....	20
Figure 3. Goodman-Kruskal's Gamma (γ) for all 22 deciduous-permanent trait pairs, sorted by magnitude.....	36
Figure 4. Gamma (γ) versus Spearman's (r_s) for all 22 trait pairs.....	47
Figure 5. Correlation heatmap of Gamma (Test 1), Tetrachoric (Test 2), and Spearman's (Test 3) for all 22 deciduous-permanent trait pairs.....	48
Figure 6. Raw score scatterplots for the four trait pairs with the strongest correlation estimates...	49

CHAPTER I: INTRODUCTION

1.1 Nonmetric Dental Morphological Traits in Biological Anthropology

Dental morphological traits have a long history as markers of biological affinity in archaeological, paleoanthropological, and forensic contexts (Scott & Turner, 1997; Hefner et al., 2016; Pilloud et al., 2016). In many prehistoric and forensic assemblages, however, subadults constitute a significant portion of the available remains. Without a clear understanding of how deciduous trait expressions correspond to permanent ones within the same individuals, those remains are either excluded from analysis entirely or their traits are treated as proxies for the permanent dentition without empirical justification. The theoretical and genetic case for correspondence is well established: both dentitions are broadly heritable, developmental theory predicts trait-specific cross-dentition patterning within morphogenetic fields, and quantitative genetic analyses of pedigreed samples confirm that homologous trait pairs share partial but meaningful genetic architecture (Paul et al., 2020, 2022b). The empirical literature directly testing that correspondence within individuals is limited and methodologically inconsistent, primarily because incompatible scoring systems for the two dentitions have made direct comparison difficult. Building a cumulative record of which trait pairs reliably correspond, to what degree, and for what developmental reasons has proven difficult. Understanding the biological basis of nonmetric dental traits, including their heritability, their developmental determinants, and the degree to which deciduous and permanent expressions are correlated within the same individuals, is foundational to interpreting them in anthropological contexts.

1.2 The Cross-Dentition Correspondence Problem

The expectation of within-individual deciduous-permanent correspondence has theoretical roots extending back to the early twentieth century. Butler's (1939) morphogenetic field theory proposes

that the mammalian dentition is organized into three developmental fields, incisor, canine, and molar, respectively. Each is governed by a developmental gradient radiating from a central key tooth. Dahlberg (1945, 1950) elaborated this framework by recognizing that the second deciduous molar (dm2) and the permanent first molar (M1) occupy analogous positions as the most stable members of their respective molar series, suggesting that the two teeth share developmental pathways within the same morphogenetic field. This relationship implies that an individual's expression of molar field traits should be broadly consistent across the two dentitions, not because the teeth are identical, but because the same developmental program influences both.

The Patterning Cascade Model (PCM; Salazar-Ciudad & Jernvall, 2010) provides an explanation for the underlying mechanism behind the morphogenetic field theory. In the PCM framework, cusp formation proceeds as a sequential cascade of enamel knot signaling events in which each cusp's spatial position is constrained by the intercusp geometry established by prior cusps. Early forming cusps set the geometric template within which later cusps develop, which means traits established early in the cascade should be more stable across dentitions than late-forming accessory cusps, whose expression depends on downstream cascade dynamics sensitive to even small geometric differences between dm2 and M1. Paul et al. (2016) applied this framework directly to the dm2/M1 metamer pair, developing the specific prediction that traits associated with the primary cusp complex should show stronger cross-dentition correspondence than late-forming accessory cusps such as the entoconulid or metaconulid.

Despite these theoretical grounds, the literature directly testing within-individual correspondence remains small. Saunders & Mayhall (1982) provided the earliest systematic longitudinal evidence, examining five traits in the Burlington Growth Centre and finding associations consistent with field theory predictions. Subsequent studies in North American and

Colombian samples have reported trait-specific patterns broadly consistent with field theory expectations, but the reported patterns vary between studies in a way that tracks the methodological differences at least as much as biological ones (Aguirre et al., 2007; Ocampo et al., 2009; Edgar & Lease, 2007; Paul & Stojanowski, 2017). The central obstacle is scoring system incompatibility: ASUDAS was developed for the permanent dentition, while deciduous morphology has typically been scored using independent systems, Hanihara (1961) and Sciulli (1998), that differ in their reference standards, ordinal scales, and presence/absence breakpoints.

1.3 Edgar and Lease (2007) as the Direct Predecessor

The most methodologically direct predecessor to this study is Edgar & Lease (2007), who tested within-individual cross-dentition morphological correspondence in a sample of 54 European Americans from the Bolton-Brush Growth Study Collection, a mid-twentieth century longitudinal dental cast series from Ohio. They scored 19 deciduous traits using Hanihara's and Sciulli's descriptions and their permanent homologues using ASUDAS, then compared them using Goodman-Kruskal gamma and tetrachoric correlation. To address scoring system incompatibility, they constructed a shared scale by mapping the two systems to equivalent grade levels and ran analyses on both the original mixed-scale data and the converted shared-scale data. Shared-scale conversion consistently produced more and stronger positive correlations, a finding they interpreted as evidence that mixed scoring systems artificially suppress detectable correspondence. Cross-dentition correspondence was trait-specific rather than general, with Carabelli's cusp producing the most consistently positive correlations across tests and scale formats. Edgar & Lease concluded that trait expressions are partially correlated across the two dentitions, but that the degree of correspondence and the identity of corresponding pairs are sensitive to the scoring system used. That sensitivity is the methodological problem this thesis aims to address.

1.4 Advances Since 2007

Quantitative genetic research since Edgar & Lease (2007) has changed the understanding of the biological foundations of deciduous dental morphology and its relationship to the permanent dentition. Paul & Stojanowski (2015) demonstrated that deciduous crown morphology distinguishes biological siblings from unrelated individuals, establishing the kinship signal in the deciduous dentition as reliable for biological inference. Paul & Stojanowski (2017) scored both dentitions using ASUDAS in the Burlington Growth Centre and found a greater number of significant cross-dentition correlations than Edgar & Lease (2007), attributing part of the difference to unified scoring. Paul et al. (2020) generated heritability estimates for both dentitions in a pedigreed Australian sample, demonstrating that deciduous traits are substantially heritable and supporting their use as proxies for genetic variation.

Two subsequent studies established the quantitative genetic benchmarks against which within-individual cross-dentition phenotypic results can now be directly interpreted. Paul et al. (2021) examined bivariate genetic correlations between deciduous and permanent anterior trait pairs in the same Australian sample, finding that approximately 70% of deciduous-permanent canine trait comparisons yielded statistically significant genetic correlation and interpreting this as evidence for a morphological canine module spanning the diphyodont complex. Paul et al. (2022b) extended this analysis to molar morphology, finding significant genetic correlations in over half of dm2-M1 homologue comparisons, with the highest estimates for Carabelli's cusp and hypocone. They also documented a negative genetic correlation between hypoconulid and entoconulid, interpreted as reflecting developmental competition for cellular territory at the distal aspect of the crown. Kenessey et al. (2024) tested PCM predictions in the lower mixed and permanent dentition, finding support for the cascade model's prediction that early forming traits show stronger

correspondence than late-forming accessory cusps. Together, these studies specify which trait pairs should show strong within-individual phenotypic correspondence, how strong that correspondence should be, and what developmental mechanisms are most likely responsible.

1.5 The Present Study: Significance of the Stucklen Collection

This thesis examines cross-dentition correspondence directly using the Stucklen Collection, a longitudinal dental cast series housed at the University of Pennsylvania Museum of Archaeology and Anthropology. Assembled by Richard H. Stucklen, a dentist based in Wilmington, Delaware, beginning in the late 1920s, the collection follows 46 individuals from early childhood through early adulthood. Both dentitions were scored using ASUDAS standards for 22 morphological trait pairs. The Stucklen Collection is the third independent longitudinal North American sample analyzed for deciduous-permanent trait correspondence, following the Bolton-Brush Growth Study Collection (Edgar & Lease, 2007; Saunders & Mayhall, 1982) and the Burlington Growth Centre (Paul & Stojanowski, 2017). In archaeological and forensic assemblages where subadults constitute a large portion of the available remains, knowing which deciduous trait expressions reliably predict their permanent homologues expands the analytical toolkit for reconstructing biological identity and population affinity. It also narrows the justification for excluding subadult remains from biodistance analyses entirely.

Here, we aim to answer two questions. First, to what degree are deciduous and permanent trait expressions correlated within the same individuals in the Stucklen Collection. This is answered through three complementary statistical approaches: Goodman-Kruskal gamma, tetrachoric correlation, and Spearman rank correlation. Second, does the pattern of correspondence align with the predictions of Butler's morphogenetic field theory, the PCM, and the quantitative

genetic literature. The first question is answered in Chapter IV; the second is addressed in Chapter V.

1.6 Organization of the Thesis

This thesis is organized into six chapters. *Chapter II: Background* provides the theoretical and empirical background for the study, reviewing Butler's field theory and the PCM as frameworks for predicting cross-dentition correspondence, synthesizing the genetic literature on deciduous and permanent trait development, and situating this study within the methodological history of cross-dentition comparison research. *Chapter III: Materials & Methods* describes the Stucklen Collection, the data collection and cast selection process, the trait scoring protocol, and the three statistical methods applied. *Chapter IV: Results* presents the results of the gamma, tetrachoric, and Spearman's rank correlation analyses for all 22 retained trait pairs. *Chapter V: Discussion* interprets the results in light of the developmental and genetic frameworks introduced in Chapter II, compares findings to Edgar & Lease (2007) and Paul & Stojanowski (2017), and addresses the limitations of this study. *Chapter VI: Conclusions* summarizes the conclusions and discusses implications for our understanding of nonmetric dental morphological variation across the human dental complex.

CHAPTER II: BACKGROUND

Four bodies of literature establish the theoretical and empirical foundation for this study. Section 2.1 introduces nonmetric dental morphological traits, their genetic basis, and the standardized scoring system used in contemporary research. Section 2.2 reviews Butler's morphogenetic field theory and the Patterning Cascade Model, which together provide the developmental logic underlying trait expression patterns within and across the two dentitions. Section 2.3 synthesizes current evidence on the genetic architecture of deciduous and permanent dental traits and the degree to which the two dentitions share heritable developmental determinants. Section 2.4 examines the methodological history of cross-dentition comparison studies and situates this study relative to the current literature.

2.1 The Biological and Methodological Basis of Nonmetric Dental Morphology

Nonmetric dental morphological traits are discrete or quasi-continuous crown and root features assessed on an ordinal scale against standardized reference casts, reflecting the degree to which a feature is developed or dichotomized as present or absent (Scott & Turner, 1997; Pilloud et al., 2016). Unlike metric variables such as crown diameters, nonmetric traits capture variation in shape and structure, and their expression is known to be under additive genetic control. Heritability is moderate to high across both the deciduous and permanent dentitions, a pattern documented consistently across twin and family samples and scoring systems (Dempsey et al., 1999; Townsend et al., 2012; Paul et al., 2020). This genetic basis is why cross-dentition correspondence within the same individual, where it exists, is most plausibly attributed to shared genetic architecture rather than coincidence: when both dentitions are significantly heritable, homologous trait expressions are positioned to covary for biological rather than incidental reasons.

Closely related to heritability is canalization, the tendency of developmental pathways to buffer consistent phenotypic outcomes against genetic and environmental perturbation. Crown morphological traits are generally considered highly canalized, particularly features established early in development, which contributes to their stability across individuals and populations and their usefulness for reconstructing biological affinity (Townsend et al., 2012). Canalization is not uniform, however. Late-forming accessory cusps show greater developmental instability and sensitivity to environmental influence than primary cusp morphology (Paul et al., 2020), a distinction directly relevant to this study's predictions about which trait pairs are most likely to show detectable cross-dentition correspondence.

The standard scoring tool for nonmetric dental traits in contemporary research is the Arizona State University Dental Anthropology System (ASUDAS), developed by Turner et al. (1991). The ASUDAS assigns ordinal grades to morphological features using standardized reference plaques and casts, and was designed explicitly for comparability across studies (Pilloud et al., 2016). Data collection convention is to record the maximum expression observed across antimeric pairs, minimizing the influence of asymmetry and maximizing observable variation within individuals (Irish & Scott, 2016). This study applies ASUDAS standards to both dentitions, a methodological difference from earlier cross-dentition work that used separate deciduous and permanent scoring systems and one that is central to the comparability of the results presented in Chapter IV.

The value of nonmetric dental data is well established across bioarchaeological and forensic contexts. Tooth enamel preserves well in the archaeological record, making dental morphological data available for populations whose biological record is otherwise limited (Pilloud et al., 2016). Trait frequency profiles have been used to characterize major dental morphological

complexes reflecting patterns of ancient human dispersal, including the Sinodont, Sundadont, Eurodont, and Afridont patterns (Turner, 1990; Hanihara, 1992; Irish, 1997). Recent genomic work has confirmed that these population-level patterns are real: Irish et al. (2020) demonstrated that ASUDAS-derived biodistance estimates correlate strongly with genome-wide genetic differentiation measures, and Rathmann & Reyes-Centeno (2020) showed that individual traits vary substantially in how well their between-population frequencies mirror neutral genomic variation, with canine accessory ridge traits and entoconulid performing best and Carabelli's cusp and tuberculum dentale among the weakest. The fact that individual traits differ in their capacity to track population genetic history reinforces the expectation that cross-dentition correspondence will also be trait-specific rather than uniform, and provides context for interpreting which pairs show the strongest and weakest phenotypic associations in the results.

2.2 Field Theory, the Patterning Cascade Model, and Cross-Dentition Correspondence

Two theoretical frameworks explain the developmental logic underlying crown morphological patterning and generate testable predictions about which trait pairs should show the strongest cross-dentition correspondence: Butler's morphogenetic field theory and the Patterning Cascade Model (PCM).

Butler (1939) proposed that the mammalian dentition is organized into morphogenetic fields, each governed by a developmental gradient radiating from a central point called the key tooth. Within each field, the key tooth is the most developmentally stable, while teeth positioned farther from it become progressively more variable as the gradient weakens. Dahlberg (1945) elaborated this framework for the human dentition by identifying the first permanent molar (M1) as the key tooth of the permanent molar series and the second deciduous molar (dm2) as its analogue within the deciduous dentition (Figure 1).

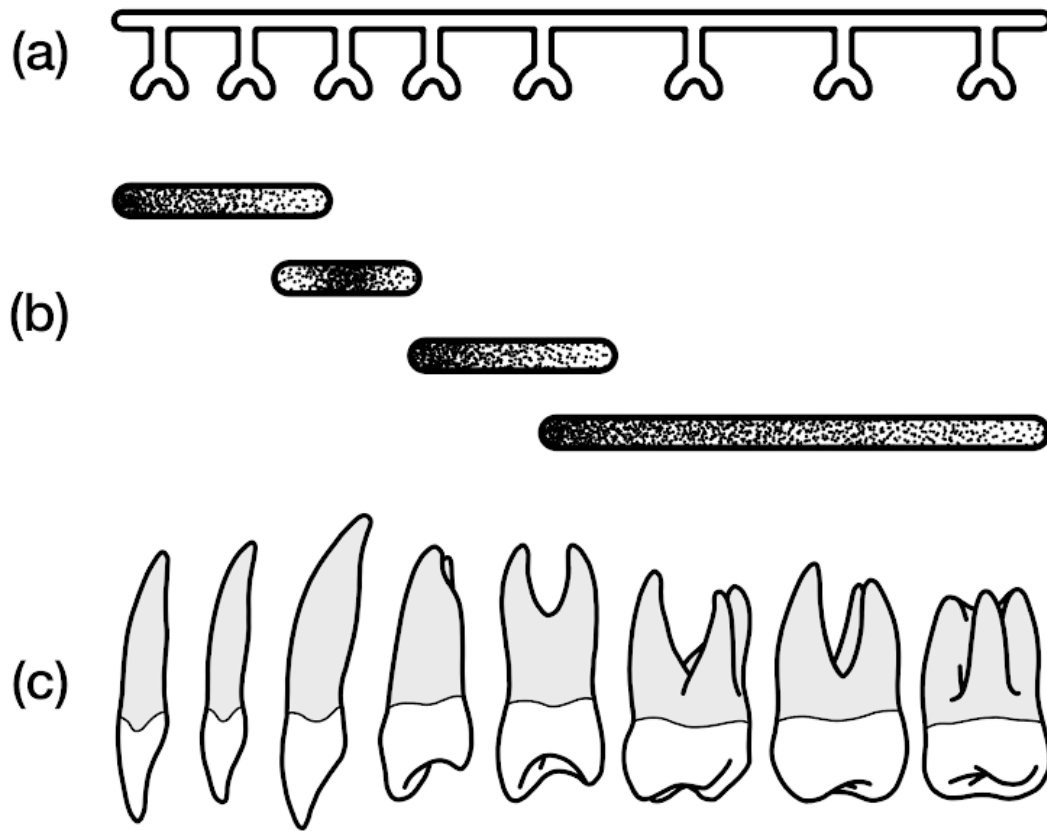


Figure 1. Application of morphogenetic field theory to the human dentition, adapted from Butler (1939) and Dahlberg (1945). (a) The dental lamina positions with indications for the permanent maxillary dentition (I1, I2, C, P3, P4, M1, M2, M3). (b) The four morphogenetic fields proposed for the human dentition each represented as a developmental gradient radiating from its respective key tooth (I1, C, P3, M1). Field intensity decreases with increasing distance from each key tooth. (c) The differentiated human

permanent dentition that results, with crown morphology reflecting the combined influence of field position and regional morphogenetic gradients.

The morphological similarity between dm2 and M1 is well documented and consistent with their shared key-tooth status: crown cusp number, general occlusal morphology, and the frequencies of several discrete traits are more similar between these two teeth than between any other deciduous-permanent pair (Dahlberg, 1950; Edgar & Lease, 2007; Bailey et al., 2014). Frequency differences do exist, with protostylid, Carabelli's cusp, and aspects of hypocone development tending to occur at higher rates in dm2, while deflecting wrinkle and marginal ridge structures are more common in M1 (Dahlberg, 1950; Smith et al., 1987; Edgar & Lease, 2007). These frequency differences reflect the distinct developmental geometries and ontogenetic timing of the two crowns rather than an absence of shared developmental programming. Field theory's prediction for this study follows directly: because dm2 and M1 share a morphogenetic field, their trait expressions should generally correspond within the same individual.

The Patterning Cascade Model (PCM) provides the mechanistic explanation for why that correspondence is trait-specific rather than uniform across the dentitions (Salazar-Ciudad & Jernvall, 2010). The PCM describes cusp formation as a sequential cascade of enamel knot signaling events, in which each successive cusp's position is constrained by the intercusp distances already established by earlier cusps. Because this cascade begins from the primary cusp complex, traits established early in the sequence are most likely to be directly shaped by shared crown geometry and are most stable across homologous teeth. Late-forming accessory cusps are most sensitive to small geometric differences between the two crowns and are the least likely to show consistent cross-dentition correspondence. Paul et al. (2016) applied this logic directly to dm2 and M1, predicting stronger correspondence for early-forming traits than for late-forming accessory

structures. Subsequent empirical work has supported this: Kondo & Townsend (2006) showed that Carabelli's cusp expression in M1 was associated with protocone area size in the direction the PCM predicts, Paul et al. (2017) found that relative intercusp distances were significant predictors of Carabelli's expression in within-individual dm2/M1 pairs, and Kenessey et al. (2024) demonstrated that intercusp distances accounted for accessory cusp variation in mandibular molar pairs.

One additional source of cross-dentition divergence is the difference in developmental timing between the two dentitions. Deciduous crown formation occurs largely prenatally, within a buffered intrauterine environment, while permanent crown formation occurs postnatally during a period of active growth when the child is exposed to nutritional variation, environmental stressors, and illness. The two dentitions develop under different degrees of environmental influence, with deciduous trait expression likely reflecting underlying genetic determinants more directly (Paul et al., 2020). The implication for this study is that deciduous scores may provide a less environmentally confounded signal of shared developmental architecture, which would help with detecting correspondence if/where it exists.

Together, these frameworks generate three *a priori* expectations against which the results in Chapter IV are evaluated. Early forming molar field traits, particularly Carabelli's cusp and hypocone, are expected to show the strongest cross-dentition correspondence given their developmental priority and the weight of prior empirical evidence (Edgar & Lease, 2007; Paul et al., 2017; Paul & Stojanowski, 2017). Late-forming accessory cusps, including cusp 5 and cusp 6 of the molars, are predicted to show weak or absent correspondence because their expression is most sensitive to geometric divergence between dm2 and M1 downstream in the cascade. Canine field traits are predicted to show strong correspondence: the permanent canine is the key tooth of its field, the deciduous canine is its direct analogue and the only tooth in the field, and canine

accessory ridge traits are established early relative to primary cusp geometry. Paul et al. (2021) found that approximately 70% of deciduous-permanent canine comparisons yielded significant genetic correlations in a pedigreed Australian sample, the highest rate observed across any tooth class.

2.3 The Genetic Architecture of Deciduous and Permanent Dental Traits

The developmental theory reviewed in Section 2.2 predicts that dm2 and M1 share a morphogenetic program; the quantitative genetic literature reviewed here asks how much of that shared program is reflected in the additive genetic architecture of specific trait pairs. The answer matters for this study because it determines which pairs are the strongest candidates for detectable phenotypic correspondence and what biological mechanism would explain it.

Paul et al. (2022b) provided the most comprehensive bivariate genetic correlation analysis currently available for deciduous and permanent molar traits scored using ASUDAS standards, using a sample of Australian twins and their families. Genetic correlations estimated for dm2/M1 homologue pairs were statistically significant in approximately 56% of comparisons, with none showing complete pleiotropy. This confirms the expectation of partial rather than complete genetic overlap, which is the baseline for interpreting phenotypic results: correspondence should be trait-specific, not uniform. Among the pairs most directly relevant to this study, Carabelli's cusp ($r_G = 0.635$) and hypocone ($r_G = 0.597$) showed the strongest genetic integration, consistent with the PCM prediction that early forming traits carry more shared developmental signals. Paul et al. (2022b) also found that cross-dentition integration between dm2 and M1 was stronger than within-row integration between adjacent teeth in either dentition, which they interpret as evidence that

dm2 and M1 share a conserved molar field developmental program that is not simply a product of positional proximity.

For the anterior dentition, Paul et al. (2021) found that approximately 70% of deciduous-permanent canine trait comparisons yielded significant genetic correlations in the same Australian sample, a higher rate than for either incisor or molar pairs. Stojanowski et al. (2018) replicated this canine integration pattern in a demographically distinct pedigreed sample, the South Carolina Gullah, finding near-complete pleiotropy between antimeres for canine mesial ridge and distal accessory ridge and strong cross-trait integration within the canine field. The consistency of the canine signal across two samples with very different demographic histories suggests it reflects a real and stable feature of canine field developmental architecture rather than a sample-specific bias. Paul et al. (2020) established that both dentitions are substantially heritable across both dentitions, with most estimates falling between 0.4 and 0.8, and that deciduous traits may reflect underlying genetic determinants more directly than permanent traits given the prenatal buffering of deciduous crown formation reviewed in Section 2.2.

This study is looking at phenotypic correlations between ASUDAS scores in the two dentitions of the same individuals, not genetic correlations, and these two are related but not equivalent. Decomposing phenotypic covariance into genetic and environmental components requires genealogical data that the Stucklen Collection does not currently have. The genetic literature reviewed here sets up some predictions: traits with high r_G , particularly Carabelli's cusp, hypocone, and canine accessory ridges, are the strongest candidates for detectable phenotypic correspondence because a shared additive genetic mechanism is in place to produce it. Traits with near-zero genetic correlations, including late-forming accessory cusps, are more affected by the perturbations in the developmental environment, and correspondence is not expected. If

phenotypic results align with the rG rankings, shared genetic architecture is the most parsimonious explanation; if they do not, shared prenatal developmental environment or scoring flaws would be a plausible explanation.

2.4 Methodological Issues in Comparing the Two Dentitions

Despite the theoretical and empirical case for cross-dentition correspondence, relatively few studies have directly examined within-individual deciduous-permanent trait correlations in human samples. This is due to two main obstacles: the rarity of longitudinal collections where both dentitions can be scored in the same individuals, and the historical practice of scoring deciduous and permanent dental morphology using separate systems with different reference standards, ordinal scales, and dichotomization breakpoints. Because numerical scores from one system cannot be directly compared to those from another, early cross-dentition studies faced an analytic problem that could not be fully resolved after the fact.

Saunders & Mayhall (1982) conducted the earliest systematic cross-dentition comparison, examining five traits in 827 children from the Burlington Growth Centre longitudinal sample. They found that shoveling in the deciduous incisors predicted shoveling in the permanent incisors and that dm2/M1 associations were consistent with the molar field hypothesis, but their study predated the ASUDAS and relied on scoring systems that precluded direct grade-level comparison across dentitions, limiting the strength of the statistical conclusions.

Edgar & Lease (2007) is the most direct predecessor to this study. Working with 54 European Americans from the Bolton-Brush Growth Study Collection, they scored 19 deciduous traits using Hanihara's and Sciulli's criteria and their permanent homologues using ASUDAS, then constructed a shared ordinal scale to partially address the incompatibility before running

Goodman-Kruskal gamma and tetrachoric correlations on both the original and converted scores. The shared-scale conversion yielded more positive correlations than the original-scale analysis, which they interpreted as evidence that mixed scoring systems artificially suppress detectable correspondence. Their overall conclusion, that cross-dentition trait expressions are partially correlated but the pattern is trait-specific with Carabelli's cusp the most consistent finding, frames the central question this study asks: to what degree does an individual's deciduous expression predict their permanent expression for the same trait?

Paul & Stojanowski (2017) addressed the scoring incompatibility more directly by applying ASUDAS standards to both dentitions in the Burlington Growth Centre collection from the outset. Their analysis found significant gamma correlations for a limited set of trait pairs, most consistently Carabelli's cusp and cusp 7, and demonstrated that a unified scoring system produces more transparent and interpretable cross-dentition comparisons than post-hoc conversion. This study follows their approach by applying ASUDAS to both dentitions in the Stucklen Collection, which allows the results to be compared directly to Paul & Stojanowski (2017) and Edgar & Lease (2007) while eliminating scale conversion as a confound.

Cross-dentition correspondence has also been documented outside of North American samples, which matters for establishing that the pattern reflects developmental architecture rather than population-specific factors. Studies of Colombian mestizo and indigenous samples found trait-specific correspondence consistent with field theory, with Carabelli's cusp the most reliable signal across population groups and scoring approaches (Aguirre et al., 2007; Ocampo et al., 2009). The replication of the same trait-specific pattern across demographically distinct samples strengthens the case that the correspondence this study tests is a real feature of shared developmental architecture rather than an artifact of any particular collection or population.

2.5 This Study in Context

Two conclusions emerge from the literature. Cross-dentition correspondence is trait-specific rather than general, with Carabelli's cusp and hypocone the most consistently detected signals across populations and methods, and late-forming accessory cusps are yielding weak or absent associations in nearly every study. Reported results also vary across studies in ways that track methodological differences at least as much as biological ones, with scoring system comparability the clearest source of that variation: studies applying ASUDAS to both dentitions produce more positive and more consistent correlations than those requiring post-hoc scale conversion.

This study addresses both points directly. The Stucklen Collection provides a larger within-individual sample than any prior ASUDAS-standardized cross-dentition study, with both dentitions scored on a common scale. The results in Chapter IV offer both a replication test of the Carabelli's cusp and hypocone findings that anchor the existing literature and a new test of whether the canine field integration documented genetically by Paul et al. (2021) is detectable at the phenotypic level in a within-individual sample.

CHAPTER III: MATERIALS AND METHODS

3.1 The Stucklen Collection

The sample examined here is from a series of dental molds housed at the University of Pennsylvania museum. Dr. Richard Stucklen was a practicing dentist and prominent early researcher on orthodontics throughout the 1920s-1970s. Stucklen helped in the creation of multiple longitudinal collections, along with taking molds of his patients undergoing orthodontic treatment. He donated all of these materials to the University of Pennsylvania upon his retirement in 1970, and these longitudinal collections were added to the Wilton M. Krogman Center for Research in Child Growth and Development. A section of those casts is this sample, hereby referred to as the Stucklen Collection. Details about the specific research plan for this collection, how the sample was selected, and the exact methodology are not known as there are no records documenting the history. The sample is believed to have been made up of children from the Wilmington/Philadelphia area in the 1950s-1960s (Rachel Watson & Janet Monge, personal communications). What is known is that individuals who consented to be involved in the study were followed from early childhood through early adulthood, with casts typically produced at approximately twelve-month intervals from roughly birth to age 12, then every two years until adulthood. This longitudinal design, in which the same individual is observed repeatedly across the full span of dental development, is what makes within-individual deciduous-permanent comparison possible and distinguishes the Stucklen Collection from cross-sectional population samples, in which the two dentitions can only be observed in different individuals.

The full collection comprises approximately 71 individuals, each represented by a series of plaster dental molds. Molds were stored in boxes that were labeled with the individual's alphanumeric identification code, sex, and the total number of dental impressions in the series. The

individual's identifier and precise age at the time of impression, recorded in years, months, and days (YY.MM.DD format) were inscribed directly in the plaster.

No formal population affinity data was available for this collection. Individual demographic records were not retained in a form accessible for this study, and no ancestry or ethnicity information is recorded on the casts or their storage boxes.

3.2 Data Collection

For each individual, the casts were arranged in chronological order by inscribed age, and the full series was reviewed before any traits were scored. This initial review was necessary because the number of casts per individual varies across the collection and the transition between dentition stages does not occur at a uniform age, so the appropriate casts for scoring had to be identified individually for each person rather than by applying a fixed age rule.

In order to minimize the effects of occlusal attrition on trait visibility, where multiple casts were equally suitable within the same series, the earliest available cast was scored. Individual teeth were excluded from scoring when occlusal surfaces were obscured by casting imperfections, primarily air bubbles or plaster imperfections, or when caries or attrition rendered the relevant morphological features unidentifiable. Fourteen individuals were excluded from the sample entirely whose cast series represented only a single dentition stage, making within-individual deciduous-permanent comparison impossible. Four additional individuals were excluded due to pathological conditions, primarily cleft palate, or caries which resulted in alterations to the occlusal surfaces or missing teeth that precluded complete trait scoring.

A subset of 17 individuals was selected opportunistically for photographic documentation, capturing cases of notable trait co-occurrence across dentitions, clear discordance, and pathological conditions of interest.

3.3 Final Sample Composition

The final paired analytical sample consists of 46 individuals: 24 male and 22 female (Supplementary Table 1). Age at the deciduous scoring observation ranged from 2.39 to 6.61 years. The distribution of deciduous scoring ages peaks between approximately three & a half to five years old, consistent with the period of complete deciduous eruption and the typical absence of permanent tooth interference at those ages (Figure 2, upper panel). Age at the permanent scoring observation ranged from 9.13 to 25.73 years, with the large majority of observations falling between 12 and 17 years (Figure 2, lower panel).

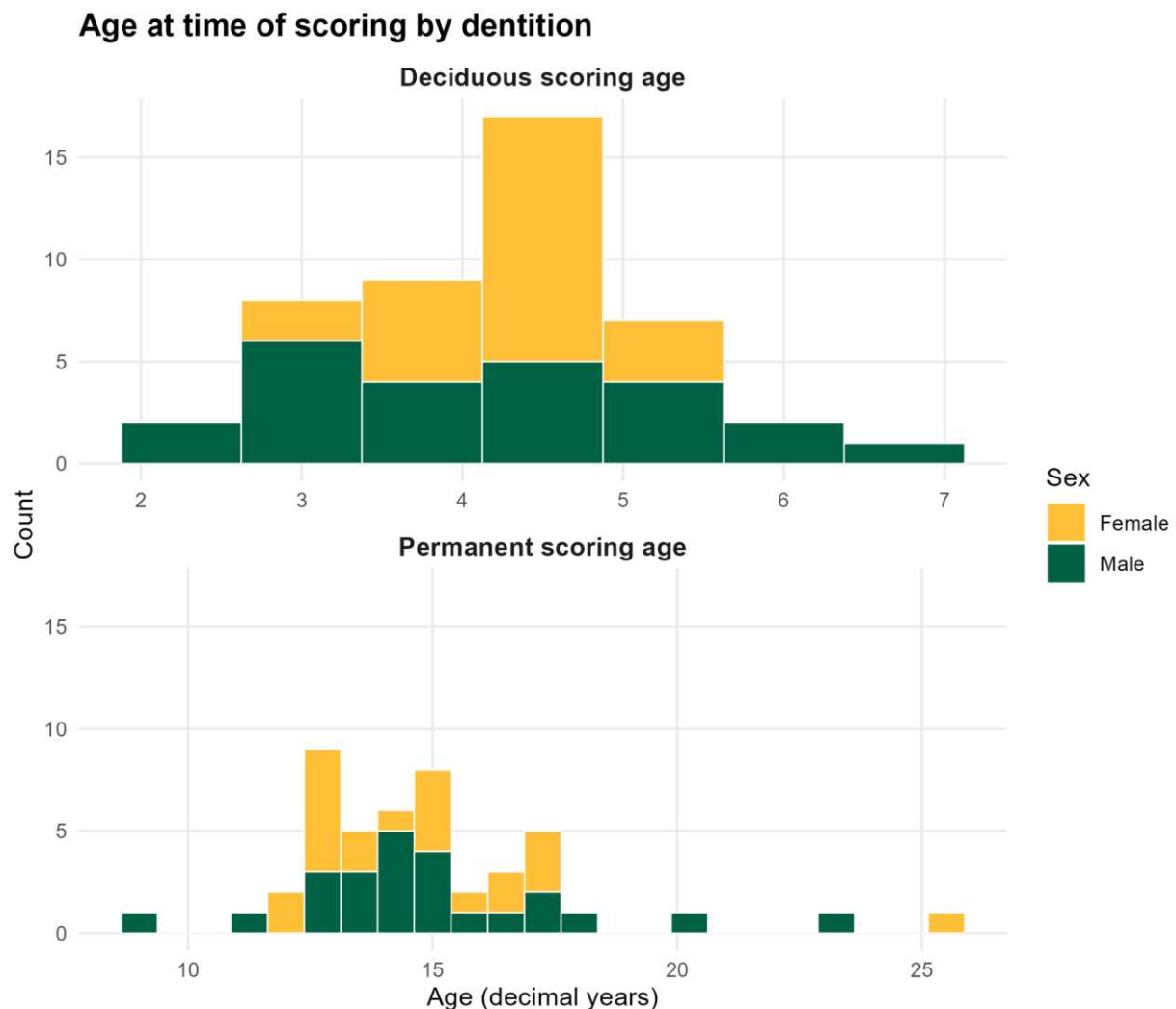


Figure 2. Age distributions of the Stucklen Collection analytical sample ($N = 46$). Upper panel: age at deciduous scoring observation (mean 4.23 years). Lower panel: age at permanent scoring observation (mean 14.87 years).

Trait-level sample sizes vary within the overall $N = 46$, ranging from a minimum of 37 complete pairs (deflecting wrinkle, dm2/M1) to a maximum of 46 complete pairs for several traits, reflecting variation in tooth absence and trait observability across individuals (Table 2).

3.4 Trait Scoring Procedure

The Arizona State University Dental Anthropology System (ASUDAS; Turner et al., 1991; Scott & Irish, 2017) was used to score all traits in both the deciduous and permanent dentitions. Scoring was performed primarily with reference to Edgar's *Dental Morphology for Anthropology: An Illustrated Manual* (Edgar, 2017), supplemented by the ASUDAS reference plaques for verification of ambiguous expressions. A total of 22 nonmetric dental traits were scored across both dentitions; the full trait list, tooth pairings, and ASUDAS grade ranges are provided in Table 1.

Table 1. Nonmetric dental traits scored in this study

Trait	Dec. Tooth	Perm. Tooth	ASUDAS Range	Breakpoint	Retained
Maxillary Molar					
Carabelli's trait	dm2	M1	0–7	0–1 / 2+	Yes
Hypocone	dm2	M1	0–5	0–2 / 3+	Yes
Metacone	dm2	M1	0–5	0–2 / 3+	Yes
Metaconule	dm2	M1	0–5	0 / 1+	Yes
Parastyle ‡	dm2	M1	0–6	0 / 1+	No ‡
Mandibular Molar					
Deflecting wrinkle	dm2	M1	0–3	0 / 1+	Yes

Trait	Dec. Tooth	Perm. Tooth	ASUDAS Range	Breakpoint	Retained
Mid-trigonid crest	dm2	M1	0–1	0 / 1+	Yes †
Metaconule	dm2	M1	0–5	0 / 1+	Yes
Entoconulid	dm2	M1	0–5	0 / 1+	Yes †
Maxillary Incisor					
Winging	di1	I1	0–3	0 / 1+	Yes
Labial curve	di1	I1	0–4	0 / 1+	Yes
Shoveling	di1	I1	0–7	0–1 / 2+	Yes
Shoveling	di2	I2	0–7	0–1 / 2+	Yes
Tuberculum dentale	di1	I1	0–6	0–1 / 2+	Yes †
Tuberculum dentale	di2	I2	0–6	0–1 / 2+	Yes
Maxillary Canine					
Canine mesial ridge	dc	C	0–3	0 / 1+	Yes
Canine distal accessory ridge	dc	C	0–5	0–1 / 2+	Yes
Shoveling	dc	C	0–7	0–1 / 2+	Yes
Mandibular Incisor / Canine					
Shoveling	di1	I1	0–7	0–1 / 2+	Yes †
Shoveling	di2	I2	0–7	0–1 / 2+	Yes †
Shoveling	dc	C	0–7	0–1 / 2+	Yes
Canine distal accessory ridge	dc	C	0–5	0–1 / 2+	Yes

N = 22, with deciduous and permanent tooth pairings, ASUDAS grade ranges, and dichotomization breakpoints. Dec. = deciduous; Perm. = permanent.

‡ Parastyle excluded (no complete deciduous-permanent pairs observed).

† Retained but interpreted with caution due to near-monomorphism in one or both dentitions.

For each trait, the relevant tooth or teeth were examined and an ASUDAS grade was assigned based on the degree of morphological expression observed. Maximum expression across left and right antimeres was recorded and used for all analyses, following standard protocol in dental anthropology (Turner et al., 1991; Irish & Scott, 2016). When one antimeres was unscorable due to casting damage or tooth absence, the score from the intact side was used. When both antimeres were unscorable, that individual was excluded from analysis for the affected trait.

The decision to apply ASUDAS to both dentitions rather than a deciduous-specific scoring system was done to address the central methodological limitation of Edgar and Lease (2007), who scored the deciduous dentition using Sciulli (1998) and Hanihara (1961) criteria and the permanent dentition using ASUDAS, then required post-hoc conversion to a shared scale for direct comparison. Scoring both dentitions on ASUDAS from the beginning places deciduous and permanent grades on the same ordinal scale without a conversion step, makes Spearman's rank correlation directly applicable, and eliminates conversion error as a source of ambiguity in the results. This is the same approach adopted by Paul & Stojanowski for their 2017 study. It should be noted that ASUDAS was developed and calibrated against permanent tooth morphology (Turner et al., 1991), and its application to deciduous teeth introduces some uncertainty at intermediate grade levels. The tradeoff accepted here is some imprecision in grade-level calibration in exchange for a directly comparable ordinal scale, a tradeoff Edgar & Lease (2007) addressed when they acknowledge the limitations of post-hoc conversion in their research.

ASUDAS scoring has been shown to produce reliable results for experienced scorers, and the use of an ordinal rather than continuous scale means that disagreements typically span only a single grade (Nichol and Turner, 1986). For traits subsequently dichotomized for tetrachoric

analysis, single-grade intra-observer disagreements would not typically alter the dichotomized value.

3.5 Pre-Analysis Data Treatment

Correlation estimates require variance on both dimensions being compared. If a trait does not vary in one dentition, there is no covariation to measure, and the resulting statistic is either incalculable or meaningless regardless of what the other dentition shows. Each scored trait pair was screened prior to the inferential analyses described in Section 3.6, following the procedure described by Paul & Stojanowski (2017). Traits were excluded when expression was fully constant in one or both dentitions after dichotomization, and retained but flagged for cautious interpretation when expression frequencies were near-extreme, typically at or below approximately 3%, because at those frequencies a single individual's scores can determine the entire correlation estimate.

Four traits were excluded entirely due to complete monomorphism in one or both dentitions: metaconule, parastyle, hypoconulid, and entoconulid. These do not appear in the results. Seven additional traits were retained but flagged. Hypocone (dm2/M1) and metacone (dm2/M1) had constant deciduous expression after dichotomization, meaning all 46 individuals were categorized as present in the deciduous dentition; tetrachoric estimation is incalculable for both because the 2×2 contingency table lacks variation on one dimension, and gamma produces only tied pairs. Cusp 5, lower (dm2/M1) had a deciduous frequency of 97.9%, leaving only one non-expresser. In the opposite direction, tuberculum dentale (di1/I1) had a deciduous frequency of 0% at the grade-2 breakpoint; mandibular shoveling (di1/I1) and (di2/I2) each had deciduous frequencies of 2.1%, meaning only one individual expressed the trait deciduously in each case. Cusp 6 (dm2/M1) and mid-trigonid crest (dm2/M1) each had expression frequencies of approximately 2% in both dentitions. Results for all seven are interpreted with caution throughout

Chapters IV and V. Score frequencies for each trait across both dentitions are listed in Table 2, modeled from Edgar & Lease (2007)

3.6 Statistical Analysis

Three statistical tests were applied to each of the 21 retained trait pairs: Goodman-Kruskal's Gamma (γ), tetrachoric correlation (r_{Tet}), and Spearman's rank correlation (r_s). This multi-test design follows Edgar & Lease (2007), who applied gamma and tetrachoric to the Bolton-Brush data, with Spearman's added as a third test which is possible by scoring both dentitions with ASUDAS. The following sections describe each procedure in turn and explain how it was applied to the Stucklen data.

Goodman-Kruskal's Gamma (γ) is an ordinal association statistic defined as:

$$(Con - Dis) / (Con + Dis)$$

where Con is the count of concordant pairs and Dis the count of discordant pairs across all possible individual comparisons (Goodman & Kruskal, 1954). Tied pairs, individuals sharing the same score in either dentition, are excluded. Gamma (γ) is a measure of ordinal association ranging from -1.0 to +1.0. A positive value indicates that individuals who score higher on the deciduous version of a trait tend to score higher on the permanent version of the same trait, while a negative value indicates an inverse relationship. A value of 0 indicates no association between the two scores. The magnitude of gamma reflects the proportion of concordant pairs minus the proportion of discordant pairs among all pairs of individuals who can be ranked differently on at least one variable. Statistical significance was assessed using the standard ASE-based z-test at $\alpha = .05$, two-tailed (Edgar & Lease, 2007). The asymptotic standard error (ASE) quantifies the precision of the gamma estimate: larger ASE values indicate greater uncertainty around the coefficient, typically reflecting smaller effective sample sizes after tied pairs are excluded. The z-statistic is the ratio of the gamma coefficient to its ASE ($z = \gamma / ASE$) and indicates how many standard deviations the

observed gamma falls from zero. A z-value greater than 1.96 or less than -1.96 corresponds to statistical significance at the two-tailed $\alpha = 0.05$ threshold. The associated p-value reflects the probability of obtaining a gamma coefficient as large as or larger than the observed value if the true association between deciduous and permanent trait expression were zero. Values below 0.05 are interpreted as statistically significant, indicating that the observed correspondence between the two dentitions is unlikely to reflect chance variation in the sample.

Tetrachoric correlation ($rTet$) estimated the latent continuous liability correlation underlying two observed binary variables, assuming a single normal threshold for each (Brown, 1977). Ordinal trait scores were dichotomized at the standard ASUDAS presence/absence breakpoints documented in Table 1. Tetrachoric correlation ranged from -1.0 to +1.0. A positive value indicated that individuals scored as present on the deciduous version of a trait tended to be scored as present on the permanent version of the same trait, while a negative value indicated the inverse relationship. A value of 0 indicated no association between the two binary classifications. Unlike gamma, tetrachoric correlation works on dichotomized data and estimates the underlying continuous correlation and reflects the latent liability correspondence between dentitions rather than the ordinal ranking correspondence. The asymptotic standard error (ASE) quantified the precision of each estimate; larger ASE values indicated greater uncertainty, typically associated with uneven cell distributions or small effective sample sizes. The z-statistic was the ratio of $rTet$ to its ASE and indicated how many standard errors the observed coefficient fell from zero. A z-value greater than 1.96 or less than -1.96 corresponded to statistical significance at the two-tailed $\alpha = .05$ threshold. The associated p-value reflected the probability of obtaining a tetrachoric coefficient as large as or larger than the observed value if the true latent correlation between

deciduous and permanent trait expression were zero, values below .05 were interpreted as statistically significant.

Spearman's rank correlation (r_s) is the counterpart to the Pearson correlation that is computed on ranked rather than raw scores, with tied observations receiving average ranks (Spearman's, 1904). Spearman's rank correlation ranged from -1.0 to +1.0. A positive value indicated that individuals who ranked higher in deciduous trait expression tended to rank higher in permanent trait expression, while a negative value indicated the inverse relationship. A value of 0 indicated no rank-order association between the two dentitions. Unlike gamma, Spearman's included all individuals in the analysis. Individuals scoring grade 0 in both dentitions received tied low ranks rather than being excluded, making the Spearman correlation sensitive to co-absence correspondence in traits with low expression frequency. This distinction was particularly relevant for rare accessory cusp traits where a substantial proportion of the sample scored absent in both dentitions. The use of a common ASUDAS ordinal scale for both dentitions made Spearman's applicable without scale conversion. The t-statistic indicated how many standard deviations the observed coefficient fell from zero under the null hypothesis of no association; a t-score exceeding the critical value at the two-tailed $\alpha = .05$ threshold was interpreted as statistically significant. The associated p-value reflects the probability of obtaining a Spearman's coefficient as large as or larger than the observed value if the true rank-order association between deciduous and permanent trait expression were zero. P-values below .05 were interpreted as statistically significant, indicating that the observed rank correspondence between the two dentitions was unlikely to reflect chance variation in the sample.

3.7 Null and Alternative Results in Context

The null hypothesis for each trait pair is that deciduous and permanent expressions are statistically independent within individuals: an individual's deciduous score carries no predictive information

about their permanent score for the same trait. What that null looks like in practice differs across the three tests.

For Goodman-Kruskal's gamma, a null result takes the form of a coefficient near zero with a z-statistic below ± 1.96 , indicating that concordant and discordant pairs are roughly balanced. Because gamma excludes tied pairs from its computation, large asymptotic standard errors are a meaningful diagnostic, they reflect a small effective sample after ties are removed rather than a true absence of association. A nonsignificant gamma should be read alongside the number of untied pairs contributing to the estimate, since the two are not equivalent.

For tetrachoric correlation, the null produces a coefficient near zero with a standard error large enough that the z-statistic falls below the significance threshold. For traits flagged in Section 3.5 as near-monomorphic in one or both dentitions, tetrachoric correlation was unable to be calculated since the contingency table lacks the variation needed to estimate a nonzero coefficient regardless of the true underlying relationship. Those results are retained for the tables but treated as uninformative rather than as evidence against correspondence.

Spearman's rank correlation presents the most demanding null condition. Because it includes all individuals rather than excluding tied pairs, it is sensitive to co-absence as well as to gradation in expression. For rare traits where a large proportion of the sample scores are absent in both dentitions, a near-zero Spearman coefficient would indicate that even systematic co-absence is insufficient to produce a detectable rank-order signal, a standard gamma cannot evaluate for those same traits. This makes Spearman's a genuinely independent test rather than simply a more conservative version of gamma.

Across all three tests, the null predicts not just nonsignificant individual coefficients but the absence of any consistent directional tendency. Convergent null results across all three carry

more evidential weight than any single nonsignificant result on its own. Diverging results are also meaningful: a significant Spearman's result alongside a nonsignificant gamma, for instance, would indicate that correspondence is driven by co-absence rather than gradation in expression, which has implications for how the biological signal should be understood.

The *a priori* developmental predictions reviewed in Chapter II, that canine field traits and early-forming molar characters such as Carabelli's cusp and hypocone should show stronger correspondence than late-forming accessory cusps, meaning that the null is not expected to hold across all 22 trait pairs. The larger question is whether the pattern of rejections tracks those predictions.

CHAPTER IV: RESULTS

4.1 Sample and Trait Frequency Descriptions

Trait-level sample sizes and expression frequencies at the selected breakpoints are reported in Table 2, where ‘Higher’ is the proportion of individuals scoring higher in the permanent than the deciduous dentition, and ‘Same’ is the proportion with equal expression across dentitions.

Table 2. Score frequencies for each trait by dentition.

Trait	Dentition	0	1	2	3	4	5	6	7	Higher (P>D)	Same (P=D)	N
Carabelli's Cusp (dm2/M1)	D	0.15	0.22		0.02	0.30	0.15	0.04	0.11	0.37	0.33	46
	P	0.15	0.33	0.02	0.02	0.13	0.17	0.11	0.07	0.30		
Hypocone (dm2/M1)	D				0.35	0.57	0.09			0.04	0.43	46
	P	0.02			0.15	0.37	0.43	0.02		0.52		
Metacone (dm2/M1)	D				0.02	0.04	0.57	0.37		0.15	0.48	46
	P					0.02	0.41	0.57		0.37		
Metaconule (dm2/M1)	D	0.63	0.37							0.24	0.52	46
	P	0.63	0.37							0.24		
Parastyle (dm2/M1)	D	0.98		0.02						0.02	0.98	46
	P	1.00										
Deflecting Wrinkle (dm2/M1)	D	0.51	0.35	0.08	0.05					0.46	0.51	37
	P	0.95	0.05							0.03		
Mid-Trigonid Crest (dm2/M1)	D	0.97	0.03							0.03	0.95	38
	P	0.97	0.03							0.03		
Hypoconulid (dm2/M1)	D	0.02			0.12	0.42	0.44			0.70	0.23	43
	P	0.21		0.07	0.35	0.28	0.09			0.07		

Trait	Dentition	0	1	2	3	4	5	6	7	Higher (P>D)	Same (P=D)	N
Entoconulid (dm2/M1)	D	0.98					0.02			0.02	0.95	43
	P	0.98	0.02							0.02		
Winging (di1/I1)	D	0.80	0.09	0.07		0.04				0.11	0.65	46
	P	0.76				0.24				0.24		
Labial Convexity (di1/I1)	D	0.17	0.35	0.37	0.09	0.02				0.54	0.37	46
	P	0.50	0.35	0.13	0.02					0.09		
Shoveling (di1/I1)	D	0.33	0.35	0.26	0.04	0.02				0.11	0.41	46
	P	0.09	0.41	0.24	0.17	0.07	0.02			0.48		
Shoveling (di2/I2)	D	0.28	0.21	0.35	0.12	0.05				0.23	0.33	43
	P	0.16	0.23	0.28	0.14	0.12	0.05	0.02		0.44		
Shoveling (dc/C)	D	0.38	0.33	0.15	0.08	0.03	0.03			0.38	0.46	39
	P	0.64	0.21	0.08	0.08					0.15		
Tuberculum Dentale (di1/I1)	D	0.98	0.02								0.30	46
	P	0.30	0.24	0.17	0.15	0.04	0.07	0.02		0.70		
Tuberculum Dentale (di2/I2)	D	0.90	0.02		0.02		0.05			0.02	0.31	42
	P	0.33	0.19	0.07	0.10		0.17	0.14		0.67		
Canine Mesial Ridge (dc/C)	D	0.40	0.43	0.17						0.10	0.55	42
	P	0.31	0.33	0.36						0.36		
Canine	D	0.56	0.34	0.10						0.05	0.05	41
Distal	P	0.07	0.17	0.29	0.29	0.17				0.90		
Accessory Ridge (dc/C)												
	D	0.93	0.07							0.07	0.91	44

Trait	Dentition	0	1	2	3	4	5	6	7	Higher r (P>D)	Same (P=D)	N
Mandibular	P	0.98	0.02							0.02		
Shoveling (di1/I1)												
Mandibular	D	0.86	0.14							0.11	0.89	44
Shoveling (di2/I2)	P	0.98	0.02									
Mandibular	D	0.89	0.07	0.02	0.02					0.09	0.86	44
Shoveling (dc/C)	P	0.93	0.05		0.02					0.05		
Mandibular	D	0.48	0.33	0.19						0.31	0.43	42
canine distal accessory ridge (dc/C)	P	0.55	0.29	0.14	0.02					0.26		

(D = deciduous, P = permanent). Higher = proportion scoring higher in permanent than deciduous dentition. Same = proportion with equal expression. N = number of complete deciduous-permanent pairs. (Modeled from Edgar & Lease, 2007)

Two aspects of the sample influence interpretation of the correlation statistics and are worth noting at the beginning. First, the overall sample size of 46 is comparable to Edgar & Lease (2007; N = 54) and is adequate for detecting moderate-to-strong correlations for commonly expressed traits, but statistical power is limited when expression frequencies are very low or very high in either dentition. When fewer than 10 individuals express a trait above the breakpoint, there is

insufficient distributional spread to detect even moderate correlations reliably. Second, gamma's exclusion of tied pairs further reduces effective sample size for rare traits; for the trait pairs where expression frequency falls below or equal to 3% in at least one dentition (cusp 6, mid-trigonid crest, tuberculum dentale, mandibular shoveling, and parastyle) the number of concordant or discordant pairs available to gamma after tie exclusion can be as low as one. Correlation estimates for these traits are not used to draw inferential conclusions but are reported where they illustrate observable trends in the data.

4.2 Goodman-Kruskal's Gamma Results

Goodman-Kruskal's gamma is applied here as the primary test of Research Question 1 because it is designed for ordinal data and evaluates the direction and strength of association between deciduous and permanent trait scores using the full ordinal scale rather than a binary dichotomy. A significant positive gamma for a given trait pair would indicate that individuals with higher deciduous expression tend to show higher permanent expression, providing direct ordinal evidence of within-individual correspondence. Under Research Question 2, the PCM and field theory predict that this correspondence should be strongest for early-forming characters, particularly Carabelli's cusp, hypocone, and the canine traits, and weakest or absent for late-forming accessory cusps.

Two of the 22 trait pairs yielded statistically significant positive gamma correlations ($p < .05$): canine mesial ridge (dc/C) ($\gamma = 0.817$, $ASE = 0.186$, $z = 4.393$, $p < .001$) and hypocone (dm2/M1) ($\gamma = 0.704$, $ASE = 0.239$, $z = 2.946$, $p = .003$). Four additional trait pairs produced boundary values of $\gamma = \pm 1.000$, for which the asymptotic standard error is undefined and significance cannot be tested: tuberculum dentale (di1/I1) and mandibular shoveling (di2/I2) produced perfect positive concordance ($\gamma = 1.000$), while mid-trigonid crest (dm2/M1) and mandibular shoveling (di1/I1) produced perfect negative concordance ($\gamma = -1.000$). These four

pairs are excluded from the count of significant results. Carabelli's cusp (dm2/M1) approached but did not reach significance ($\gamma = 0.421$, $p = .070$). The remaining estimable trait pairs were non-significant. Full results are provided in Table 3 and displayed in Figure 3.

Table 3. Goodman-Kruskal's Gamma (γ) results

Trait	N	γ	ASE	z	p
Maxillary Molar (dm2/M1)					
Carabelli's cusp (dm2/M1)	46	0.421	0.232	1.814	0.070
Hypocone (dm2/M1)*	46	0.704	0.239	2.944	0.003*
Metacone (dm2/M1)	46	0.279	0.380	0.734	0.463
Metaconule (dm2/M1)	46	-0.057	0.447	-0.127	0.899
Parastyle (dm2/M1)	46	—	—	—	—
Mandibular Molar (dm2/M1)					
Deflecting wrinkle (dm2/M1)	37	-0.100	0.957	-0.104	0.917
Mid-trigonid crest (dm2/M1)	38	-1.000 †	N/A	N/A	N/A
Hypoconulid (dm2/M1)	43	0.318	0.301	1.056	0.291
Entoconulid (dm2/M1)	43	-1.000†	N/A	N/A	N/A
Maxillary Anterior					
Winging (di1/I1)	46	0.500	0.448	1.116	0.264
Labial convexity (di1/I1)	46	0.350	0.292	1.199	0.231
Shoveling (di1/I1)	46	0.417	0.258	1.617	0.106
Shoveling (di2/I2)	43	0.228	0.267	0.854	0.393
Tuberculum dentale (di1/I1)	46	1.000†	N/A	N/A	N/A

Trait	N	γ	ASE	z	p
Tuberculum dentale (di2/I2)	42	0.504	0.493	1.022	0.307
Canine mesial ridge (dc/C)*	42	0.817	0.186	4.392	<.001*
Canine distal accessory ridge (dc/C)	41	0.264	0.319	0.828	0.408
Shoveling (dc/C)	39	0.438	0.315	1.392	0.164
Mandibular Anterior					
Mandibular shoveling (di1/I1)	44	-1.000†	N/A	N/A	N/A
Mandibular shoveling (di2/I2)	44	1.000†	N/A	N/A	N/A
Mandibular shoveling (dc/C)	44	0.686	0.676	1.015	0.310
Mandibular canine distal accessory ridge (dc/C)	42	0.282	0.337	0.838	0.402

Significant results ($p < .05$) are shown in bold and marked with an asterisk (*). N = complete deciduous-permanent pairs. ASE = asymptotic standard error. N/A = value not computable. — = test not run (monomorphic or tetrachoric only).

† $\gamma = \pm 1.000$; ASE undefined. Not counted among significant results

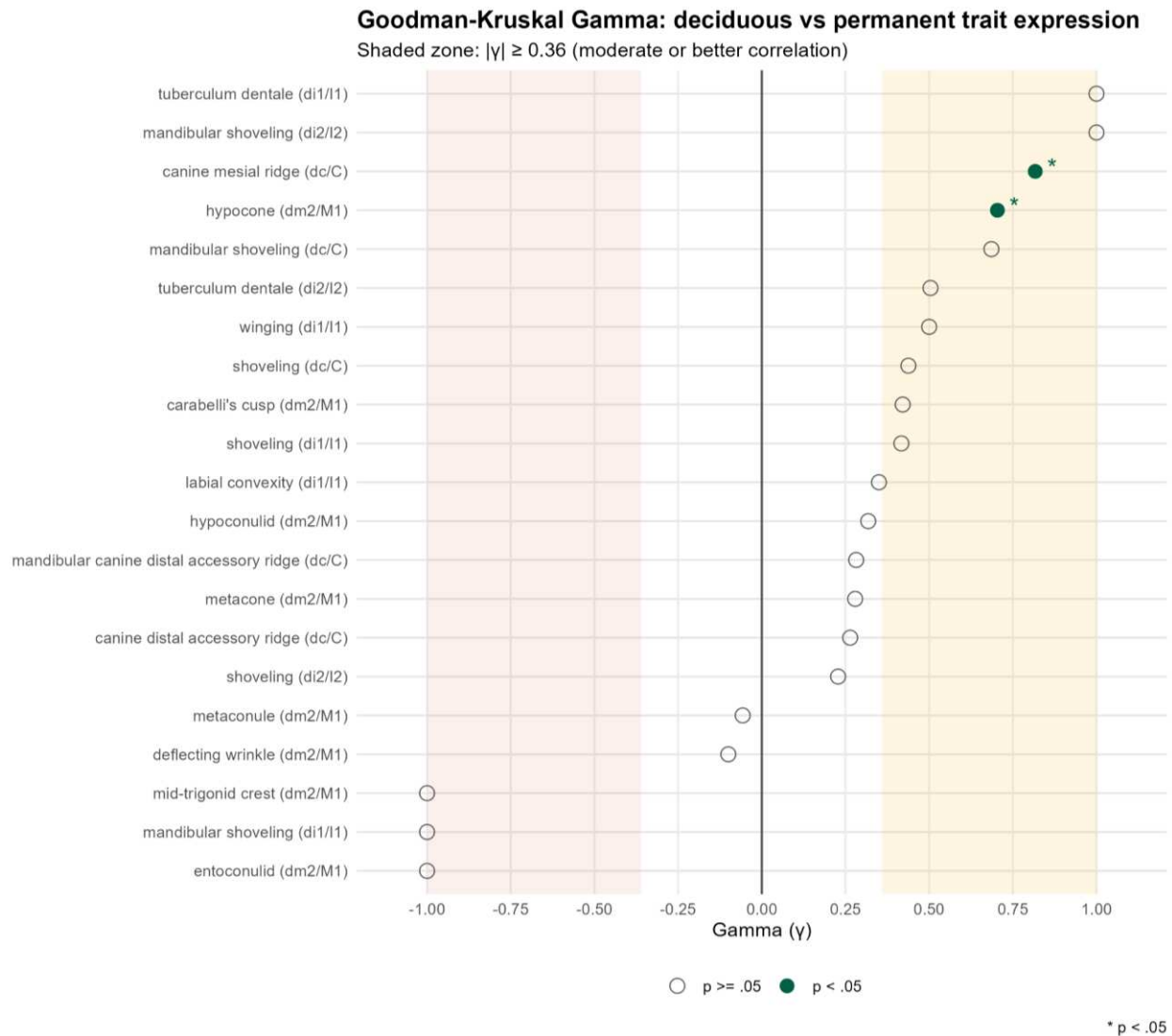


Figure 3. Goodman-Kruskal's Gamma (γ) for all 22 deciduous-permanent trait pairs, sorted by magnitude. Shaded zone indicates $|\gamma| \geq 0.36$ (moderate or better correlation). Filled points = $p < .05$; open points = $p \geq .05$. Traits with $\gamma = \pm 1.000$ are plotted but non-testable due to undefined ASE; see text.

4.2.1 Molar Traits

Among maxillary molar traits, hypocone (dm2/M1) produced the only significant result ($\gamma = 0.704$, $p = .003$). Carabelli's cusp (dm2/M1) produced a positive but non-significant estimate ($\gamma = 0.421$, $p = .070$). Metacone ($\gamma = 0.279$) and metaconule ($\gamma = -0.057$) were non-significant, and parastyle was monomorphic across the sample and could not be tested.

Among mandibular molar traits, all four were non-significant. Deflecting wrinkle ($\gamma = -0.100$) and hypoconulid ($\gamma = 0.318$) were weakly positive, while entoconulid and mid-trigonid crest each produced $\gamma = -1.000$, which was non-testable because the ASE is undefined. Both traits had expression frequencies of approximately 2% in each dentition (Table 3), meaning only one or two individuals expressed each trait at all. In both cases the individual expressing deciduously differed from the individual expressing permanently, generating a perfectly discordant arrangement in the two-by-two scoring table. Given sample sizes this small, these extreme negative values reflect the absence of overlap between individuals expressing the trait rather than a biologically meaningful inversion, and cannot be interpreted as evidence of developmental antagonism.

4.2.2 Anterior Traits

Among anterior traits, canine mesial ridge (dc/C) produced the only statistically significant result in the dataset ($\gamma = 0.817$, $p < .001$). The remaining anterior trait pairs were non-significant, with positive gamma values ranging from near zero up to 0.686 for mandibular shoveling (dc/C), and mildly positive values for the incisor traits.

Three anterior trait pairs produced boundary gamma values that could not be significance-tested. Tuberculum dentale (di1/I1) and mandibular shoveling (di2/I2) each produced $\gamma = 1.000$. For tuberculum dentale (di1/I1), no individual reached the formal presence threshold deciduously (0.0% at the grade-2 breakpoint; Table 3), while 46.0% expressed permanently; the gamma value reflects concordance across a very narrow ordinal range and carries limited interpretive weight. Mandibular shoveling (di1/I1) produced $\gamma = -1.000$ for the same structural reason as entoconulid and mid-trigonid crest: a single deciduous expresser who did not express permanently, with no permanent expressers in the sample, generating a perfectly discordant cell arrangement that precludes significance testing.

4.3 Tetrachoric Correlation Results

Tetrachoric correlation is applied as a complementary test to gamma, operating on the dichotomized presence/absence version of each trait rather than the full ordinal scale. Where gamma asks whether the rank ordering of deciduous scores predicts the rank ordering of permanent scores, tetrachoric correlation asks whether individuals who express a trait above the breakpoint in one dentition are more likely to do so in the other. A significant positive tetrachoric correlation would corroborate the gamma finding and add a second line of evidence for a trait's significance. Convergence between the two tests for the same trait pair would strengthen the case that the correspondence reflects genuine biological signals rather than an artifact of scale choice.

Three tetrachoric correlations reached statistical significance ($p < .05$) in this dataset. Estimation was not possible for 5 of the 22 trait pairs (Table 4). Estimation failure was the result of two distinct situations. The first involved traits where the expression frequency was 0% or 100% at the dichotomization breakpoint in one or both dentitions (hypocone, metacone, tuberculum dentale di1/I1, and mandibular shoveling di1/I1 and di2/I2), leaving a row or column of the 2×2 table empty. The second involved traits where low expression frequency in both dentitions produced too few observations in one or more cells for stable estimation. Among the 17 estimable pairs, the direction of tetrachoric estimates was broadly consistent with gamma and Spearman's results.

The largest positive estimates were obtained for canine mesial ridge (dc/C) ($r_{Tet} = 0.723$), Carabelli's cusp (dm2/M1) ($r_{Tet} = 0.531$), and shoveling (di1/I1) ($r_{Tet} = 0.510$), all directionally consistent with their significant Spearman's results. Five traits produced negative tetrachoric estimates: hypoconulid ($r_{Tet} = -0.826$), mid-trigonid crest ($r_{Tet} = -0.620$), entoconulid ($r_{Tet} = -0.606$), canine distal accessory ridge ($r_{Tet} = -0.367$), and metaconule ($r_{Tet} = -0.112$), also consistent with their gamma values. Mandibular shoveling (dc/C) produced $r_{Tet} = 1.000$, reflecting

near-complete concentration of observations in the "absent in both dentitions" cell of the 2×2 table rather than a biologically meaningful correlation; with so few expressers, any agreement among them produces a boundary estimate. The failure of tetrachoric correlation to reach significance for most traits could reflect the constraints of low expression frequencies in this sample rather than an absence of directional association. Full results are provided in Table 4.

Table 4. Tetrachoric correlation (rTet) results.

Trait	N	rTet	p
Maxillary Molar (dm2/M1)			
Carabelli's cusp (dm2/M1)*	46	0.531	0.187*
Hypocone (dm2/M1)	46	N/A	N/A
Metacone (dm2/M1)	46	N/A	N/A
Metaconule (dm2/M1)	46	−0.043	−0.043
Parastyle (dm2/M1)	46	—	—
Mandibular Molar (dm2/M1)			
Deflecting wrinkle (dm2/M1)	37	0.017	0.425
Mid-trigonid crest (dm2/M1)	38	−0.632	11.431
Hypoconulid (dm2/M1)	43	−0.881	92.485
Entoconulid (dm2/M1)	43	−0.617	11.736
Maxillary Anterior			
Winging (di1/I1)	46	0.411	0.245
Labial convexity (di1/I1)	46	0.212	0.265
Shoveling (di1/I1)*	46	0.51	0.195*
Shoveling (di2/I2)	43	0.397	0.215

Trait	N	rTet	p
Tuberculum dentale (di1/I1)	46	N/A	N/A
Tuberculum dentale (di2/I2)	42	0.251	0.352
Canine mesial ridge (dc/C)*	42	0.723	0.151*
Canine distal accessory ridge (dc/C)	41	-0.393	0.309
Shoveling (dc/C)	39	0.375	0.282
Mandibular Anterior			
Mandibular shoveling (di1/I1)	44	N/A	N/A
Mandibular shoveling (di2/I2)	44	N/A	N/A
Mandibular shoveling (dc/C)	44	1.000†	—
Mandibular canine distal accessory ridge (dc/C)	42	0.478	0.260

Significant results ($p < .05$) are marked with an asterisk (*). ASE was non-estimable for all computed values. N/A = non-estimable due to empty or sparse cells. — = test not applicable (monomorphic in raw scores).

† $r_{Tet} = 1.000$ is a boundary estimate arising from near-complete concentration of observations in the co-absent cell; standard error is undefined (Inf) and the value should not be interpreted as a strong positive correlation.

4.4 Spearman's Rank Correlation Results

Spearman's rank correlation provides a third, non-parametric measure of ordinal association that differs from gamma in one analytically important respect: unlike gamma, it does not exclude individuals who score grade zero in both dentitions. In a sample where many traits have low expression frequencies, a test like this one is capable of analyzing more of the sample. A significant Spearman's result where gamma is non-significant does not necessarily mean stronger biological

correspondence. It may instead reflect the contribution of co-absent pairs to the rank-based concordance. Interpreting the two tests together allows the source of any correspondence signal to be identified, whether driven by variation among expressers or by the weight of shared absence, which is directly relevant to evaluating the strength and nature of the correspondences bearing on Research Questions 1 and 2.

Six of the 22 trait pairs yielded statistically significant Spearman's rank correlations ($p < .05$): canine mesial ridge (dc/C) ($r_s = 0.635$, $p < .001$), hypocone (dm2/M1) ($r_s = 0.489$, $p = .001$), Carabelli's cusp (dm2/M1) ($r_s = 0.427$, $p = .003$), mandibular shoveling (di2/I2) ($r_s = 0.384$, $p = .010$) (interpreted as a co-absence artifact in Section 5.2), shoveling (di1/I1) ($r_s = 0.346$, $p = .018$), and shoveling (dc/C) ($r_s = 0.329$, $p = .041$). Full results are provided in Table 5.

Table 5. Spearman rank correlation (r_s) results.

Trait	N	r_s	p
Maxillary Molar (dm2/M1)			
Carabelli's cusp (dm2/M1)*	46	0.427	.003*
Hypocone (dm2/M1)*	46	0.489	.001*
Metacone (dm2/M1)	46	0.154	.307
Metaconule (dm2/M1)	46	-0.026	0.862
Parastyle (dm2/M1)	46	—	—
Mandibular Molar (dm2/M1)			
Deflecting wrinkle (dm2/M1)	37	-0.025	0.885
Mid-trigonid crest (dm2/M1)	38	-0.027	0.872
Hypoconulid (dm2/M1)	43	0.249	0.107

Trait	N	rs	p
Entoconulid (dm2/M1)	43	−0.024	0.880
Maxillary Anterior			
Winging (di1/I1)	46	0.239	0.110
Labial convexity (di1/I1)	46	0.277	0.063
Shoveling (di1/I1)*	46	0.346	0.018*
Shoveling (di2/I2)	43	0.222	0.153
Tuberculum dentale (di1/I1)	46	0.259	0.082
Tuberculum dentale (di2/I2)	42	0.221	0.161
Canine mesial ridge (dc/C)*	42	0.635	<.001*
Canine distal accessory ridge (dc/C)	41	0.202	0.206
Shoveling (dc/C)*	39	0.329	0.041*
Mandibular Anterior			
Mandibular shoveling (di1/I1)	44	−0.041	0.790
Mandibular shoveling (di2/I2)*	44	0.384	0.010*
Mandibular shoveling (dc/C)	44	0.227	0.139
Mandibular canine distal accessory ridge (dc/C)	42	0.197	0.212

Significant results ($p < .05$) are shown in bold and marked with an asterisk (). — = test not run.*

Note: Parastyle (dm2/M1) was monomorphic in raw scores and excluded. Hypoconulid and Entoconulid values to be updated upon analysis completion.

4.4.1 Molar Traits

Among molar traits, the Spearman's results corroborate the Goodman-Kruskal's gamma findings: hypocone ($rs = 0.489$, $p = 0.001$) and Carabelli's cusp ($rs = 0.427$, $p = 0.003$) were both significant.

The remaining molar pairs were non-significant. Entoconulid ($r_s = -0.031$) and mid-trigonid crest ($r_s = -0.024$) were both near zero, confirming that the extreme negative gamma values for these traits reflect a handful of discordant individuals rather than any dataset-wide negative trend.

4.4.2 Anterior Traits

Among anterior traits, canine mesial ridge (dc/C) produced the strongest Spearman's correlation in the dataset ($r_s = 0.635$, $p < .001$) and mandibular shoveling (di2/I2) was also significant ($r_s = 0.384$, $p = .010$), both corroborating their gamma results. Two additional traits were significant with Spearman's but not with gamma: shoveling (di1/I1) ($r_s = 0.346$, $p = .018$) and shoveling (dc/C) ($r_s = 0.329$, $p = .041$). For both traits, gamma produced positive but non-significant estimates ($\gamma = 0.417$ and 0.438 , respectively). The discrepancy arises because deciduous shoveling frequency in this sample was below 35% for upper incisors and below 27% for the canine (Table 2), which means the majority of individuals score grade 0 deciduously. The discrepancy arises not from a power deficit but from a structural feature of gamma: co-absent pairs (individuals scoring grade 0 in both dentitions) are excluded by definition from the calculation, as gamma is computed solely from concordant and discordant ordinal pairs. When the majority of individuals in the sample score absent deciduously, gamma is effectively computed on a small residual subset, whereas Spearman's incorporates the full rank distribution including those co-absent observations. Spearman incorporates them as concordant observations and reaches significance. The remaining anterior traits showed non-significant Spearman's results, with most producing positive estimates below 0.25.

4.5 Cross-Method Comparison

Table 6 and Figure 5 summarize results across all three tests. Four trait pairs were significant on at least two tests. Canine mesial ridge (dc/C) was the only trait significant on all three ($\gamma = 0.817$, $r_{Tet} = 0.723$, $r_s = 0.635$). Carabelli's cusp (dm2/M1) was significant on tetrachoric and Spearman's

($r_{Tet} = 0.531$, $r_s = 0.427$). Hypocone (dm2/M1) was significant on gamma and Spearman's ($\gamma = 0.704$, $r_s = 0.489$). Shoveling (di1/I1) was significant on tetrachoric and Spearman's ($r_{Tet} = 0.510$, $r_s = 0.346$). Two traits were significant on Spearman's only: shoveling (dc/C) ($r_s = 0.329$) and mandibular shoveling (di2/I2) ($r_s = 0.384$). No traits were significant on gamma or tetrachoric alone.

Figure 4 plots the gamma coefficient against the Spearman's correlation for each of the 22 trait pairs, with a dashed diagonal representing perfect 1:1 agreement. Points are color-coded by significance outcome: blue indicates agreement between methods (either both significant or both non-significant) and orange indicates a disagreement. Gamma values systematically exceed Spearman's correlations across the dataset, with the large majority of points falling above the diagonal. This reflects gamma's restriction to expressing individuals only: by excluding tied pairs who scored grade zero in both dentitions, gamma is computed on a smaller, positively selected subset, which inflates its estimates relative to Spearman's. The three orange points, shoveling (di1/I1), shoveling (dc/C), and mandibular shoveling (di2/I2), fall near the diagonal, meaning the two methods returned numerically similar values yet only Spearman's reached significance. This occurs because the majority of individuals scored grade zero deciduously for those traits: co-absent pairs excluded from gamma are treated by Spearman's as concordant tied ranks, pushing its correlation across the threshold. The four traits yielding $\gamma = \pm 1.000$ are excluded from the plot; those extreme gamma estimates carry no interpretable signal and illustrate how gamma can produce extreme values from very small numbers of pairs when a trait is rare.

Figure 5 displays the same results as a correlation heatmap, with each row representing one of the 22 trait pairs and each column representing one of the three statistical tests. Cell color encodes the direction and magnitude of association: dark teal indicates a strong positive

association, gold a strong negative association, and values near zero appear as pale teal or yellow; gray cells indicate the statistic was non-estimable for that trait-test combination. Asterisks mark cells where $p < 0.05$. Two patterns are immediately visible. First, Gamma column cells are consistently darker teal than the corresponding Spearman's cells, confirming the systematic upward inflation visible in Figure 4. Second, the most robustly supported traits, canine mesial ridge, hypocone, Carabelli's cusp, and shoveling (di1/I1), stand out as a cluster of consistently colored, asterisked cells, while the majority of traits show pale, non-significant values across all three tests. The gold cells for entoconulid, mid-trigonid crest, and mandibular shoveling (di1/I1) under Gamma and Tetrachoric visually underscore that those extreme values reflect the results of sparse data rather than genuine negative correspondence.

Figure 6 displays the raw grade-by-grade distributions for these four trait pairs, illustrating both the degree of ordinal correspondence and the placement of the dichotomization breakpoints relative to where individuals cluster..

Table 6. Cross-method summary for all trait pairs.

Trait	γ	rTet	rs
Maxillary Molar (dm2/M1)			
Carabelli's cusp (dm2/M1)	0.421	0.531*	0.427*
Hypocone (dm2/M1)	0.704*	N/A	0.489*
Metacone (dm2/M1)	0.279	N/A	0.154
Metaconule (dm2/M1)	-0.057	-0.043	-0.026
Parastyle (dm2/M1)	—	—	—
Mandibular Molar (dm2/M1)			

Trait	γ	rTet	rs
Deflecting wrinkle (dm2/M1)	-0.100	0.017	-0.025
Mid-trigonid crest (dm2/M1)	-1.000 †	-0.632	-0.027
Hypoconulid (dm2/M1)	0.318	-0.881	0.249
Entoconulid (dm2/M1)	-1.000 †	-0.617	-0.024
Maxillary Anterior			
Winging (di1/I1)	0.500	0.411	0.239
Labial convexity (di1/I1)	0.350	0.212	0.277
Shoveling (di1/I1)	0.417	0.510*	0.346*
Shoveling (di2/I2)	0.228	0.397	0.222
Tuberculum dentale (di1/I1)	1.000 †	N/A	0.259
Tuberculum dentale (di2/I2)	0.504	0.251	0.221
Canine mesial ridge (dc/C)	0.817*	0.723*	0.635*
Canine distal accessory ridge (dc/C)	0.264	-0.393	0.202
Shoveling (dc/C)	0.438	0.375	0.329*
Mandibular Anterior			
Mandibular shoveling (di1/I1)	-1.000 †	N/A	-0.041
Mandibular shoveling (di2/I2)	1.000 †	N/A	0.384*
Mandibular shoveling (dc/C)	0.686	1.000	0.227
Mandibular canine distal accessory ridge (dc/C)	0.282	0.478	0.197

Significant results ($p < .05$) are marked with an asterisk (*). Bold trait names indicate significance on at least one test. † = $\gamma = \pm 1.000$, significance not testable. N/A = non-estimable. — = test not run.

$\dagger \gamma = \pm 1.000$; ASE undefined. Not counted among significant results. N/A = Non-estimable. — = Monomorphic or test not applicable.

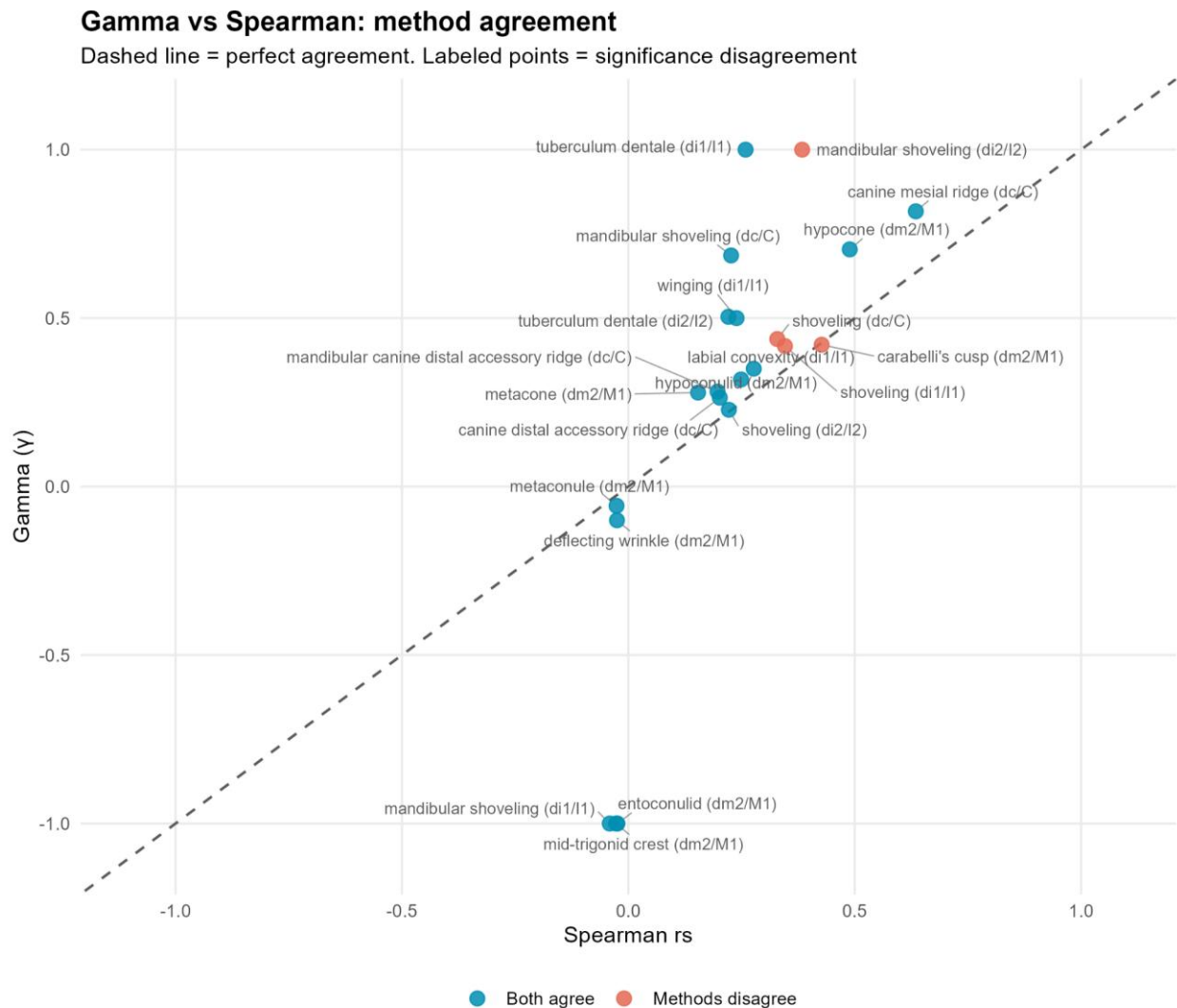


Figure 4 Gamma (γ) versus Spearman's (r_s) for all 22 trait pairs. Dashed line = 1:1 agreement. Points above the line indicate $\gamma > r_s$, reflecting gamma's restriction to expressed individuals and its exclusion of co-absent pairs; points below the line indicate $r_s > \gamma$, reflecting co-absent pairs contributing concordance to the rank correlation. Blue = methods agree on significance; orange = methods disagree.

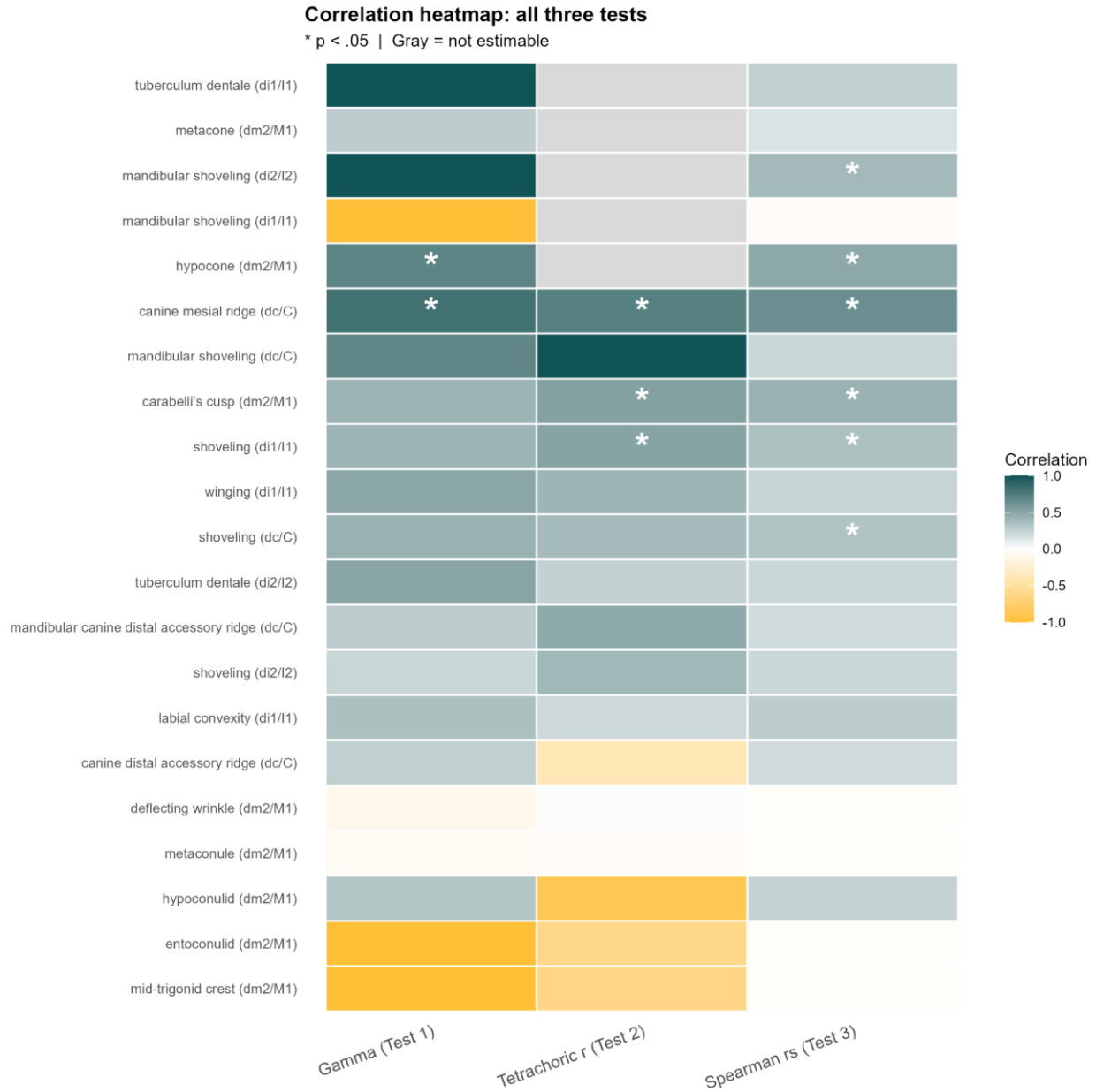


Figure 5. Correlation heatmap of Gamma (Test 1), Tetrachoric (Test 2), and Spearman's (Test 3) for all 22 deciduous-permanent trait pairs. Dark teal = strong positive correlation; gold = strong negative correlation; gray = non-estimable. * = $p < .05$.

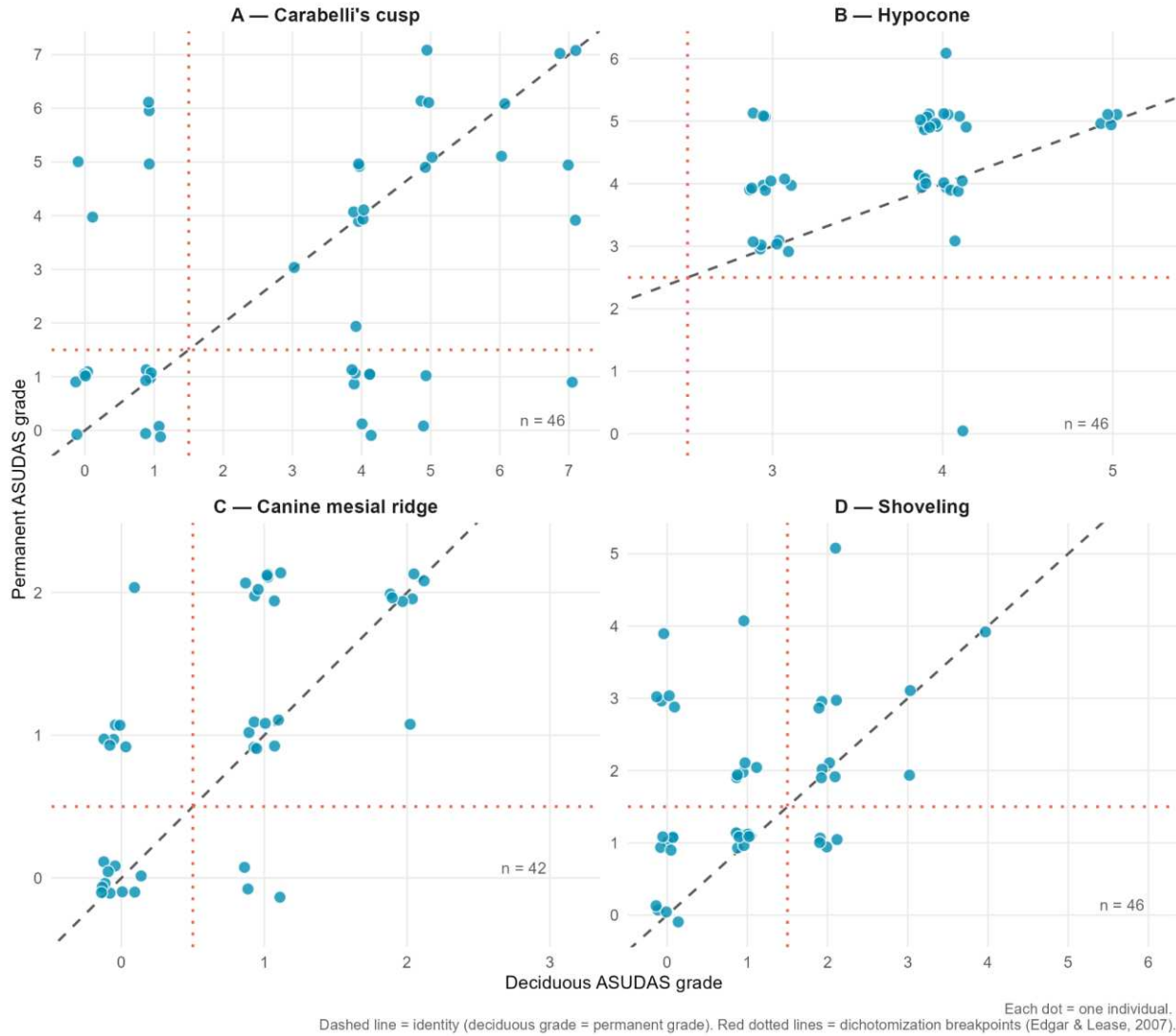


Figure 6. Raw score scatterplots for the four trait pairs with the strongest correlation estimates: (A) Carabelli's cusp $dm2/M1$ ($\gamma = 0.421$), (B) hypocone $dm2/M1$ ($\gamma = 0.704$), (C) canine mesial ridge dc/C ($\gamma = 0.817$), and (D) shoveling $di1/I1$ ($\gamma = 0.417$). Each dot represents one individual. Dashed diagonal = identity line (deciduous score = permanent score). Red dotted lines = dichotomization breakpoints following Edgar & Lease (2007). Bottom left quadrant = absent in both dentitions. Top right quadrant = present in both dentitions.

4.6 Research Questions

Across the three statistical approaches, a consistent but limited pattern of deciduous-permanent correspondence emerges from the Stucklen Collection data. The results can be organized around the two research questions introduced in Chapter I.

Research Question 1: *To what degree are the expressions of nonmetric dental morphological traits correlated between the deciduous and permanent dentitions of the same individuals?*

The degree of correspondence varies substantially by trait. Of the 22 retained trait pairs, four were robustly corroborated, meaning significant on at least two of the three tests, and can be regarded as the most reliable findings of this analysis. Canine mesial ridge (dc/C) was the single trait significant on all three methods ($\gamma = 0.817$, $r_{Tet} = 0.723$, $r_s = 0.635$), representing the strongest and most consistently supported cross-dentition association in the dataset. Hypocone (dm2/M1), Carabelli's cusp (dm2/M1), and shoveling (di1/I1) each reached significance on two tests. Two additional traits, shoveling (dc/C) and mandibular shoveling (di2/I2), were significant on Spearman's only, suggesting moderate associations that gamma's structural exclusion of co-absent pairs obscured. The remaining trait pairs produced non-significant, generally small positive correlations, with the exception of four boundary cases ($\gamma = \pm 1.000$) arising from near-monomorphic expression in at least one dentition; these are not interpretable as meaningful biological signals.

The data do not support a global or uniform pattern of cross-dentition correspondence across nonmetric dental morphology. Correspondence is trait-specific, with the most consistent associations concentrated among molar and anterior traits with high heritability and early morphogenetic timing. For most traits, the null expectation that deciduous and permanent expressions are statistically independent in this sample cannot be rejected.

Research Question 2: *Does the pattern of correspondence align with the predictions of field theory, the Patterning Cascade Model, and the genetic literature?*

A full evaluation is reserved for Chapter V, but the distribution of significant results is consistent with several developmental predictions. The traits predicted to show the strongest cross-dentition correspondence based on earlier morphogenetic onset and shared genetic pathways (namely canine mesial ridge, shoveling, and Carabelli's cusp) are the ones with the most robust statistical support. Molar traits regulated later in the patterning cascade and incisor traits with limited variance in this sample produce weaker or undetectable correlations, consistent with field theory's expectation that correspondence weakens as the morphogenetic gradient dissipates across the dental field. The overall pattern is not random but structured in ways the theoretical frameworks predicted, even if the statistical signal across the full set remains small given the sample's size and trait frequency constraints.

CHAPTER V: DISCUSSION

5.1 Research Questions

Cross-dentition correspondence in the Stucklen Collection is trait-specific (Table 7). Of the 22 trait pairs analyzed, two produced statistically significant positive gamma correlations ($p < 0.05$): canine mesial ridge (dc/C) ($\gamma = 0.817$, $p < .001$) and hypocone (dm2/M1) ($\gamma = 0.704$, $p = 0.003$). Carabelli's cusp (dm2/M1) approached but did not reach gamma significance ($\gamma = 0.421$, $p = 0.070$). Three tetrachoric correlations reached significance: canine mesial ridge ($r_{Tet} = 0.723$), Carabelli's cusp ($r_{Tet} = 0.531$), and shoveling di1/I1 ($r_{Tet} = 0.510$). Spearman's rank correlation produced six significant results: canine mesial ridge ($r_s = 0.635$, $p < 0.001$), hypocone ($r_s = 0.489$, $p < 0.001$), Carabelli's cusp ($r_s = 0.427$, $p = 0.003$), and shoveling di1/I1 ($r_s = 0.346$, $p = 0.018$). For the shoveling traits, the Spearman signal is driven by co-absence correspondence that gamma cannot detect: where the majority of individuals score grade zero in both dentitions, Spearman's incorporates these co-absent pairs as concordant observations while gamma operates on a small subset of expressers. Four trait pairs were robustly significant on two or more tests: canine mesial ridge (significant on all three), Carabelli's cusp (tetrachoric and Spearman's, with gamma approaching significance), hypocone (gamma and Spearman's), and shoveling di1/I1 (tetrachoric and Spearman's). These results are phenotypic correlations only; without genealogical data it is not possible to decompose the observed covariance into additive genetic and environmental components, and the results are interpreted as consistent with, rather than direct evidence of, shared genetic architecture.

Table 7. Summary of deciduous–permanent correlation results for all 22 trait pairs analyzed in the Stucklen Collection, with a priori predictions and hypothesis conformance.

Trait Pair	Prediction	N	Goodman's γ (p)	Tetrachoric (rTet)	Spearman (rs, p)	Conforms to Hypothesis?	Plain-Language Meaning
Maxillary Molar Traits (dm2 / M1)							
Carabelli's cusp (dm2/M1)	Strong	46	$\gamma = 0.421$, p = .070	rTet = 0.531*	rs = 0.427*	Partial	Individuals who express Carabelli's cusp on their deciduous molar tend to express it on their permanent molar. Two of three tests reach significance and gamma narrowly misses the threshold, making this the most consistently supported finding in the dataset and consistent with Carabelli's cusp's status as an early-forming trait with a strong shared developmental basis.
Hypocone (dm2/M1)	Strong	46	$\gamma = 0.704^*$	N/A	rs = 0.489*	Yes	The degree of hypocone expression tracks across dentitions: individuals with greater hypocone development on their deciduous molar tend to show greater development on their permanent molar. This confirms the prediction that early-forming primary cusp complex traits show the strongest cross-dentition correspondence.
Metacone (dm2/M1)	Moderate	46	$\gamma = 0.279$, p = .463	N/A	rs = 0.154, p = .307	Yes	No significant correspondence is detected. Although the metacone is a primary cusp, it shows little size variation in modern humans, which reduces the variance available to detect correspondence. The null result does not clearly contradict theoretical predictions.

Trait Pair	Prediction	N	Goodman's γ (p)	Tetrachoric (rTet)	Spearman (rs, p)	Conforms to Hypothesis?	Plain-Language Meaning
Cusp 5 (dm2/M1)	Weak	46	$\gamma = -0.057$, p = .899	$r_{Tet} = -0.043$	$r_s = -0.026$, p = .862	Yes	No significant correspondence is detected on any test, consistent with the prediction that late-forming accessory cusps are most sensitive to geometric divergence between dm2 and M1 and least likely to show cross-dentition correspondence.
Parastyle (dm2/M1)	Weak	46	Non-estimable	Non-estimable	Non-estimable	N/A	Near-zero expression in this sample makes stable statistical estimation impossible. The result is uninformative about correspondence but does not contradict theoretical predictions.
Deflecting wrinkle (dm2/M1)	Weak	37	$\gamma = -0.100$, p = .917	$r_{Tet} = 0.017$	$r_s = -0.025$, p = .885	Yes	No significant correspondence is detected, consistent with predictions for a late-forming accessory ridge whose expression depends heavily on downstream intercusp geometry that diverges between dm2 and M1.
Mid-trigonid crest (dm2/M1)	Weak	38	Extreme ($\gamma = -1.0$)	$r_{Tet} = -0.632$	$r_s = -0.027$, p = .872	Yes	The extreme gamma value is a statistical artifact produced by near-zero expression collapsing the contingency table. The more reliable Spearman result is non-significant. No interpretable correspondence is detected, consistent with theoretical predictions.
Cusp 5 mandibular (dm2/M1)	Weak	43	$\gamma = 0.318$, p = .291	$r_{Tet} = -0.881$ (unstable)	$r_s = 0.249$, p = .107	Yes	No significant correspondence is detected. The tetrachoric estimate is highly unstable due to a near-singular contingency table and is uninformative. The Spearman result, while non-significant, is directionally positive. The overall pattern is consistent with the weak correspondence predicted for late-forming accessory cusps.

Trait Pair	Prediction	N	Goodman's γ (p)	Tetrachoric (rTet)	Spearman (rs, p)	Conforms to Hypothesis?	Plain-Language Meaning
Cusp 6 (dm2/M1)	Weak	43	Extreme ($\gamma = -1.0$)	$r_{Tet} = -0.617$ (unstable)	$r_s = -0.024$, $p = .880$	Yes	The extreme gamma value is a statistical artifact from near-zero expression; the Spearman result is non-significant. No correspondence is detected, consistent with the prediction that late-forming accessory cusps show the weakest cross-dentition signal.
Maxillary Incisor Traits (di1 / I1 and di2 / I2)							
Winging (di1/I1)	Moderate	46	$\gamma = 0.500$, $p = .264$	$r_{Tet} = 0.411$	$r_s = 0.239$, $p = .110$	No	No test reaches significance despite a moderately sized gamma estimate. The null result may reflect limited statistical power rather than a genuine absence of correspondence, but no positive conclusion can be drawn from this sample.
Labial curve (di1/I1)	Moderate	46	$\gamma = 0.350$, $p = .231$	$r_{Tet} = 0.212$	$r_s = 0.277$, $p = .063$	No	No test reaches significance, though Spearman approaches the threshold ($p = .063$). The result is inconclusive: the moderate positive estimates suggest a possible correspondence that this sample lacks the power to confirm.
Shoveling (di1/I1)	Moderate	46	$\gamma = 0.417$, $p = .106$	$r_{Tet} = 0.510^*$	$r_s = 0.346^*$	Yes	Two tests reach significance. The correspondence reflects a shared developmental tendency toward non-expression: individuals who do not express the trait on their deciduous incisor also tend not to express it on their permanent incisor, rather than matching degrees of expression among those who do express the trait.
Tuberculum dentale (di1/I1)	Moderate	46	Extreme ($\gamma = 1.0$)	Non-estimable	$r_s = 0.259$, $p = .082$	No	The extreme gamma value is a statistical artifact; the Spearman result is non-significant. The trait approaches near-universal expression in both dentitions in this sample, leaving no discriminating variation against which to detect correspondence..

Trait Pair	Prediction	N	Goodman's γ (p)	Tetrachoric (rTet)	Spearman (rs, p)	Conforms to Hypothesis?	Plain-Language Meaning
Shoveling (di2/I2)	Moderate	43	$\gamma = 0.228$, p = .393	rTet = 0.397	rs = 0.222, p = .153	No	No significant correspondence is detected. Estimates are in the expected positive direction but fall short of significance, suggesting a possible relationship that this sample cannot confirm.
Tuberculum dentale (di2/I2)	Moderate	42	$\gamma = 0.504$, p = .307	rTet = 0.251	rs = 0.221, p = .161	No	No significant correspondence is detected despite a moderately sized gamma estimate. Limited statistical power likely contributes to the null result.
Canine Traits (dc / C)							
Canine mesial ridge (dc/C)	Strong	42	$\gamma = 0.817^*$	rTet = 0.723*	rs = 0.635*	Yes	The strongest and most consistent result in the dataset, significant on all three tests. Individuals with a well-developed mesial accessory ridge on their deciduous canine reliably express a comparable feature on their permanent canine. Prior studies failed to detect this correspondence because they relied on incompatible scoring systems; unified ASUDAS scoring reveals a robust biological signal consistent with the high degree of canine field integration reported in the quantitative genetic literature.
Canine distal accessory ridge (dc/C)	Moderate	41	$\gamma = 0.264$, p = .408	rTet = -0.393	rs = 0.202, p = .206	No	No significant correspondence is detected and the tetrachoric estimate is negative, likely reflecting a scoring artifact or asymmetric expression pattern between dentitions. The distal accessory ridge does not behave like the mesial ridge despite sharing a field position.

Trait Pair	Prediction	N	Goodman's γ (p)	Tetrachoric (rTet)	Spearman (rs, p)	Conforms to Hypothesis?	Plain-Language Meaning
Canine shoveling (dc/C)	Moderate	39	$\gamma = 0.438$, p = .164	rTet = 0.375	rs = 0.329*	Partial	Only Spearman's reaches significance, and as with maxillary incisor shoveling, the signal partly reflects co-absence in the sample with low trait frequencies. The result should be interpreted cautiously.
Mandibular Incisor and Canine Traits							
Mandibular shoveling (di1/I1)	Weak	44	Extreme ($\gamma = -1.0$)	Non- estimable	rs = -0.041, p = .790	Yes	The extreme gamma value and non-estimable tetrachoric are statistical artifacts of near-zero expression in this sample. No meaningful correspondence is detected or expected.
Mandibular shoveling (di2/I2)	Weak	44	Extreme ($\gamma = 1.0$)	Non- estimable	rs = 0.384*	Partial	The extreme gamma value is a statistical artifact. The significant Spearman result reflects co-absence: the large majority of individuals show no expression in either dentition. The pattern is driven by shared non-expression rather than graded correspondence among expressers.
Mandibular shoveling (dc/C)	Moderate	44	$\gamma = 0.686$, p = .310	rTet = 1.0 (unstable)	rs = 0.227, p = .139	No	A large gamma estimate but non-significant, with a numerically perfect but highly unstable tetrachoric. Near-zero expression in this sample makes estimation unreliable across all three tests. No interpretable correspondence can be concluded.
Mandibular canine distal acc. ridge (dc/C)	Moderate	42	$\gamma = 0.282$, p = .402	rTet = 0.478	rs = 0.197, p = .212	No	No significant correspondence is detected. Estimates are in the expected positive direction but fall short of significance, likely reflecting sample size constraints.

*Statistical significance assessed at $p < .05$. * = $p < .05$. Note: Hypothesis conformance codes: Yes = result matches prediction; Partial = result partially matches prediction; No = result does not match prediction; N/A = non-estimable (insufficient expression frequency). 'Extreme' gamma values ($\gamma = \pm 1.0$) indicate statistical artifacts caused by near-zero expression frequencies and are not interpreted as meaningful correlations. Results are phenotypic only; without genealogical data, genetic and environmental contributions to the observed covariance cannot be separated.*

The pattern of correspondence partially confirms the predictions generated by field theory, the Patterning Cascade Model, and the quantitative genetic literature. Field theory predicts that trait pairs sharing the same morphogenetic field should correspond across dentitions, with the strongest signal expected between key tooth analogues such as dm2 and M1 in the molar field and deciduous and permanent canine in the canine field. The PCM adds a more specific prediction: early-forming traits associated with the primary cusp complex should show stronger correspondence than late-forming accessory cusps, whose expression is sensitive to downstream geometric differences between dm2 and M1 that accumulate through the cascade. Paul et al. (2021) provides the most directly relevant genetic prediction, when she found that approximately 70% of deciduous-permanent canine trait comparisons yielded significant genetic correlations in a pedigreed Australian sample and that shared genetic architecture underlies incisor shoveling expression across both dentitions.

The results are consistent with all three sets of predictions in their broad outlines. The two significant molar traits, Carabelli's cusp and hypocone, are both early-forming characters associated with the primary cusp complex, and they correspond as predicted. The four late-forming accessory cusp traits, cusp 5, cusp 6, mid-trigonid crest, and deflecting wrinkle, produced no significant correspondence, also as predicted. The significant result for canine mesial ridge is consistent with Paul et al. 's (2021) prediction of strong canine field cross-dentition integration, and the shoveling co-absence signal is consistent with their finding of shared genetic architecture for incisor shoveling across dentitions.

Where predictions are not confirmed, the most likely explanation is sample size and trait frequency constraints rather than a failure of developmental theory. Several trait pairs with near-zero expression frequencies in one or both dentitions produced statistically uninterpretable results

regardless of any underlying correspondence. This matters for how the non-significant results are interpreted. Field theory and the PCM make predictions about how trait expression should track across dentitions when a trait is present and variable, not about why a trait fails to appear. When nearly everyone in the sample scores absent in both dentitions, there is no variation in expression to track, and the question of correspondence cannot be tested. Shared absence neither confirms nor denies the developmental predictions, it simply falls outside their ability to predict.

The shoveling co-absence results are consistent with the strong cross-dentition genetic integration reported by Paul et al. (2021), but the nature of that signal differs fundamentally from the correspondence seen in traits like Carabelli's cusp or canine mesial ridge and requires a different interpretation. For Carabelli's cusp and canine mesial ridge, the correspondence is graded: individuals who express more of the trait deciduously also tend to express more of it permanently, meaning the signal reflects within-individual developmental tracking across tooth generations. For shoveling in this sample, there is no graded variation to track. The statistical signal picks up only the fact that individuals who score absent deciduously also score absent permanently, which is a population-level genetic signature reflecting the rarity of strong shoveling alleles in European-ancestry groups rather than evidence that any individual's degree of lingual ridge development is tracking across dentitions. The Paul et al. (2021) finding that the same genes influence shoveling expression in both dentitions is consistent with the co-absence pattern observed here, but because those genes produce little to no expression in this sample, there is no within-individual variation against which to demonstrate correspondence in the sense that developmental theory requires.

Canine shoveling (dc/C) and mandibular shoveling (di2/I2) present the same interpretive problem. For a cross-dentition correlation to carry developmental meaning, there must be actual variation in trait expression to compare across tooth generations. Two individuals who both score

zero on mandibular shoveling deciduously and permanently are not demonstrating coordinated developmental programs; they are demonstrating only that the trait did not appear, which could reflect any number of factors unrelated to how the two dentitions relate within that individual. Mandibular shoveling produced extreme gamma values ($\gamma = -1.000$ at di1/I1, $\gamma = 1.000$ at di2/I2) that are artifacts of this situation rather than biological signal, and the Spearman result for di2/I2 ($r_s = 0.384$, $p = .010$) reflects the same co-absence dynamic as maxillary shoveling. Canine shoveling (dc/C) produced only a marginal Spearman's correlation ($r_s = 0.329$, $p = .041$) with non-significant gamma and tetrachoric results, and should be treated with the same caution for the same reason.

5.2 Comparison to Other Cross-Dentition Correspondence Studies

Carabelli's cusp is the most robustly replicated finding in the cross-dentition correspondence literature. Saunders and Mayhall (1982) found significant association for Carabelli's cusp in their Burlington Growth Centre sample using chi-square. Edgar and Lease (2007) found it to be the most consistently significant trait across test formats and scale conversions in the Bolton-Brush Growth Study sample (Table 8, $\gamma = 0.68$, $r_{Tet} = 0.67$ on their original scale). Paul and Stojanowski (2017) found significant gamma under unified ASUDAS scoring in the Burlington Growth Centre. This study adds significant tetrachoric ($r_{Tet} = 0.531$) and Spearman's ($r_s = 0.427$) results in the Stucklen Collection, with gamma approaching significance ($\gamma = 0.421$, $p = .070$). Across all four independent longitudinal collections, Carabelli's cusp is the most consistently detected deciduous-permanent molar correspondence in the available literature.

Table 8. γ and tetrachoric results for original data from Edgar & Lease

Trait	N	Γ	ASE	z	Tet	ASE	Breakpoints	
							D	P
UI1SS	53	0.30	0.14	1.07				
UI2SS	52	0.18	0.18	0.63				
UCSS	51	0.19	0.19	0.77				
UI1TD	50	0.25	0.25	0.71	0.12	0.24	0/1–4	0–2/3–6
UI2TD	43	0.23	0.23	0.24				
UCTD	42	0.00	0.19	0.00	0.04	0.24	0/1–4	0/1
UCMR	44	–1.00 ^a	0.00					
UCDAR	51	–1.00 ^a	0.00					
UMC5	45	0.19	0.57	0.23	0.09	0.36	0/1	0/1–5
UMCB	53	0.68 ^a	0.08	3.86 ^b	0.67 ^a	0.15	0–1/2–6	0–4/5–7
UMHC								
LI1SS	52	–0.13	0.55	–0.17				
LI2SS	53	0.65 ^a	0.22	1.52 ^c				
LMCN	53	–0.27	0.29	–0.08				
LMGP	42	0.24	0.55	0.32	0.12	0.34	X, +/Y	X, +/Y
LMDW	49	0.66 ^a	0.13	2.24 ^b				
LMPS	52	–1.00 ^a	0.00					
LMC6	52	–1.00 ^a	0.00					
LMC7	50	0.37	0.22	1.03	0.23	0.26	0/1–5	0/1

ASE, asymptotic error. ^a Significant correlation. ^b Significant z-score. ^c Nearly significant z-score.

From Edgar & Lease (2007, Table 3).

Hypocone correspondence was significant in this study ($\gamma = 0.704$, $p = .003$; $r_s = 0.489$, $p < .001$), a result consistent with Paul & Stojanowski (2017) and with the genetic correlation of approximately $r_G = 0.597$ reported by Paul et al. (2022b) for the dm2/M1 hypocone pair. The fact that Edgar & Lease (2007) could not estimate this result in their data, most likely due to extreme

expression frequencies in their sample, does not contradict these findings and instead illustrates the same sample-composition sensitivity discussed for rare traits. Taken together, the phenotypic correspondence detected here and the genetic architecture identified by Paul et al. (2022b) reinforce the interpretation that hypocone tracks across dentitions because of genuine shared developmental programming, not statistical coincidence.

Canine mesial ridge is a unique finding. Edgar & Lease (2007) found their canine mesial ridge result (UCMR) to be $\gamma = -1.00$, which they attributed to their mixed scoring system: an artifact of scale incompatibility rather than a real biological signal. With both dentitions scored on ASUDAS, this study does not suffer from the same issue. Paul & Stojanowski (2017) did not report on this trait in their work. This study finds a strongly significant positive correspondence for canine mesial ridge, the strongest result in the entire dataset. This is the result Paul et al. 's (2021) canine module predicts: approximately 70% of deciduous-permanent canine trait comparisons yielded significant genetic correlations in their Australian pedigreed sample, substantially higher than for incisors or molar accessory cusps. The prior failure to detect canine mesial ridge correspondence was a scoring system artifact. Its extremely high correspondence is worth investigating in other longitudinal samples.

Maxillary shoveling (di1/I1) produced a significant Spearman's correlation ($r_s = 0.346$, $p = 0.018$) and a significant tetrachoric correlation ($r_{Tet} = 0.510$), with a moderately positive but non-significant gamma ($\gamma = 0.417$, $ASE = 0.258$, $p = 0.106$). Unlike the mandibular shoveling results, this finding is interpretable as a genuine biological correspondence. Expression frequencies were substantial in both dentitions (67% deciduous and 91% permanent) with the permanent dentition scoring higher than the deciduous in 48% of individuals and identically in 41%, indicating overlapping and graded ordinal variation in both teeth. Saunders & Mayhall (1982)

reported a significant chi-square association between di1 and I1 shoveling in the Burlington Growth Centre sample ($p < .001$). Paul & Stojanowski (2017) also found significant gamma ($\gamma = 0.523$, $p = .027$) in the same sample. Edgar & Lease (2007) did not reach significance for maxillary central incisor shoveling ($\gamma = 0.30$). The genetic architecture analysis of Paul et al. (2021) is the most direct explanation: incomplete pleiotropy was detected for di1/I1 shoveling homologues in their Australian pedigreed sample, indicating that a shared genetic pathway drives expression in both dentitions.

5.3 Developmental Mechanisms: The Patterning Cascade Model and Activator-Inhibitor Dynamics

The pattern of significant and non-significant results is not arbitrary but can be understood within the developmental framework of the PCM (Salazar-Ciudad and Jernvall, 2002, 2010) and the molecular activator-inhibitor dynamics that govern it. That early-forming molar and canine field traits show cross-dentition correspondence while late-forming accessory cusps do not reflect a coherent developmental logic running from molecular signaling through crown geometry to individual trait expression.

In the PCM framework, tooth crown morphogenesis begins with a sequence of secondary enamel knot (SEK) formation events, in which each new knot is established through the balance of activator and inhibitor signals from previously established knots. Activator molecules, including FGF4 and SHH, promote epithelial cell differentiation into non-proliferative knot cells and stimulate growth of the surrounding mesenchyme. Inhibitor molecules, including BMP4 and WNT6, suppress new knot formation immediately adjacent to an established knot and instead stimulate lateral mesenchymal expansion (Jernvall and Thesleff, 2000; Kenessey et al., 2024; Salazar-Ciudad and Jernvall, 2002). The spatial reach of inhibitory signaling from each knot determines a minimum intercusp distance: no new knot can form within the inhibitory zone of a

previous one. The position of each successive cusp is geometrically constrained by all prior cusps, making crown morphogenesis a cascade in which the earliest events determine the outcome for all later ones. Because the activator-inhibitor ratio and the diffusion parameters of these molecules are genetically encoded, the cascade geometry is significantly heritable. This is the molecular mechanism through which genetic architecture becomes phenotypic morphology.

Early-forming cusps, those initiated from the primary enamel knot or in the first rounds of SEK formation, establish the inhibitory landscape of the crown. Because dm2 and M1 develop from the same morphogenetic field under the same genetic program, the primary cusp complex geometry is replicated between the two teeth: the same activator-inhibitor parameters operate from the same field position at two successive ontogenetic stages. Late-forming cusps depend on the space remaining after all prior knots have formed, and any small geometric divergence between dm2 and M1 arising from their size difference, their different developmental timing, and their distinct prenatal versus postnatal environments accumulates through the cascade to produce greater divergence in late-forming traits. Early-forming traits show stronger cross-dentition correspondence than late-forming accessory cusps because the shared genetic pathway controlling the activator-inhibitor cascade is most consistently expressed at the beginning of tooth formation, before geometric divergence between the two crowns has had the opportunity to accumulate..

Carabelli's cusp illustrates this mechanism most clearly. Carabelli's cusp is a lingual accessory cusp or groove on the protocone of the maxillary first molar cusp and its expression depends on the geometry of the protocone-paracone and hypocone-protocone intercuspal distances established early in the cascade. Paul et al. (2016) showed directly that these relative intercuspal distances are significant predictors of Carabelli's expression in between dm2 & M1. When the protocone region is tightly spaced, the inhibitory field of the primary protocone knot reaches the

lingual fossa and suppresses Carabelli's formation, but when spacing moves the inhibitory field, accessory cusp growth is possible. The four-study replication of significant Carabelli's correspondence results reflects this genetic program as seen across populations with European ancestry.

The genetic determinants of these traits is still a topic of active research. Erbil and Merriwether (2024) identified variants in *SOSTDC1*, a sclerostin domain-containing inhibitor of BMP signaling expressed in the dental mesenchyme during morphogenesis, and in *FGF3* and *FGF4* as candidates for Carabelli's expression in a pilot sequencing study. While their sample size limits interpretation, the biological mechanism is consistent with the activator-inhibitor framework: *SOSTDC1* modulates the inhibitory BMP signal that suppresses accessory knot formation in the protocone region, and variations producing reduced inhibition would increase Carabelli's expression in the same direction in both dentitions developing from the same morphogenetic field.

The hypocone is subject to similar mechanisms as Carabelli's cusp. As the fourth primary cusp of the maxillary molars, established in the early rounds of the SEK cascade from the trigone geometry, hypocone expression is constrained by the same geometric relationships operating across dm2 and M1. The significant correspondence observed in this sample, together with the genetic correlation reported by Paul et al. (2022b) ($r_G = 0.597$), supports the interpretation that the hypocone is governed by the same activator-inhibitor cascade geometry and that its expression tracks reliably across both dentitions. The near-universal deciduous frequency in this sample (100% at the breakpoint) reflects the hypocone's position as an early cascade trait in a population where the geometric conditions for its formation are nearly always met. The variation that does

exist is in grade rather than presence/absence, and the significant gamma confirms that grade variation tracks across dentitions.

The late-forming accessory traits, entoconulid, mid-trigonid crest, hypoconulid, and deflecting wrinkle, produce no significant correspondence, consistent with PCM predictions. Cusp 6 (entoconulid) and mid-trigonid crest are among the last traits to form in the mandibular molar cascade, positioned at the distal-most aspect of the crown where inhibitory fields from the four primary cusps are most geometrically complex and sensitivity to small perturbations is highest. Paul et al. (2022b) found a negative genetic correlation between cusp 5 (hypoconulid) and cusp 6 in the permanent dentition. The near-zero Spearman values in this sample ($r_s = -0.024$ for cusp 6) are consistent with the interpretation that whatever correspondence exists at the genetic level is not detectable as a phenotypic signal in a small sample where these traits are already rare. The non-significant deflecting wrinkle result reflects a similar dynamic, as a complex fissure trait whose expression is highly sensitive to downstream cascade geometry.

In East Asian populations, the EDAR V370A variant explains approximately 18.9% of shoveling variance (Kimura et al., 2009), with pleiotropic effects extending to double shoveling, crown size, and canine accessory ridge traits (Park et al., 2012). In a sample where EDAR V370A is rare or absent, shoveling variation is likely to be polygenic, reflecting the cumulative effect of many different alleles. The consistent co-absence of shoveling across dentitions in this sample is best understood as a neutral population genetic signal rather than evidence for or against the developmental correspondence that the PCM predicts.

5.4 What Does Correspondence Mean at the Individual Level?

The statistical results in Chapter IV establish which trait pairs show ordinal concordance across dentitions. The practical interpretation of these results is whether an individual who expresses a

trait deciduously is likely to express it permanently, and whether an individual who does not express it deciduously is likely to not express it permanently.

Even for the most robustly significant trait, Carabelli's, the two dentitions are not perfectly correlated at the individual level. The deciduous frequency at the breakpoint was 66.0% and the permanent frequency was 54.0%. A considerable number of individuals expressed Carabelli's cusp deciduously but not permanently, or did not express it deciduously but did express it permanently. Significant tetrachoric and Spearman's results confirm a real ordinal correlation: individuals with stronger deciduous Carabelli's expression tend towards stronger permanent expression, even though gamma does not reach significance ($\gamma = 0.421$, $p = .070$). This does not mean that deciduous presence always predicts permanent presence. This is probably due to Carabelli's cusp operating under partial, rather than complete, genetic pleiotropy. Paul et al. (2022b) reported $r_G \approx 0.635$ for Carabelli's cusp, indicating that the same genes are substantially but not entirely shared between deciduous and permanent expression. The environmental component of phenotypic expression is independent across the two dentitions: deciduous crowns form largely prenatally under limited environmental influence, while permanent crowns form postnatally under considerably greater environmental exposure (Paul et al., 2020; Smith et al., 1997). This asymmetry in the developmental environment means that even genetically predisposed individuals may fail to manifest a trait across both dentitions.

For traits without significant correspondence, the deciduous and permanent expressions are effectively decoupled at the phenotypic level in this sample. This does not necessarily mean the two dentitions share no genetic overlap. Paul et al.'s (2022b) genetic correlation data show significant r_G for several molar trait pairs that produce no significant phenotypic correspondence in this sample. However, whatever shared genetic architecture exists is not enough to produce

detectable concordance within individuals at this sample size. Environmental and developmental noise between the two dentitions is probably larger relative to the shared signal. For these traits, deciduous and permanent expressions are better understood as independent phenotypic observations than as correlated expressions of shared genetic pathways.

The shoveling results require a different interpretation though. Shoveling is among the most heritable dental traits, and Paul et al. (2021) reported near-complete genetic pleiotropy for di1/I1 shoveling across dentitions. The significant Spearman result for shoveling (di1/I1) in this sample reflects systematic co-absence: the large majority of individuals score grade zero in both the deciduous and permanent dentitions. In a North American sample with likely predominantly European-ancestry where co-absence is the most likely result, that shared absence carries genuine genetic information, reflecting a population-level tendency toward reduced lingual ridging at the incisor-canine complex. Co-absence is informative for population comparisons and is consistent with the shared genetic architecture Paul et al. (2021) document, but individual-level correspondence among expressers is not detectable in a sample of this size.

5.5 Non-Significant Traits and Limitations

Non-significant results & limitations in this study arise from three distinct sources. The first is the issue of small sample size with rare traits. For cusp 6 (entoconulid), mid-trigonid crest, mandibular shoveling (di1/I1 & di2/I2), and tuberculum dentale (di1/I1), deciduous or permanent expression frequencies were at or below 2.1% at the breakpoint. For these traits, the number of individuals expressing the trait in either dentition was just one or two. The extreme gamma values for cusp 6 ($\gamma = -1.000$), mid-trigonid crest ($\gamma = -1.000$), mandibular shoveling di1/I1 ($\gamma = -1.000$), and tuberculum dentale di1/I1 ($\gamma = 1.000$) are entirely due to this situation: a single discordant or concordant expressing pair produces a perfect extreme gamma when there are no other pairs to

average it with. The near-zero Spearman correlations for all four of these traits (which include all individuals and are not dominated by a single pair) confirms that no dataset-wide correspondence exists. These results do not tell us anything meaningful as they are artifacts of the inherent issues around statistical tests on small samples.

Table 9. Sample sizes and estimability status for all 22 deciduous–permanent trait pairs.

Trait	N	Estimability Status	Extreme γ
Molar (dm2/M1)			
Deflecting wrinkle (dm2/M1)	37	All 3 tests ran	No
Mid-trigonid crest (dm2/M1)	38	All 3 tests ran	Yes
Hypoconulid (dm2/M1)	43	All 3 tests ran	No
Entoconulid (dm2/M1)	43	All 3 tests ran	Yes
Carabelli's cusp (dm2/M1)	46	All 3 tests ran	No
Hypocone (dm2/M1)	46	Tetrachoric skipped	No
Metacone (dm2/M1)	46	Tetrachoric skipped	No
Metaconule (dm2/M1)	46	All 3 tests ran	No
Parastyle (dm2/M1)	46	No tests ran	No
Maxillary Anterior			
Winging (di1/I1)	46	All 3 tests ran	No
Labial convexity (di1/I1)	46	All 3 tests ran	No
Shoveling (di1/I1)	46	All 3 tests ran	No
Shoveling (di2/I2)	46	Tetrachoric skipped	Yes
Tuberculum dentale (di1/I1)	43	All 3 tests ran	No
Tuberculum dentale (di2/I2)	42	All 3 tests ran	No
Canine mesial ridge (dc/C)	39	All 3 tests ran	No

Trait	N	Estimability Status	Extreme γ
Canine distal accessory ridge (dc/C)	41	All 3 tests ran	No
Shoveling (dc/C)	42	All 3 tests ran	No
Mandibular Anterior			
Mandibular shoveling (di1/I1)	44	Tetrachoric skipped	Yes
Mandibular shoveling (di2/I2)	44	Tetrachoric skipped	Yes
Mandibular shoveling (dc/C)	44	All 3 tests ran	No
Mandibular canine distal accessory ridge (dc/C)	42	All 3 tests ran	No

N = number of complete deciduous–permanent pairs available for analysis. Estimability Status indicates which of the three correlation tests were computable. Extreme γ indicates whether the trait produced a $\gamma = \pm 1.000$. Note: Extreme $\gamma = \pm 1.000$ arises when all concordant or discordant pairs are on one side; ASE is undefined and significance cannot be tested.

The second source is genuine sources of discordance seen between the two dentitions. For the non-significant molar accessory cusp traits and many incisor traits, the PCM and the underlying genetic architecture suggest that whatever shared genetic influence exists is not as powerful as environmental variation, developmental timing differences between the prenatal deciduous and postnatal permanent dentitions, or the geometric divergence between dm2 and M1 in the downstream cascade. For these traits, non-significance is not only an issue of sample size. It may reflect a real biological signal: the deciduous and permanent dentitions express these traits differently at the individual level, even if their population-level frequencies carry information about the same underlying genetic variation.

There are limitations due to the scoring imprecision when using ASUDAS references to score deciduous morphology. ASUDAS was developed for permanent tooth morphology, and its

grade scoring reflects permanent crown proportions and dimensions (Turner et al., 1991). Paul et al. (2020) noted that ASUDAS standards require augmentation for deciduous application and found that ASUDAS yields lower heritability estimates for deciduous postcanine traits than deciduous-specific mixed standards, suggesting that grade-level imprecision in deciduous scoring reduces the genetic signal captured by ASUDAS relative to scoring standards made for the deciduous dentition. This limitation was most apparent in practice for a couple of traits. For example, tuberculum dentale, which are scored on small deciduous incisor and canine crowns, was difficult to grade because the traits themselves are proportionally smaller and more compressed than the permanent crown-based traits seen in the ASUDAS references. Paul et al. (2020) specifically note that tuberculum dentale on the deciduous canine as the only anterior trait for which deciduous specific scoring standards outperform ASUDAS. Intra-observer error testing was not conducted for this study, which is a recognized limitation (Nichol & Turner, 1986; Pilloud et al., 2019); formal error testing in future replications would allow this source of uncertainty to be quantified rather than estimated.

Two other limitations affect the generalizability of the results. The Stucklen Collection is most likely made of individuals who are of predominantly European descent (though this cannot be confirmed), and the expression frequency profile of most traits in this sample reflects the low-frequency of traits seen in populations of European-ancestry. Traits that are near-monomorphic in this sample might show very different cross-dentition correspondence patterns in populations where more individuals noticeably express these traits. Replication of this kind of study in a non-European ancestry sample is needed to confirm if any of these results are universal.

CHAPTER VI: CONCLUSION

This project aimed to characterize the degree of cross-dentition correspondence in nonmetric dental morphological trait expression between the deciduous and permanent dentitions of the same individuals in the Stucklen Collection. The analysis applied three complementary statistical approaches, Goodman-Kruskal's gamma, tetrachoric correlation, and Spearman's rank correlation, to 22 deciduous-permanent trait pairs, generating a multi-method assessment that allowed for comparison of results across tests and evaluation of results against the predictions of field theory, the Patterning Cascade Model, and the quantitative genetic literature.

The results indicate that cross-dentition correspondence in this sample is trait-specific and limited in overall extent. Canine mesial ridge (dc/C) was the most robustly corroborated correspondence in the dataset, reaching significance across all three statistical tests ($\gamma = 0.817$; $r_{Tet} = 0.723$; $r_s = 0.635$). Hypocone (dm2/M1) was significant on gamma and Spearman's ($\gamma = 0.704$; $r_s = 0.489$), and Carabelli's cusp (dm2/M1) was significant on tetrachoric and Spearman's with gamma approaching significance ($r_{Tet} = 0.531$; $r_s = 0.427$; $\gamma = 0.421$, $p = .070$). Shoveling (di1/I1) was significant on tetrachoric and Spearman's, though the Spearman signal reflects co-absence correspondence in the sample rather than graded expression correspondence in the expressing subset. Late-forming accessory cusp traits produced no significant correspondence across any test, and several mandibular shoveling pairs yielded extreme gamma values that are statistical artifacts of near-zero expression frequencies rather than biologically meaningful findings. These results are phenotypic correlations only; without genealogical data it is not possible to decompose the observed covariance into additive genetic and environmental components, and they are interpreted

as consistent with, rather than direct evidence of, shared genetic architecture across the diphyodont dentition.

The pattern of significant results partially confirms the predictions of field theory, the Patterning Cascade Model, and the quantitative genetic literature. Carabelli's cusp and hypocone are both early-forming traits associated with the primary cusp complex, and their correspondence is precisely what field theory and the PCM anticipate. The consistent failure of late-forming accessory cusp traits to reach significance also aligns with theoretical expectations. The strong correspondence for canine mesial ridge is consistent with the high degree of cross-dentition genetic integration reported by Paul et al. (2021). Where theoretical predictions are not confirmed, the most likely explanation is sample size and expression frequency constraints rather than a failure of the developmental or genetic theory. Several trait pairs had too few expressing individuals in one or both dentitions to support stable or interpretable estimates regardless of any underlying correspondence.

This project also demonstrates the practical consequences of statistical test selection in cross-dentition correspondence research. Gamma's structural exclusion of co-absent pairs inflates estimates for rare traits while making it insensitive to co-absence signals that carry genuine biological information in low-frequency populations. Tetrachoric correlation's requirement for sufficient cell counts in the dichotomized 2x2 table makes it unusable for a decent portion of trait pairs in this sample. Spearman's rank correlation, by incorporating the full rank distribution including co-absent observations, recovers signals that gamma cannot detect but conflates two distinct types of correspondence, graded expression and co-absence, that require different interpretive frameworks.

6. 1 Future Directions

Dental anthropology sits at an intersection of developmental biology, quantitative genetics, and bioarchaeology, and the results presented here raise questions that warrant continued investigation. The most immediate need is replication in a larger and more diverse sample. The Stucklen Collection, while valuable for its longitudinal dental cast data, is constrained in size and skewed toward low expression frequencies for many ASUDAS traits due to its composition. A larger sample, or one drawn from a population with higher expression frequencies for traits like shoveling and accessory cusps, would allow for a more robust estimation across all three methods and more powerful tests of correspondence in the expressing subset. This is particularly relevant for canine distal accessory ridge, labial convexity, and the mandibular shoveling complex, all of which produced directionally positive but non-significant estimates that may reflect real biological signals hidden by sample size.

The findings also have implications for the incorporation of subadults into bioarchaeological research. In many prehistoric and forensic assemblages, subadults are a significant portion of the available remains, but without a clear understanding of how deciduous trait expressions correspond to permanent ones within the same individuals, those remains are often either excluded from analysis entirely or their traits are treated as proxies for the permanent dentition without the understanding of how strong of proxy they might be. If deciduous and permanent trait expressions are correlated within the same individual, as this study and the genetic literature suggest, then deciduous morphology recorded from subadult individuals in mortuary assemblages carries information relevant to population reconstruction that is currently not being utilized. Expanding the pool of samples for cross-dentition correspondence and integrating it with the heritability and genetic correlation literature (Paul et al., 2020, 2021, 2022) would strengthen the theoretical foundation for protocols that use deciduous and permanent dental data

interchangeably in biodistance analyses. Pedigreed longitudinal cast samples represent a rare opportunity to evaluate phenotypic correspondence against known genealogical relationships. Further work is needed to build a cumulative empirical record of which trait pairs reliably correspond, to what degree, and for what developmental reasons, a gap with direct consequences for how subadult dental remains are interpreted in archaeological and forensic contexts.

REFERENCES

- Aguirre L, Castillo D, Solarte D, Moyano M, Moreno F. 2007. Analysis of three non-metric dental traits in a living population from Colombia. *Int J Dent Anthropol* 9:24–35.
- Bailey SE, Benazzi S, Hublin JJ. 2014. Allometry, merism, and tooth shape of the upper deciduous M2 and permanent M1. *Am J Phys Anthropol* 154:104–114.
- Butler PM. 1939. Studies of the mammalian dentition: differentiation of the post-canine dentition. *Proc Zool Soc Lond* 109B:1–36.
- Dahlberg AA. 1945. The changing dentition of man. *J Am Dent Assoc* 32:676–690.
- Dahlberg AA. 1950. The evolutionary significance of the protostylid. *Am J Phys Anthropol* 8:15–24.
- Dempsey PJ, Townsend GC, Martin NG. 1999. Insights into the genetic basis of human dental variation from statistical modelling analyses. *Perspect Hum Biol* 4:9–17.
- Edgar HJH, Lease LR. 2007. Correlations between deciduous and permanent tooth morphology in a European American sample. *Am J Phys Anthropol* 133:726–734.
- Erbil FN, Merriwether DA. 2024. Identification of the genetic determinants of shovel-shaped incisors and Carabelli's cusp. *Anthropol Rev* 87(3):1–17.
- Garn SM, Lewis AB, Kerewsky RS. 1966. Extent of sex influence on Carabelli's polymorphism. *J Dent Res* 45:1823.
- Gross JM, Edgar HJH. 2019. Informativeness of dental morphology in ancestry estimation in African Americans. *Am J Phys Anthropol* 170:408–416.
- Hanihara K. 1961. Criteria for classification of crown characters of the human deciduous dentition. *J Anthropol Soc Nippon* 69:27–45.

- Hanihara K. 1963. Crown characters of the deciduous dentition of the Japanese-American hybrids. In: Brothwell DR, editor. Dental anthropology. Oxford: Pergamon. p 103–124.
- Hanihara K. 1967. Morphological pattern of deciduous dentition in the Japanese-American hybrids. *J Anthropol Soc Nippon* 75:222–241.
- Hanihara T. 1992. Dental and cranial affinities among populations of East Asia and the Pacific: the basic populations in East Asia, IV. *Am J Phys Anthropol* 88:163–182.
- Hefner JT, Pilloud MA, Buikstra JE, Vogelsberg CCM. 2016. A brief history of biological distance analysis. In: Pilloud MA, Hefner JT, editors. Biological distance analysis: forensic and bioarchaeological perspectives. Amsterdam: Elsevier. p 3–22.
- Hughes TE, Townsend GC, Bockmann MR. 2016. An overview of dental genetics. In: Irish JD, Scott GR, editors. A companion to dental anthropology. Hoboken: Wiley-Blackwell. p 122–138.
- Irish JD. 1997. Characteristic high- and low-frequency dental traits in Sub-Saharan African populations. *Am J Phys Anthropol* 102:455–467.
- Irish JD, Morez A, Girdland Flink L, Phillips ELW, Scott GR. 2020. Do dental nonmetric traits actually work as proxies for neutral genomic data? Some answers from continental- and global-level analyses. *Am J Phys Anthropol* 172:347–375.
- Jernvall J, Thesleff I. 2000. Reiterative signaling and patterning during mammalian tooth morphogenesis. *Mech Dev* 92:19–29.
- Kenessey DE, Stojanowski CM, Paul KS. 2024. Evaluating predictions of the patterning cascade model of crown morphogenesis in the human lower mixed and permanent dentition. *PLoS ONE* 19(6):e0304455.
- Kimura R, Yamaguchi T, Takeda M, et al. 2009. A common variation in EDAR is a genetic determinant of shovel-shaped incisors. *Am J Hum Genet* 85:528–535.

- Kondo S, Townsend GC. 2006. Associations between Carabelli trait and cusp areas in human permanent maxillary first molars. *Am J Phys Anthropol* 129:196–203.
- Marado LM, Campanacho V. 2013. Carabelli's trait: definition and review of a commonly used dental non-metric variable. *Cad GEEvH* 2(1):24–39.
- Moes E, O'Donnell L. 2026. Comparing biodistance estimates from deciduous and permanent dental morphology in the pre-Spanish US Southwest. *Dent Anthropol* 39(1):3–10.
- Ocampo AM, Sánchez JD, Martínez C, Moreno F. 2009. Correlación de diez rasgos morfológicos dentales coronales entre molares deciduos y permanentes en tres grupos étnicos colombianos. *Rev Estomatol* 17(2):7–16.
- Park J-H, Yamaguchi T, Watanabe C, et al. 2012. Effects of an Asian-specific nonsynonymous EDAR variant on multiple dental traits. *J Hum Genet* 57:508–514.
- Paul KS, Astorino CM, Bailey SE. 2017. The patterning cascade model and Carabelli's trait expression in metameres of the mixed human dentition: exploring a morphogenetic model. *Am J Phys Anthropol* 162:3–18.
- Paul KS, Feezell R, Hughes T, Brook AH. 2022a. Integrating genealogy and dental variation: contributions to biological anthropology. *Yearb Biol Anthropol* 181(S76):145–179.
- Paul KS, Stojanowski CM, Hughes TE, Brook AH, Townsend GC. 2016. The patterning cascade model and Carabelli's trait expression in metameres of the human molar field. *Am J Phys Anthropol* 159:468–480.
- Paul KS, Stojanowski CM, Hughes TE, Brook AH, Townsend GC. 2020. Patterns of heritability across the human diphyodont dental complex: crown morphology of Australian twins and families. *Am J Phys Anthropol* 172:1–15.

- Paul KS, Stojanowski CM, Hughes TE, Brook AH, Townsend GC. 2021. The genetic architecture of anterior tooth morphology in a longitudinal sample of Australian twins and families. *Arch Oral Biol* 129:105168.
- Paul KS, Stojanowski CM, Hughes TE, Brook AH, Townsend GC. 2022b. Genetic correlation, pleiotropy, and molar morphology in a longitudinal sample of Australian twins and families. *Genes* 13:996.
- Paul KS, Stojanowski CM. 2015. Performance analysis of deciduous morphology for detecting biological siblings. *Am J Phys Anthropol* 157:615–629.
- Paul KS, Stojanowski CM. 2017. Comparative performance of deciduous and permanent dental morphology in detecting biological relatives. *Am J Phys Anthropol* 164:97–116.
- Pilloud MA, Adams DM, Hefner JT. 2019. Observer error and its impact on ancestry estimation using dental morphology. *Int J Legal Med* 133:949–962.
- Pilloud MA, Edgar HJH, George R, Scott GR. 2016. Dental morphology in biodistance analysis. In: Pilloud MA, Hefner JT, editors. *Biological distance analysis: forensic and bioarchaeological perspectives*. Amsterdam: Elsevier. p 109–131.
- Rathmann H, Reyes-Centeno H. 2020. Testing the utility of dental morphological trait combinations for inferring human neutral genetic variation. *Proc Natl Acad Sci USA* 117:10769–10777.
- Salazar-Ciudad I, Jernvall J. 2010. A computational model of teeth and the developmental origins of morphological variation. *Nature* 464:583–586.
- Saunders SR, Mayhall JT. 1982. Developmental patterns of human dental morphological traits. *Arch Oral Biol* 27:45–49.
- Sciulli PW. 1998. Evolution of the dentition in prehistoric Ohio Valley Native Americans: II. Morphology of the deciduous dentition. *Am J Phys Anthropol* 106:189–205.

- Scott GR, Turner CG II. 1997. The anthropology of modern human teeth: dental morphology and its variation in recent human populations. Cambridge: Cambridge University Press.
- Smith P, Gomorri JM, Spitz S, Becker J. 1997. Model for the examination of evolutionary trends in tooth development. *Am J Phys Anthropol* 102:283–294.
- Smith P, Koyoumdjisky-Kaye E, Kalderon W, Stern D. 1987. Directionality of dental trait frequency between human second deciduous and first permanent molars. *Arch Oral Biol* 32:5–9.
- Stojanowski CM, Paul KS, Seidel AC, Duncan WN, Guatelli-Steinberg D. 2018. Heritability and genetic integration of anterior tooth crown variants in the South Carolina Gullah. *Am J Phys Anthropol* 167:124–143.
- Townsend GC, Bockmann M, Hughes T, Brook A. 2012. Genetic, epigenetic and environmental influences on human tooth number, size and shape. *Odontology* 100:1–9.
- Turner CG II. 1990. Major features of Sundadonty and Sinodonty, including suggestions about East Asian microevolution, population history, and late Pleistocene relationships with Australian Aborigines. *Am J Phys Anthropol* 82:295–317.
- Turner CG II, Nichol CR, Scott GR. 1991. Scoring procedures for key morphological traits of the permanent dentition: the Arizona State University Dental Anthropology System. In: Kelley MA, Larsen CS, editors. *Advances in dental anthropology*. New York: Wiley-Liss. p 13–31.

SUPPLEMENTARY MATERIALS

Supplementary Table 1. Final analytical sample ($N = 46$).

ID	Sex	Age at deciduous scoring	Age at permanent scoring
AA 7	M	4.42	16.02
AB 70	M	6.22	14.70
AD 2104C	F	4.30	16.26
AD 33	F	3.60	12.56
AF 10	M	4.00	17.67
AR R51	F	4.65	17.31
AS 1A	F	4.60	14.97
AV 12	F	4.44	14.19
BC 543	M	4.55	14.00
BC R319B	M	4.25	14.01
BH 21	F	4.19	12.08
CB 15	F	3.81	13.40
CBE 26A	F	4.18	12.81
CF 3	F	3.89	17.06
DB 15A	M	2.52	13.36
DB 71	M	3.53	10.95
DKR 556	M	3.34	9.13
DL 661	F	2.80	15.04
DM 22	M	5.43	13.03
EH 23A	F	5.12	15.18
ER 464	F	4.86	15.56
ES 52	F	5.40	12.36
FD 2104B	M	3.32	13.71
FL 4A	M	5.23	14.13

ID	Sex	Age at deciduous scoring	Age at permanent scoring
FS 1	M	6.04	16.90
JA 238	M	2.79	14.42
JBE 26	F	3.53	12.49
JE 284	F	4.36	13.21
JS 268	M	3.93	17.32
JT 13	M	5.24	15.01
KC 319K	M	5.06	15.08
LA 25	F	4.51	16.31
LD 14L	M	2.39	14.36
LO 16	F	4.34	25.73
LR 18	F	4.26	15.08
LS 11	F	4.04	16.94
MF 2106	F	5.24	13.07
PDa 14	M	4.58	12.51
PH 23	M	6.61	16.54
PL 4	F	3.33	13.00
PaH 23	M	3.43	19.95
RAC R319RA	F	4.33	12.39
RD 14	M	4.82	22.88
SD 2104A	M	3.00	12.83
SL 2	M	2.94	13.50
WC R319W	M	3.25	14.87

Sex and age at deciduous scoring observation, and age at permanent scoring observation for each individual. Ages in decimal years, converted from YY.MM.DD format inscribed on each cast. F = female; M = male.