

**Bioarchaeological analyses of mobility, demography, and
pathology in Final Neolithic and Early Bronze Age
populations in Baden-Württemberg (Southwest Germany)**

Dissertation

der Mathematisch-Naturwissenschaftlichen Fakultät

der Eberhard Karls Universität Tübingen

zur Erlangung des Grades eines

Doktors der Naturwissenschaften

(Dr. rer. nat.)

vorgelegt von

Stephanie Lismann

aus Miltenberg

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Dekan:

Prof. Dr. Thilo Stehle

1. Berichterstatter/-in:

Prof. Dr. Katerina Harvati

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Abstract

Several migration events during the third to mid-second millennia BC mark a major turning point in Central European prehistory, leading to the emergence of the Final Neolithic cultural complexes of the Corded Ware and Bell Beaker, as well as multiple Early Bronze Age cultural groups. In Southwest Germany, their partial coexistence fostered complex trajectories of cultural transmission, adaptation, and genetic exchange, making the region particularly relevant for bioarchaeological research. This dissertation aims to reconstruct the local population development of Corded Ware and Neckar Group societies in the Tauber and Neckar River regions. Three case studies apply distinct palaeoanthropological methods to human skeletal remains, with a particular focus on diachronic comparison.

In the first case study, a newly developed software tool was used to perform biodistance analyses based on dental metric and non-metric traits. The results support previous archaeological, genetic, and isotopic findings from neighbouring regions, suggesting population continuity. Temporal variation in dental traits points to possible isolation of particular populations. Evidence of childhood mobility further indicates interactions between neighbouring sites and the practice of fostering children. These findings provide a nuanced perspective on gene flow and sociocultural practices between local groups.

The second study investigated demographic patterns using life table analysis. Mortality profiles and life expectancy indicate diachronic changes, with female individuals of infant, juvenile, and adult age most affected. These patterns likely reflect sociocultural factors such as potential female child neglect or infanticide, juvenile pregnancies, and improving living conditions for adult females, which is consistent with observations from other regions. The results offer insights into sex related mortality risks during cultural transitions.

The third study focused on biological stress indicators through palaeopathological analyses and examined their association with mortality and cultural practices. Results show sex-specific patterns in dental disease, suggesting differences in diet and tooth use. Degenerative joint diseases indicate sex division of labour, different subsistence strategies in the Final Neolithic, which shifts towards greater task specialisation and occupational homogenisation in the Early Bronze Age. Non-specific stress markers reflect childhood stress and sex-related weaning practices. Evidence of trauma includes the practice of trepanation in the Final Neolithic, increasing strenuous labour through traumatic joint disease, and constant fracture rates. The presence of neoplastic disease in the Early Bronze Age may be linked to lifestyle,

working conditions, or genetic predisposition. These findings underscore the sociocultural impact on biological stress.

In conclusion, this dissertation employs diverse palaeoanthropological approaches to explore population development and assess the impact of cultural change on past lives. It emphasises the value of localised studies in contributing to scientific discussions of prehistoric societies across Central Europe.

Zusammenfassung

Mehrere Migrationsereignisse während des dritten bis mittleren zweiten Jahrtausends v. Chr. markieren einen bedeutenden Wendepunkt in der zentraleuropäischen Vorgeschichte. Sie führten zur Entstehung der endneolithischen Kulturkomplexe der Schnurkeramik und der Glockenbecher sowie mehrerer frühbronzezeitlicher Kulturgruppen. In Südwestdeutschland begünstigte ihre teilweise Koexistenz komplexe Entwicklungen der kulturellen Übertragung, Anpassung und des genetischen Austauschs, wodurch diese Region besonders relevant für bioarchäologische Forschung ist. Ziel dieser Dissertation ist es, die lokale Bevölkerungsentwicklung der Schnurkeramiker und der Neckargruppen in der Tauber- und Neckarregion zu rekonstruieren. In drei Fallstudien wurden unterschiedliche paläoanthropologische Methoden auf menschliche Skelettreste angewendet, wobei ein besonderer Fokus auf dem diachronen Vergleich lag.

In der ersten Fallstudie wurde ein neu entwickeltes Softwaretool verwendet, um Biodistanzanalysen auf der Grundlage metrischer und nicht-metrischer Zahnmerkmale durchzuführen. Die Ergebnisse bestätigen frühere archäologische, genetische und isotopische Studien aus benachbarten Regionen und deuten auf eine Bevölkerungskontinuität hin. Zeitliche Unterschiede in den Zahnmerkmalen weisen auf eine mögliche Isolation bestimmter Populationen hin. Hinweise auf Mobilität im Kindesalter deuten zudem auf Interaktionen zwischen benachbarten Gruppen sowie auf die Praxis der Aufnahme von Ziehkindern hin. Diese Ergebnisse liefern eine nuancierte Perspektive auf den Genfluss und die soziokulturellen Praktiken im lokalen Kontext.

Die zweite Fallstudie untersuchte demographische Muster mithilfe von Sterbetafeln. Die Analyse von Mortalität und Lebenserwartung zeigt diachrone Veränderungen auf, wobei weibliche Individuen im Säuglings-, Jugend- und Erwachsenenalter am stärksten betroffen waren. Diese Muster spiegeln vermutlich soziokulturelle Faktoren wider, wie mögliche Kindesvernachlässigung oder Infantizid von Mädchen, Jugendschwangerschaften sowie verbessernde Lebensbedingungen für erwachsene Frauen, die mit Beobachtungen aus anderen Regionen übereinstimmen. Die Ergebnisse bieten Einblicke in geschlechtsspezifische Mortalitätsrisiken während kultureller Übergangsphasen.

Die dritte Fallstudie fokussiert sich auf biologische Stressindikatoren anhand paläopathologischer Analysen und untersuchte deren Zusammenhang mit Mortalität und kulturellen Praktiken. Die Ergebnisse zeigen geschlechtsspezifische Muster bei

Zahnpathologien, die auf Unterschiede in der Ernährung und der Zahnnutzung hinweisen. Degenerative Gelenkerkrankungen deuten auf eine geschlechtsspezifische Arbeitsteilung hin, sowie unterschiedliche Subsistenzstrategien im Endneolithikum, während in der Frühbronzezeit eine stärkere Spezialisierung und Vereinheitlichung der Tätigkeiten zu erkennen ist. Nicht-spezifische Stressindikatoren belegen Stress während der frühen Kindheit und geschlechtsspezifische Abstillpraktiken. Traumatische Befunde umfassen Hinweise auf Trepanationen im Endneolithikum, zunehmend körperliche Belastung durch gelenkbezogene Traumata, sowie konstante Frakturnraten. Das ausschließliche Auftreten neoplastischer Erkrankungen in der Frühbronzezeit könnte mit Lebensstil, Arbeitsbedingungen oder genetischer Prädisposition in Verbindung stehen. Diese Ergebnisse unterstreichen den soziokulturellen Einfluss auf biologischen Stress.

Zusammenfassend wendet diese Dissertation verschiedene paläoanthropologische Ansätze an, um die Populationsentwicklung zu untersuchen und den Einfluss kultureller Veränderungen auf vergangene Lebensrealitäten zu analysieren. Sie hebt die Bedeutung lokaler Studien hervor und leistet einen wichtigen Beitrag zum wissenschaftlichen Diskurs über prähistorische Gesellschaften in Zentraleuropa.

List of Abbreviations

aDNA	ancient DNA/ancient deoxyribonucleic acid
ASUDAS	Arizona State University Dental Anthropology System
BC	before Christ
BL	buccolingual
CE	cervical
CR	crown
CW	Corded Ware complex
EBA	Early Bronze Age
EIA	Early Iron Age
FN	Final Neolithic
LC	lower canine
LI	lower incisor
LM	lower molar
LP	lower premolar
MBDL	mesiobuccal-distolingual
MCA	multiple correspondence analysis
MD	mesiodistal
MLDB	mesiolingual-distobuccal
NG	Neckar group
PCA	principal component analysis
UC	upper canine
UI	upper incisor
UM	upper molar

UP upper premolar

v. Chr. vor Christus

List of Publications

Two publications and one manuscript in preparation are included in this cumulative dissertation in fulfilment of the requirements. The own contribution to the articles or manuscripts is shown in numbers in parentheses as a percentage (scientific idea/data generation/analysis and interpretation/paper writing).

Accepted articles:

Paper I (0/100/50/40):

Rathmann, H.*, **Lismann, S.***, Francken, M., Spatzier, A., 2023. Estimating Inter-Individual Mahalanobis Distances from Mixed Incomplete High-Dimensional Data: Application to Human Skeletal Remains from 3rd to 1st Millennia BC Southwest Germany. *Journal of Archaeological Science* 156, 105802.

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* shared first co-authorship, as both authors contributed equally to this work.

Paper II (50/100/90/80):

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Manuscript ready for submission:

Paper III (50/100/90/80):

Lismann, S., Francken, M., Harvati, K., Bartelheim, M., Spatzier, A., (*in prep.*). Evaluating the impact of Final Neolithic-Early Bronze Age transition on pathology prevalence in populations from Southwest Germany. Manuscript close to submission.

1. Introduction

Human bones and teeth can reveal a wide range of information through osteological and bioarchaeological analyses, including, among other things, habitual activities, disease prevalence, demographic structure, and diet. From such data, it is possible to infer aspects of behaviour, lifestyle, and sociocultural practices. When contextualised with archaeological lines of evidence, such as settlement patterns, material culture, and burial practice, these inferences can be strengthened, contributing to a more holistic understanding of past populations. Accordingly, the study of human remains not only significantly contributes to our understanding of individuals and their communities, but also provides critical insights into the lifestyles and socioeconomic structures of past societies.

The period from the third to mid-second millennium BC in European prehistory is of particular interest. During this time, the Final Neolithic cultural complexes of the Corded Ware and Bell Beaker emerged and gave rise to the subsequent Early Bronze Age and its various cultural groups. This dynamic phase was characterised by complex interplays of migrants and native populations, cultural transmission and adaptation, and social and material developments, all of which profoundly shaped the demographic and sociocultural landscape of Europe.

1.1 Third-Millennium BC Migration and the Beginning of Complex Societies in Europe

Between 3100 and 2450 BC, three major east-to-west migration events were identified in Europe through ancient DNA (aDNA) studies (Allentoft et al., 2015; Haak et al., 2015; Heyd, 2023; Olalde et al., 2018), leading to considerable demographic and cultural transformations. The first migrants of the Yamnaya culture, originating from the Pontic-Caspian steppe northwest of the Black Sea, expanded westwards between 3100 and 3050 BC; these groups mixed with the indigenous populations of Early Neolithic farmers and Western Hunter-Gatherer ancestry (Heyd, 2023), likely driven by socioeconomic and climatic factors, such as technological innovations namely the wheel and wagon, and increasing aridity (Frînculeasa et al., 2015; Heyd, 2019). These movements may also have been directed by rulers in response to rising conflict levels (Anthony, 2020).

Between 2950 and 2750 BC, migrants adapted to new environments and cultural settings, leading to the formation of the Corded Ware cultural complex in Europe, with the Rhine River marking its western most expansion (Heyd, 2023). Interestingly, archaeology and

aDNA studies noticed a discrepancy in Y chromosome types associated with these groups (e.g., Furtwängler et al., 2020; Juras et al., 2020; Papac et al., 2021). Although the majority of the Corded Ware burials exhibit high levels of steppe ancestry and carry distinct Y chromosome types (R1a and R1b), the typical Yamnaya Y chromosome (R1b-Z2103) is comparatively rare. This suggests that Corded Ware groups were not direct descendants of the Yamnaya, but instead of various other steppe populations from the Dniester-Dnieper frontier (Heyd, 2023). Nonetheless, the Yamnaya finds expression in the burial traditions of early Corded Ware communities, namely mounds, east-west orientation, supine upper body position, and emphasise of the individual (Furholt, 2019). However, other important cultural aspects, like gender differentiation, grave goods, and weapon display, seemingly stem from other cultural influences (Heyd, 2023). Hence, both the variety of haplogroups and cultural factors, and radiocarbon dates as early as 2900 BC highlight Bohemia as a centre of cultural emergence and further dispersal of the Corded Ware culture (Papac et al., 2021). In the following centuries, several regional Corded Ware networks dominated the landscape, accompanied by an increasing homogenisation of burial customs (Heyd, 2023). Recent aDNA studies suggest the possibility of an additional migration event, indicated by Y chromosome lineages rich in steppe ancestry (e.g., Haak et al., 2015; Papac et al., 2021), though further validation is still required.

Finally, between 2600 and 2450 BC the Bell Beaker component emerged at the Rhine River frontier, originating from the Iberian Peninsula (Heyd, 2023), blending eastern (e.g., ceramics decoration styles, gender differentiation) and western (e.g., origin of Beaker vessels, long distance trade) sociocultural aspects in Central Europe. However, a substantial genetic contribution from Iberian Bell Beaker populations has been ruled out and steppe ancestry remained dominant (Olalde et al., 2018). As with the Corded Ware culture in Bohemia, the presence of frequent Beaker-associated findings along the Upper Rhine suggests an earlier emergence around 2550 BC compared to other regions, indicative of a leapfrog pattern of dispersal of Bell Beaker culture (Heyd, 2023).

Consequently, during these transformative 600 years, successive migration and transmission events occurring approximately every 150 to 200 years formed parts of Europe's genetic and cultural landscape to varying degrees (Heyd, 2023). This complex situation of co-existing Corded Ware and Bell Beaker groups, the intensification of supraregional contacts and trade, the use of bronze, and the emergence of craftsmanship around 2200 BC ultimately contributed to the formation of various Early Bronze Age cultural expressions in Central Europe, that differ in geographical location, burial customs, and archaeological findings. However, even within Early Bronze Age cultural groups, differences are discernible. This lack

of uniformity highlights the complexity of cultural development during this period, emphasising the importance of context-specific analyses when attempting to reconstruct biological and sociocultural dynamics.

1.2 Importance of the Neckar and Tauber Region during the 3rd to Mid-2nd Century BC

Many insights into cultural and population development have been derived from interregional perspectives, which often obscure smaller-scale, localised dynamics. As a result, several recent researches have challenged the theory of near-complete population replacement during the third to mid-second millennia BC (e.g., Furtwängler et al., 2020; Knipper et al., 2017; Mitnik et al., 2019), as initially proposed by aDNA analyses (Allentoft et al., 2015; Haak et al., 2015; Olalde et al., 2018). This underscores the importance of examining regional contexts in greater detail. Despite growing scholarly interest and numerous studies focusing on Central Europe (e.g., Furtwängler et al., 2025, 2020; Hukelova, 2016; Knipper et al., 2016; Nicklisch, 2017; Sjögren et al., 2020, 2016), certain regions, such as Southwest Germany, remain underexplored in terms of bioarchaeological research. This region occupies a geographically and culturally significant position, as it represents the westernmost expansion of Corded Ware societies and lies adjacent to a key area of Bell Beaker dispersal, which contributed to the emergence of Early Bronze Age cultural traditions. The diverse topography would have supported a range of subsistence strategies, and the river systems likely played a crucial role in the movement of people, goods, and ideas, fostering both population and cultural development. In the past decades, several archaeological excavations in this area have uncovered a considerable number of human skeletal remains from Final Neolithic and Early Bronze Age cemeteries. However, the majority of these finds have not yet been systematically analysed, regarding both the burial context and the human remains. Existing bioarchaeological investigations have been limited in scope, often focusing on smaller sites, addressing only age and sex, and results remained unpublished in preliminary internal reports or in university theses. Only a few studies examined larger sites more thoroughly (Dresely, 2004; Trautmann, 2012) offering valuable insights into Corded Ware societies in the Tauber River valley. Yet, comprehensive diachronic comparisons across other sites and time periods are still missing, preventing a deeper understanding of the regional population history in the Tauber and Neckar River areas. It therefore offers a valuable opportunity to explore how the supraregional phenomena of the Corded Ware and Bell Beaker, and the subsequent Neckar group, were locally adapted, modified, and expressed.

This research gap provides a strong basis for in-depth bioarchaeological analyses aimed at reconstructing the population development during a period of high cultural historical relevance. To address this, a research project led by the State Office for Cultural Heritage in Esslingen seeks to apply a systematic and multidisciplinary approach. As part of this initiative, the present doctoral thesis comprises three studies focused on the anthropological analysis of skeletal remains from two regions in the state of Baden-Württemberg, Southwest Germany. The Tauber River valley, in northern Baden-Württemberg, provides most of the Final Neolithic sites associated with the Corded Ware cultural complex, while the Early Bronze Age sites of the Neckar group are located in the upper and middle Neckar River region. Unfortunately, the limited availability of skeletal remains from the Final Neolithic Bell Beaker culture in this area preclude their inclusion in this study.

The human remains examined for this thesis originate from both recent and older excavations, mostly of which had not undergone prior osteological analysis, except for the Tauber region (Dresely, 2004; Trautmann, 2012). The remains were analysed through a combination of dental biodistance, demographic, and pathological methods to reconstruct, for the first time, the population history and to provide a comprehensive basis for future bioarchaeological investigations in the region.

In conclusion, this doctoral research aims to investigate the population history of individuals associated with the Corded Ware culture and Neckar group, spanning the Final Neolithic and Early Bronze Age (2900 to 1600 BC). It specifically focuses on diachronic developments within a small-scale regional context, contributing to a broader understanding of cultural and biological transformations in prehistoric Central Europe.

2. Research Strategy

2.1 Objectives

The overall aim of this dissertation was to anthropologically analyse selected burial sites in order to reduce the gaps in our knowledge about past human lives during the 3rd to mid-2nd millennia BC in the regions of the upper and middle Neckar River and Tauber River valley, in the state of Baden-Württemberg.

The three studies presented here are the first that contextualise these skeletal remains in a comprehensive frame while focusing on specific bioarchaeological aspects. The following objectives were pursued for all three studies:

- (1) To reconstruct the population development of the consecutive periods of the Final Neolithic and Early Bronze Age in a small regional scale in Southwest Germany.
- (2) To infer potential diachronic changes both in bioarchaeological and sociocultural aspects.

2.2 Research Questions

Study I: What does the regional population history of Baden-Württemberg reveal based on biodistance analyses of dental metric and non-metric traits?

Numerous studies revealed that the third to mid-second millennia BC in Central Europe was highly dynamic in regards of different migration processes (e.g., Allentoft et al., 2015; Haak et al., 2015; Olalde et al., 2018; Sjögren et al., 2016). However, these inferences about the population history in Final Neolithic and Early Bronze Age Europe are mainly based on large scale sampling strategies which obscure complex small-scale trends and the role of individuals. This consideration is particularly important since the Final Neolithic cultural complexes of the Corded Ware (ca. 2900-2100 BC) and the Bell Beaker (ca. 2750-2000 BC) founded several cultures and regional groups that emerged in the Early Bronze Age (ca. 2300-1600 BC). Studies of regional settings demonstrated different mobility patterns ranging from age- and sex-specific mobility to rapid DNA change or residential communities with low mobility (e.g., Furtwängler et al., 2020; Knipper et al., 2017; Mittnik et al., 2019). Especially the regions of the upper and middle Neckar River and Tauber River valley, Southwest Germany, remain understudied in this regard. Therefore, the first study investigates for the first time the diachronic regional affinity patterns on human dental remains from six archaeological locations in Southwest-Germany in an inter-individual comparative framework. The sites are attributed to the Final Neolithic Corded Ware culture, Early Bronze Age Neckar group and Early Iron Age Hallstatt culture. The latter one is included as comparative sample for an extended depiction. Therefore, the aim of this study was to investigate the population history of different partly co-existing cultural groups in order to detect regional trends by utilising dental morphometrics.

Study II: Did the transition from the Final Neolithic to the Early Bronze Age have a concomitant demographic impact on populations in Baden-Württemberg?

Studies from various disciplines have made it clear that the 3rd to mid-2nd millennia BC in Europe underwent complex population developments and social interactions, as also demonstrated in Study I. This spread of new ideologies also shaped the populations biological

profile in various extents. Another approach to investigate the life history of past populations are palaeodemographic analyses. By constructing life tables, group differences in age- and sex-specific mortality and life expectancy can be observed, as demonstrated for Eastern Europe and Central Germany (Hukelova, 2016; Nicklisch, 2017). The density of sites from different cultural groups along the rivers Tauber and Neckar in Baden-Württemberg are of particular interest, since previous analyses in the Tauber region revealed valuable demographic insights of Corded Ware cultures (Dresely, 2004; Trautmann, 2012). However, systematic diachronic analyses are missing. Therefore, taking individual sites into account to cover regional manifestations is even more crucial. This study compared the demographic profile based on life table reconstructions of the Corded Ware culture and Neckar group societies from the first study. By including further sites, it aims to identify potential inter- and intra-population differences in mortality, life expectancy, and sociocultural consequences related to diachronic change.

Study III: Are there observable changes in morbidity among populations during the transition from the Final Neolithic to the Early Bronze Age?

While Study II focused on demographic trends in Corded Ware culture and Neckar group societies, Study III takes up these findings in order to identify potential correlations between mortality and morbidity. Furthermore, the development and introduction of new tools in the Early Bronze Age required specialisations in tasks, which potentially led to different subsistence strategies and differences in labour and lifestyle between the periods (Harding, 2002; A. A. Macintosh et al., 2014; Sjögren et al., 2016). This affects and demands the human skeleton in various ways, relating to dietary habits, habitual tasks, stress due to infectious disease or malnutrition. Consequently, this allows for a comprehensive evaluation of the biological stress level in populations. Relatively few studies in neighbouring regions directly compared pathological data of populations from different cultural and temporal background (e.g., Hukelova, 2016; Nicklisch, 2017). Even though palaeopathological analyses of Corded Ware culture populations in the Tauber valley revealed interesting results (Dresely, 2004; Trautmann, 2012), a diachronic comparison with Early Bronze Age sites has not been conducted yet. Therefore, this study investigates different palaeopathological conditions among the Final Neolithic and Early Bronze Age populations to compare their morbidity. It aims to identify differences in skeletal lesions and examine potential correlations with mortality, sociocultural and ecological changes.

3. Materials and Methods

The skeletal material originates from different geographically and temporally separated archaeological sites in Baden-Württemberg. The Final Neolithic sites cluster along the Tauber River, except for the site of Heilbronn, which aligns with the Early Bronze Age sites in the Neckar River region, totalling 340 individuals, of which 322 were suitable for anthropological analysis, from 17 sites (cf. Study II: Map and List of skeletal samples in Figure 1 and Table 1. Note that one female individual was added to Ammerbuch-Reusten “Grüninger” after the data analysis, totalling 340 individuals instead of 339 as reported in Study II). Thirteen cemeteries are associated with the culture of the Corded Ware complex (ca. 2900–2100/1800 BC) of the Final Neolithic, and four with the culture of the Neckar group (ca. 2200–1600 BC) of the Early Bronze Age in this region.

The Final Neolithic samples are totalling 250 skeletons. Twelve Final Neolithic sites in the Tauber River valley comprise three large (Tauberbischofsheim-Impfingen, Tauberbischofsheim-Dittigheim, and Lauda-Königshofen) and nine small (Bad-Mergentheim-Althausen, Grünsfeld-Krensheim, Lauda-Königshofen/Gerlachsheim, Tauberbischofsheim (three sites), Weikersheim, Werbach-Wenkheim and Wertheim-Reicholzheim) burial sites (Dresely, 2004; Trautmann, 2012). Heilbronn is the fourth large burial site located in the northern middle Neckar region. They generally share similar burial practices with rectangular to oval grave pits, in which individuals were buried in crouched position. Bipolar gender differentiation was practiced, with bodies predominantly oriented along a northeast-southwest axis or east-west axis. Males were typically positioned on their right, while females were placed on their left side. Albeit, a considerable number of inverted gender positions were observed (Dresely, 2004; Ortolf, 2014; Trautmann, 2012).

The Early Bronze Age samples encompass 73 skeletal remains from two larger cemeteries (Ammerbuch-Reusten, Remseck-Aldingen) and two cemeteries (Kirchheim unter Teck, Gerlingen) with only few graves. Typical burial customs of the Neckar region were followed, characterised by rectangular grave pits frequently containing stone constructions. Individuals were interred in a crouched position according to bipolar gender differentiation, with orientations along the northeast-southwest, east-west, or north-south axes. Males were typically placed on their left side, and females on their right (Krause, 1988; Lau, 1950; Zürn, 1975). However, Ammerbuch-Reusten deviates from this pattern marked by the absence of stone constructions, a scarcity of grave goods, and numerous exceptions to body orientation

and gender differentiation (Spatzier, 2023, p. 169).

However, not all sites and skeletons were used for each study, decision was based on accessibility and preservation of skeletons, comparability of skeletal data, and research question.

Each of the three studies presented here applied different methods of classic palaeoanthropology to address the research questions outlined above. Previous to the respectively used research method, age-at-death and sex was estimated for each skeletal remain based on standard macroscopic osteological techniques as detailed in each study, or where available taken from the literature (cf. Study II; Dresely, 2004; Trautmann, 2012). More detailed information is provided in the manuscripts included in this cumulative dissertation.

3.1 Study I (Appendix A)

The dental remains of four Final Neolithic (Heilbronn, Tauberbischofsheim-Impfingen, Tauberbischofsheim two sites) and three Early Bronze Age (Remseck-Aldingen, Ammerbuch-Reusten, Kirchheim unter Teck) sites presented in this cumulative dissertation were included in the first study. In order to cover a subsequent chronological period, a comparative sample of individuals from the Early Iron Age Hallstatt culture (ca. 750-450 BC) were included. The skeletons originate from the same cemetery as the Corded Ware culture individuals from Tauberbischofsheim-Impfingen (for detailed sample descriptions see Study I: Appendix A). For analysis, the Corded Ware cemeteries of Tauberbischofsheim-Impfingen and Tauberbischofsheim were combined. This sums up to 144 human skeletal remains from six archaeological locations dating between ca. 2900-1600 BC and ca. 750-450 B. (cf. Study I: map and list of sites in Figure 1 and Table 1).

To identify biological relatedness, dental morphological features were used as they are regarded to be heritable and selectively neutral (Irish et al., 2020; Rathmann et al., 2017; Rathmann and Reyes-Centeno, 2020; Scott et al., 2018). For this, two types of dental data were collected: continuous data (metric traits) and discontinuous data (non-metric traits). All dental traits were recorded on the permanent dentition following standard procedures (Buikstra and Ubelaker, 1994; Hillson et al., 2005; Mayhall, 1992; Scott and Irish, 2017; Turner II et al., 1991). The continuous data comprises 88 variables of the upper and lower dentition, consisting of maximum length, width, and diagonal diameter at the tooth crown and cement-enamel junction. All measurements were taken preferably on left teeth with a Mitutoyo pointed blade digital sliding calliper with 0.01 mm accuracy. All available measurements were used for

analysis. The discontinuous data involves 111 nominal and ordinal trait variables of the crown, root, and jawbone following the Arizona State University Dental Anthropology System (ASUDAS) (Scott and Irish, 2017; Turner II et al., 1991). If both antimeric teeth were present, the tooth with the highest expression was scored (individual count method) and only key teeth, which are most stable in expression of traits, were used for analysis (Scott et al., 2018; Scott and Irish, 2017). Furthermore, ordinal traits were not dichotomised to capture as much variation as possible in small-scale inter-individual relationships. Subsequently, several standard data pre-processing and quality control procedures were applied to exclude intra-observer error, sexual dimorphism, surplus and redundant data (for details see Study I pre-processing procedure, and Study I: Appendix B Table B.1 to B.6). These steps reduced the sample to 64 individuals from five archaeological sites and 85 variables (56 metric, and 29 non-metric traits; cf. Study I: Table 2 and 3). Finally, it was required to re-code specific trait variables for coherence (i.e., if some grade expressions were missing) and treat particular ordinal-scale variables as nominal-scale variables (i.e., if only two grade expressions were represented).

Pearson correlations were applied to the final pre-processed dataset to visualise correlations structures, revealing a high amount of integration within dental continuous variables and independence within dental discontinuous variables as well as between both variable types (cf. Study I: Figure 2).

The dental data set was then analysed in the statistics program R using the new FLEXDIST tool. It is a flexible software tool for estimating inter-individual distances from correlated, mixed, fragmented, and high-dimensional data that constitutes an alternative to the Gower distance measurements. However, FLEXDIST and the simulation framework where FLEXDIST was compared to the Gower coefficient was conceptualised and carried out by a collaborator and its methodologies will not be discussed in this dissertation (for details see Study I in Appendix A).

3.2 Study II (Appendix B)

Study II examines the demographic pattern of the total Final Neolithic and Early Bronze Age sample (cf. Study II: map and list of sites in Figure 1 and Table 1), which was based on age-at-death and sex data. With the exception of the Final Neolithic sites examined in Study I, data for the remaining Corded Ware skeletons were obtained from previous publications (Dresely, 2004; Trautmann, 2012) as the methods were similar and results assumed to be comparable. Individuals without age determination and skeletal fragments without clear assignment to a

buried individual were excluded from analysis, which sums up to 250 Final Neolithic skeletal remains and 72 Early Bronze Age individuals from 17 sites.

To reconstruct the demographic history of these populations, life tables were calculated (Acsádi and Nemeskéri, 1970). To ensure a sufficient sample size, life tables were constructed for the four large Corded Ware cemeteries (Heilbronn, Tauberbischofsheim-Impfingen, Tauberbischofsheim-Dittigheim, Lauda-Königshofen), the two large Neckar group sites (Ammerbuch-Reusten, Remseck-Aldingen), and two composite samples representing all sites from each cultural period. For analysis, individuals were attributed to age categories in 5-year intervals and equally distributed if spanning more than one category (Bocquet-Appel, 2002). Adult individuals with insecure sex determination were still included in the sex-differentiated life tables to increase sample size and improve statistical reliability. The Friedman rank sum test and the Wilcoxon rank sum test were used to assess significant differences in the number of dead, mortality, and life expectancy across the two composite samples and the six large cemeteries.

3.3 Study III (Appendix C)

This study includes the skeletal and dental remains of 72 individuals from five Final Neolithic sites (Heilbronn, Tauberbischofsheim-Impfingen, Tauberbischofsheim (two sites), Weikersheim), and 72 individuals from four Early Bronze Age sites (Ammerbuch-Reusten, Remseck-Aldingen, Kirchheim unter Teck, Gerlingen) (cf. Study III: map and list of sites in Figure 1 and Table 1).

All individuals were examined macroscopically for a range of pathological conditions. Dental pathologies, including calculus, caries, and abrasion, were recorded following established protocols (Brothwell, 1981; Grupe et al., 2015; Smith and Knight, 1984). Periapical lesions and signs of periodontitis were assessed based on their presence or absence. Degenerative joint disease was evaluated in adult individuals across ten joint systems (jaw, shoulder, elbow, wrist/hand, cervical spine, thoracic spine, lumbar spine, hip, knee, and ankle/foot), with severity scored according to Brothwell (1981) and Steckel et al. (2006). Schmorl's nodes were also documented, with attention to their location and size within the vertebral bodies. Non-specific stress indicators included cribra cranii, cribra orbitalia, linear enamel hypoplasia, and periosteal reactions on lower limb bones. Cribrotic lesions and periosteal reactions were recorded as present or absent. Linear enamel hypoplasia was further assessed for severity and estimated age of formation, based on the criteria by Grupe et al. (2015)

and Reid and Dean (2006). Traumatic lesions were categorised into fractures, osteochondritis dissecans, and trepanation. Fractures and trepanations were recorded according to their location, type, timing, and stage of healing. Osteochondritis dissecans was evaluated only in adults, following Vikatou et al. (2017). Neoplastic lesions were surveyed across the entire skeleton, with any observed cases recorded by location and lesion type. For further discussion, detailed descriptions, and individual adaptations of established recording protocols, see Study III in Appendix C. Due to conservational constraints and small sample sizes ordinarily scored pathologies, except for dental wear, were dichotomised prior to statistical analysis (Mardini et al., 2023; Vergidou et al., 2022). For dental wear and vertebral degenerative joint disease, in which multiple anatomical regions were scored, a single average score was calculated for tooth type and vertebral region. To increase sample size, subadults transitioning to adulthood and adults with uncertain sex determination were included in the adult sex sample. Moreover, although pathological conditions tend to accumulate or express more severely with age, no age group distinctions were made due to limited sample sizes. Specimens with insufficient bone or tooth preservation for the identification of a specific condition were excluded from analysis. Pathology frequencies were calculated per individual, for dental calculus and caries additionally per tooth. Several statistical comparisons were conducted to test the association of each pathology with sex and cultural period using Chi-square test, Fisher's exact test, Wilcoxon rank-sum test, and Kruskal-Wallis test.

4. Results and Discussion

This chapter outlines the key findings from the three articles and reviews the main contributions of this PhD project to the diachronic analysis of population development in Southwest Germany.

4.1 Study I (Appendix A): Reconstructing the Population History

The first study evaluated genetic affinities between the Corded Ware and Neckar group individuals from the Taubertal and Neckar River regions, supplemented with an Early Iron Age sample, using inter-individual biodistance analysis based on dental metric and non-metric traits. Previous anthropological research focused primarily on Corded Ware populations, while the Neckar group remained understudied and potential diachronic trends remained unnoticed.

Hence, this pilot study provides a foundation for subsequent bioarchaeological analyses of these populations, with the aim of identifying patterns of diachronic biological and sociocultural change and development.

The results indicate a high level of overlap in the PC plot in individuals both in temporal and geographical dimension, suggesting biological resemblance and population continuity in the Final Neolithic, Early Bronze Age, and Early Iron Age in Southwest Germany (see Study I: Figure 4). This is supported by biodistance studies from neighbouring regions that show similarity in populations during these time periods and a clear separation from pre-Neolithic samples (Coppa et al., 2007; Cucina et al., 1999), which is reinforced by aDNA findings in central Europe (Allentoft et al., 2015; Brunel et al., 2020; Fischer et al., 2022; Haak et al., 2015; Olalde et al., 2018).

When considering each of the five sites separately, four individuals from Heilbronn, Tauberbischofsheim-Impfingen, Remseck-Aldingen, and Tauberbischofsheim-Impfingen (Early Iron Age) appear slightly more divergent, despite overall overlap in PC space within archaeological contexts (see Study I: Figure 5). Notably, these four individuals are subadults or in transition to adulthood. Their distinct appearance may reflect childhood mobility or non-local origins, possibly as foster children from different communities (Knipper et al., 2017; Mittnik et al., 2019; Müller-Scheeßel et al., 2015; Sjögren et al., 2020). The subadult from Heilbronn also stands out due to an atypical orientation along the northeast-southwest axis. However, a relation to sex was not observed in the subadult individuals.

As different levels of variation are discernible, yet only 13% of total variance is accounted for by the first two PCs, intra-site variation was quantified as the average distance of each individual to the respective group centre (see Study I: Figure 6). Intra-site variation decreased over time from the Final Neolithic to the Early Bronze Age, which is also reported in aDNA studies. They argue the Neolithic ancestry, comprising Mesolithic hunter-gatherers, early Neolithic farmers, and Steppe pastoralists, shows a gradual decline in the Steppe pastoralists component alongside an increase in early Neolithic farmer ancestry, resulting in a genetic homogenisation and reduced variation from the Final Neolithic onwards (Furtwängler et al., 2020; Mittnik et al., 2019; Patterson et al., 2022). Striking is the low variation observed in Remseck-Aldingen, which may indicate an isolated group that experienced restricted gene flow from those gene pools. The uncommon north-south burial orientation, more typical of other regions in Central Europe, further support this theory. In contrast, the increase in intra-site variation from the Early Bronze Age onwards could reflect rising mobility and varying degrees of admixture, as reported in aDNA analyses (Brunel et al., 2020; Feldman et al., 2021;

Fischer et al., 2022; Loog et al., 2017; Stolarek et al., 2018).

Nevertheless, it needs to be noted that the small sample sizes may limit the ability to draw meaningful conclusions about intra-site variation and diachronic trends, particularly given that biodistance studies are generally more effective at broader spatial scales than at regional levels (Hubbard et al., 2015; Irish et al., 2020; Paul and Stojanowski, 2017; Rathmann et al., 2017; Rathmann and Reyes-Centeno, 2020; Stojanowski and Hubbard, 2017). Thus, although the results generally align with findings from various disciplines, future research should incorporate additional samples with larger sample sizes to enable more detailed inferences about population history in Southwest Germany.

4.2 Study II (Appendix B): Demographic Characterisation

The second study examined the demography of Corded Ware and Neckar Group populations. By re-evaluating previously published data from the Tauber valley and incorporating the new populations from the Neckar region, it was possible to establish a more comprehensive overview of demographic developments from the Final Neolithic to the Early Bronze Age. The analysis demonstrated diachronic trends and regional variations in number of dead, mortality and life expectancy (see Study II: Figure 2 to 5).

Differences between sites are most pronounced in the subadult age categories, particularly during the Early Bronze Age. The near absence of individuals in the youngest age group at Ammerbuch-Reusten may reflect poor skeletal preservation due to agricultural activity or different burial practices for non-adults. In contrast, Remseck-Aldingen is characterised by a predominance of the youngest age group, especially 2-4-year-olds. This pattern may reflect stress or specific weaning practices, as preliminary results of enamel hypoplasia indicate an earlier occurrence in this sample, corroborated by findings in Study III. Additionally, the site's distinctive features and potential isolation were noted in Study I. Yet, in both time periods, female infants exhibit higher mortality rates than males. In patrilocal societies, where male offsprings were potentially more culturally valued, reduced parental investment or female infanticide may have contributed to this pattern (Rebay-Salisbury et al., 2020; Trautmann, 2012). Trautmann has also hypothesised this explanation for sites in the Tauber region. However, a preferred sex in burial practices or signs of trauma against children are not indicated, albeit preservation, especially of cranial bones, and violent deaths without skeletal involvement hamper interpretations. Additionally, the morphological sexing of subadults is prone to error and the high number of unsexed individuals may account for the apparent excess

of females.

Adolescence emerges as the next critical period in life of the Early Bronze Age sample, although this is evident only in females from Ammerbuch-Reusten. Combined with high mortality among young adult females in both Early Bronze Age sites, this likely reflects risks of pregnancies and parturition. Studies indicate frequent adolescent pregnancies in Early Bronze Age Europe (Pany-Kucera et al., 2020; Rebay-Salisbury, 2017; Rebay-Salisbury et al., 2018), however, this is not a general trend, as increased female mortality related to the reproductive period varies across regions and time (Nicklisch, 2017; Staskiewicz, 2018a, 2018b; Tornberg and Vandkilde, 2025). These variations suggest differing cultural perceptions of womanhood, leading to regionally and chronologically distinct ages for marriage and first pregnancies.

Further sex-based differences become apparent in the Final Neolithic, where females consistently exhibit higher mortality and lower life expectancy than males. In the Early Bronze Age, however, female conditions improve after the reproductive period, resulting in more balanced mortality and life expectancy between the sexes. This suggests that cultural and social transformations from the Final Neolithic to the Early Bronze Age positively affected female living conditions. While this may reflect a regional pattern, it is important to note that diachronic trends in sexual dimorphism vary across different geographic areas (Alison A. Macintosh et al., 2014; Macintosh et al., 2016; Nicklisch, 2017).

Despite the relative demographic uniformity of the Final Neolithic, the site of Heilbronn deviates from this pattern, exhibiting low numbers of infants and elevated numbers of middle-aged adults. Epidemics or natural disasters appear unlikely, given the unsuitable distribution of deceased. The low number of infants may be explained by the aforementioned reasons. While warfare or conflicts could account for the increased number of middle adult individuals (Fernández-Crespo et al., 2023; Fibiger et al., 2023; Meyer et al., 2018), the presence of both sexes and absence of trauma make this hypothesis improbable and, currently unexplained. Interestingly, this observation coincides with the inverted bipolar burial practice. This may reflect mutually adaptive processes between the Corded Ware and Bell Beaker culture indicated from 2480 cal BC onwards (Großmann, 2016). However, the majority of the radiocarbon-dated atypical graves predate this interaction, highlighting the complexity of the underlying social and cultural dynamics and underscoring the need for further investigation.

The long-standing debate surrounding limited sample sizes and inaccuracies in age and sex estimation in palaeodemographic analyses raises concerns about how accurately skeletal samples reflect past populations (Bocquet-Appel and Masset, 1982; Boldsen et al., 2022;

DeWitte, 2018; DeWitte and Stojanowski, 2015; Wood et al., 1992; Wright and Yoder, 2003). To enhance statistical validity while accounting for regional variation, we combined samples from culturally similar contexts but treated each site individually in the analysis. Additionally, the application of multiple well-established methods for age and sex estimation helped to mitigate methodological limitations. While our findings generally align with previous European studies, demographic patterns among subadults, particularly regarding sex, should be interpreted cautiously and ideally supported by chemical or genetic validation.

4.3 Study III (Appendix C): Palaeopathological Characterisation

The third study investigates different pathological conditions in Corded Ware and Neckar group individuals. The aim was to obtain a comprehensive and detailed understanding of the physical burdens experienced by these populations. Additionally, this research investigates correlations with mortality patterns identified in the previous study and cultural changes. The results show a complex interrelation of chronological, regional, and sex-related factors influencing disease prevalence, while mortality patterns seemed to be less correlated (see Study III: Tables 2-7, Figures 2-6, as well as Tables A1-3 and Figure A1 in the Appendix).

Dental pathologies provide direct insights into dietary habits and suggest sex-based differences in the present samples. Due to the frequent post mortem loss of calculus, frequencies were likely more stable over time than preserved remains indicate. Among subadults, increased calculus frequencies in the Early Bronze Age could reflect a calculus inducing weaning diet, or may be the result of a higher proportion of juveniles in the sample. Caries frequencies were comparable over time, despite some site-specific variation. Most notably, Tauberbischofsheim-Impfingen shows the lowest rates that could be attributed to higher meat consumption, as indicated in a previous study (Trautmann, 2012). An increase in caries in Early Bronze Age males and females, and particularly per tooth among females, could imply a shift towards more cariogenic diets, or frequent snacking during preparation in females (Lukacs and Largaespada, 2006). Tooth abrasion patterns also reveal dietary differences by sex. Corded Ware men showed nearly identical and consistently higher wear scores than women. In contrast, Neckar Group males from Remseck-Aldingen exhibit the lowest abrasion. Different preparation techniques for men and women, or food reserved for men may explain this pattern, which is in agreement with evidence from Central and South Germany (Münster et al., 2018; Sjögren et al., 2016). Yet, elevated tooth wear in Corded Ware females from Tauberbischofsheim-Impfingen and Neckar Group males from Ammerbuch-Reusten may also indicate manipulative use of teeth.

Increased abrasion and an associated periapical lesion with tooth loss of the central incisors further hints at teeth used as tools in a male individual from Ammerbuch-Reusten. Since periapical lesions were only found in men, this may reflect more versatile and strenuous use of the teeth among males, or females had better oral hygiene. The latter one, however, does not account for the higher prevalence of periodontal disease in Neckar Group females. This also contrasts findings in eastern Central Europe, where males were predominantly affected through time (Hukelova, 2016), suggesting temporal or cultural shifts in diet or hygiene practices.

Degenerative joint disease reveals shifts in chronology, sex, and affected joints, indicating different physical activities from the Final Neolithic to the Early Bronze Age and male-female role division. In Corded Ware men, affected joints varied by site, reflecting population-specific activity patterns. Cervical spine and one-sided shoulder degeneration in Tauberbischofsheim-Impfingen suggests overhead tasks in throwing or lifting motions, such as carpentry, hunting, and herding or hide-processing (Schmitt et al., 2003; Shaw et al., 2012; Villotte and Knüsel, 2014). In Heilbronn habitual use of the left elbow and hand, lower limbs, and primarily thoracic joints imply a wide range of activities which involve mobile one-handed tool use related to agricultural fieldwork and livestock tending (A. A. Macintosh et al., 2014; Alison A. Macintosh et al., 2014). Findings from other Final Neolithic samples support our results (A. A. Macintosh et al., 2014; Sládek et al., 2006a, 2006b; Trautmann, 2012) and we conclude, that the Corded Ware populations had regional specialisations and pursued diverging subsistence strategies, as also indicated by isotope analyses (Sjögren et al., 2016). Corded Ware females show a more uniform pattern by bilateral upper limb loading and involvement of foot joints, consistent with repetitive tasks such as cereal processing using saddle querns in squatted or seated positions. Even though our results are in agreement with other studies (Macintosh et al., 2017; Trautmann, 2012), high levels of mobility as hypothesised for the Tauber region (Großmann, 2021) are not indicated or might go unnoticed due to low preservation of lower limb joints. Spinal joints were underrepresented and not included in the interpretation. In the Neckar group different joints were affected, but role divisions were still observable. Men showed a less diverse pattern that was more accentuated in the cervical spine and opposing shoulder and elbow. This suggests specialised manual tasks like construction and woodworking, metal processing, and leatherworking, which played a pivotal role in the Bronze Age socio-economic developments (Harding, 2002; Alison A. Macintosh et al., 2014). Furthermore, degenerative processes in the jaw corroborate the hypothesis of teeth used as tools. Neckar Group females exhibited greater involvement of the hip and knee, compared to the Corded Ware females, suggesting additional lower limb loading, possibly stationary or mobile, which is also

reflected in increased thoracic and lumbar degeneration. The results are in concordance with findings from other regions during the Early Bronze Age (Hukelova, 2016; A. A. Macintosh et al., 2014; Macintosh et al., 2017), suggesting a shift from Neolithic agricultural processing to settlement bound tasks such as pottery, textile and leather production. Schmorl's nodes were rare and evenly distributed across cultures, reflecting either isolated cases of strenuous labour or individual susceptibility. This contradicts the increasing prevalence over time in eastern Central Europe (Hukelova, 2016), indicating geographical lifestyle differences or preservation bias.

Nonspecific stress indicators were generally more prevalent during the Final Neolithic, with distinct patterns across populations. *Cribra cranii* and *cribra orbitalia*, which develop during the subadult growth period, and particularly orbital lesion frequency indicate widespread stress in early life among all groups. The different distribution of cribrotic lesions, also noted in other Tauber region sites (Dresely, 2004), may reflect their distinct aetiologies (Rivera and Mirazón Lahr, 2017). Notably, adult females exhibit a higher prevalence of *cribra orbitalia*, while males were largely unaffected, except in Tauberbischofsheim-Impfingen, aligning with a higher survivorship among subadult females reported in Study II. The population of Tauberbischofsheim-Impfingen appears to have endured prolonged stress, affecting all age groups, potentially linked to the before mentioned distinct subsistence strategy and nutritional impairment. Elevated frequencies of linear enamel hypoplasia in all samples further support evidence of increased childhood stress. Most defects accumulate between 2.7 and 3.0 years, likely reflecting the weaning and post-weaning period. While Corded Ware populations showed a constant average, the Neckar group populations displayed greater variability, spanning the youngest and oldest age of occurrence. This corroborates the assumed earlier weaning age of Remseck-Aldingen in Study II and their unique socio-cultural characteristic in Study I. Sex-based differences in linear enamel hypoplasia timing were also observed: in the Neckar group, defects developed earlier in females than in males, which is less pronounced in the Corded Ware. This may suggest sex-specific child rearing and weaning during the Early Bronze Age culture, but also for the region in general as similar findings were reported from a neighbouring Corded Ware site (Trautmann, 2012). In contrast, periosteal reactions, which can develop throughout life, were most frequent among Corded Ware adults, particularly females, indicating elevated adult stress levels. Lower rates in the Neckar group could be explained by earlier mortality before lesions could develop, but demographic data from Study II does not fully support this. Instead, the lesions may reflect labour-related stress or movement across landscapes (Caruso and Nikita, 2024; Pilloud and Schwitalla, 2020) consistent with subsistence

strategies in the Corded Ware population. A notable high prevalence of periosteal reactions in subadults from Ammerbuch-Reusten further points to harsh living conditions in some Early Bronze Age groups, a pattern that is consistent with observed from a contemporaneous site in Austria (Furtwängler et al., 2025; Rebay-Salisbury et al., 2018).

Trauma prevalence varied by population and sex. Fracture rates among adults remained relatively stable over time, though men were more frequently affected than women. The occurring fracture type suggests accidental indirect force rather than interpersonal violence. The anatomical distribution indicates sex-specific labour activities, with forearm fractures more common in females and clavicular and rib fractures in males. The postcranial frequencies align with other Final Neolithic sites in Europe (Dresely, 2004; Hukelova, 2016; Trautmann, 2012), but differ from the increased rates reported for the Early Bronze Age in eastern Central Europe (Hukelova, 2016). Contrary to these studies, fractures of the skull and in subadults were not observed most likely due to poor preservation. Trepanation was observed in two Corded Ware male individuals, the one from Tauberbischofsheim was analysed in an earlier study (Dresely, 2004) and not further considered. The individual from Heilbronn survived the surgery, as indicated by remodelled margins. Poor preservation prevents a definitive interpretation of fresh cut marks as peri- or postmortem, or taphonomic artifact. The purpose of the trepanation remains speculative, with therapeutic, ritual, or experimental motives. Nevertheless, the procedure implies medical knowledge, as it was conducted near the superior sagittal sinus. Two nearly identical trepanations from neighbouring sites (Dresely, 2004; Trautmann, 2012) suggest shared techniques and regional specialisation. Frequencies and anatomical distribution of osteochondritis dissecans lesions increased over time, except for foot joints, which were consistently affected across sites. Sex-differences were observed particularly in the Early Bronze Age, likely reflecting role division in daily labour and task specialisation in the Early Bronze Age. Females commonly show lesions in elbow, hand and knee, and males in shoulder and elbow, which is similar to the findings in degenerative joint disease.

Neoplastic diseases were observed only in the Early Bronze Age. Their absence in the Final Neolithic may be partly due to taphonomic factors, as preservation decreases over time, and evidence of neoplasms older than four millennia are very rare (David and Zimmerman, 2010; Hunt et al., 2018; Lieverse et al., 2014). However, greater genetic predisposition due to increased migration, or changes in lifestyle, culture, and environment, such as food preparation and smoke exposure during labour, likely increased carcinogenic risk in the Early Bronze Age.

Palaeopathological analyses can be affected by several sources of bias. Disease frequencies are directly dependent on skeletal preservation. Using only well-preserved

skeletons would improve data quality but also reduce sample size and potentially omit relevant pathologies. We therefore included all skeletons and assessed individually whether preservation was sufficient in combination with completeness thresholds for specific bones. Moreover, disease prevalence can have different meanings, requiring consideration of various influential factors and careful interpretations. By analysing several stress indicators and including demographic data and archaeological context, we aimed to provide a more holistic understanding. Finally, our two-category age classification limits the identification of age-related disease patterns. Larger sample sizes would allow for more precise age groups in future studies.

5. Concluding Remarks and Future Directions

This dissertation evaluated human skeletal remains from different cultural background of the Final Neolithic and Early Bronze Age in Southwest Germany. The aim was to reconstruct population development using both innovative and traditional anthropological techniques, applied to largely understudied material. This approach allowed us to identify not only diachronic trends but also to recognise regional development as a decisive factor in shaping population histories. In Study I, dental data provided initial insights into the population history and revealed population continuity from the Final Neolithic to the Early Bronze Age, excluding large-scale population migrations. The presence of comparatively non-local subadult individuals suggests movement during childhood, potentially as foster children from neighbouring populations. Changes in genetic variability over time were most pronounced in the Early Bronze Age site of Remseck-Aldingen, possibly indicating a relatively isolated community. Through demographic analyses in Study II, we identified chronological shifts and, more importantly, regional patterns. Most changes are likely related to sociocultural factors, with the strongest impact observed among females. Increased rates of early female infant mortality in both periods suggest neglect or possible female infanticide, although secure sex identification through DNA or proteomic analysis is required to confirm this. High mortality among Early Bronze Age female juveniles may reflect adolescent pregnancies, possibly due to shifts in perceptions of womanhood and marital ages. Female life expectancy in both periods was initially lower than that of males, with the disparity persisting in the Final Neolithic. In contrast, the Early Bronze Age shows more equal mortality rates from middle adulthood onwards, potentially indicating improving living conditions. Study III offered deeper insights

into sociocultural developments through the analysis of pathologies. Dental diseases suggest sex-related dietary variation and the use of teeth as tools. Degenerative joint disease also indicates both sex-specific labour and temporal shifts in habitual activity. This is linked to local specialisation followed by homogenisation of tasks. Evidence of non-specific stress suggests persistent childhood stress and differing weaning practices between sexes and populations, corroborating assumptions for the potentially genetic and sociocultural distinctiveness of Remseck-Aldingen. Trauma patterns varied: trepanations prevailed in the Final Neolithic; traumatic joint lesions became more diverse, and both more frequent and sex-dependent, during the Early Bronze Age; whereas fracture rates remained stable over time, suggesting non-intentional causes. The emergence of neoplastic diseases in the Early Bronze Age may reflect genetic predisposition or an accumulation of risk factors related to socioeconomic changes. Notably, overall pathology rates do not correlate directly with mortality patterns observed in Study II, suggesting that resilience, cultural practices, and lifestyle changes played a more decisive role.

These studies contribute to the growing interest in population development during the third to mid-second millennia BC in Europe by addressing significant gaps in the Southwest Germany anthropological record. While previous research (Dresely, 2004; Trautmann, 2012) has offered valuable insights into Corded Ware societies in this region, the studies presented here highlight the importance of diachronic comparisons for detecting sociocultural trends over time. Future research should therefore incorporate skeletal remains from the Final Neolithic Bell Beaker culture to include all major cultural complexes in that region and achieve more comprehensive insights into local sociocultural developments.

Although we were able to corroborate some of our conclusions, and our results are generally consistent with findings from neighbouring regions, focusing on isolated factors risks misinterpretation. The significance of our results would be strengthened by multivariate approaches, including secure sex identification through genetics or proteomics, particularly in subadults, as well as isotope analyses for diet reconstruction and mobility studies.

In conclusion, this dissertation contributes to the growing interest in population development during the Final Neolithic and Early Bronze Age in Germany. The findings offer important insights into the biological responses of past populations to sociocultural changes. However, there is significant potential for future comparative research in the form of further unstudied skeletal material from both older and recent excavations.

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Appendix A

Paper I

Estimating inter-individual Mahalanobis distances from mixed incomplete high-dimensional data: Application to human skeletal remains from 3rd to 1st millennia BC Southwest Germany

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Estimating inter-individual Mahalanobis distances from mixed incomplete high-dimensional data: Application to human skeletal remains from 3rd to 1st millennia BC Southwest Germany

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ABSTRACT

Biological distance, or biodistance, analysis aims to identify relatedness among human skeletal remains from archaeological contexts. However, analyses are often hindered by the fragmentary and heterogeneous nature of the data. Here, we introduce FLEXDIST, a flexible software tool for estimating inter-individual distances. FLEXDIST takes correlations among variables into account, works with multiple variable scales (i.e., nominal, ordinal, continuous, or any mixture thereof), handles missing values, and allows for high-dimensional data. Conceptually, FLEXDIST computes Mahalanobis-type distances using mixed data PCA iterated over multiple randomly imputed datasets to take uncertainty resulting from incomplete cases into account. Using a simulation framework, we demonstrate the performance of FLEXDIST compared to the Gower coefficient. We then apply FLEXDIST to a newly collected dataset comprising heritable and neutrally evolving dental morphological features from 64 archaeological human remains from Southwest Germany in order to explore population history along a temporal transect spanning the Final Neolithic to Early Iron Age (2900-450 BC). In agreement with previous archaeological, genetic, and isotopic studies from neighbouring regions, we find evidence for population continuity, alternating levels of variability through time, and mobility during childhood. A fully automated R script for performing FLEXDIST is available at <https://doi.org/10.5281/zenodo.7869075>.

1. Introduction

Biological distance, or biodistance, analysis is an integral component of bioarchaeological research and aims to identify relatedness among human skeletal remains based on heritable and neutrally evolving cranial and dental features (Buikstra et al., 1990; Larsen 2015; Hefner et al., 2016). Biodistance analysis is widely used for reconstructing past kinship structures and social organisation within archaeological sites (Alt and Vach 1995; Shimada et al., 2004; Stojanowski and Schillaci 2006; Pilloud and Larsen 2011; Paul et al., 2013; Nikita et al., 2019; Rathmann et al., 2022; Maaranen et al., 2022), for assessing ancient population structure and history on regional to global scales (Irish et al., 2017; Reyes-Centeno et al., 2017; Rathmann et al., 2019; Fidalgo et al., 2022; López-Onaindia et al., 2022; Akbar et al., 2023; Mardini et al.,

2023), or for investigating hominin phylogenies across taxa in palaeo-anthropological research (Athreya and Wu 2017; Irish et al., 2018; Bermúdez et al., 2023). Analytically, the degree of relatedness among observations (either single individuals or groups of individuals) is quantified with a multivariate distance measure that transforms the phenotypic data into numerical distance values between pairs of observations, summarised in a symmetrical distance matrix, where small values indicate similarity, and high values indicate dissimilarity.

Biodistance datasets have several characteristics that can make them challenging to analyse. First, skeletal expressions are highly integrated systems, and correlations among variables need to be taken into account analytically to avoid over-representing variation from expressions that co-occur, for example by using the well-known Mahalanobis (1936) distance. However, thanks to more refined data collection protocols,

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datasets are increasingly high-dimensional and comprise more variables than individuals, which can hamper many classical multivariate analyses, including the typical Mahalanobis solution. Second, datasets are often heterogeneous and comprise a mix of variables recorded on different scales, including continuous, ordinal, and nominal data (Howells 1973; Hauser and De Stefano 1989; Hillson 1996; Scott and Irish 2017). The different variable scales are routinely analysed separately, as many standard statistical tests do not accept or do not work well with mixed data, although more holistic approaches combining the different scales in a single analysis capture more variation (Lease and Sciulli 2005; Hefner et al., 2014). Third, datasets from archaeological contexts are typically highly fragmented and comprise excessive amounts of missing values, sometimes exceeding 30% (Mardini et al., 2023) or even 70% (Rathmann et al., 2022). As deletion of incomplete individuals and variables leads to significant data loss, missing values must be estimated, ideally using effective imputation techniques to predict plausible values (Kenyhercz and Passalacqua 2016; Kenyhercz et al., 2019; Wissler et al., 2022). However, imputation performance has been demonstrated to be higher for continuous than for discontinuous data (Wissler et al., 2022), perhaps related to differential degrees of integration and modularity within and between data scales.

Several inter-group distance measures have been developed to overcome these hurdles and be directly applicable to correlated, mixed, and fragmented datasets, most of them based on extensions of the Mahalanobis distance (Königsberg 1990; Bedrick et al., 2000; De Leon and Carrière 2005; Nikita 2015; Mardini et al., 2023). However, inter-individual distance measures that work in such cases are less visible in biodistance research. Among the most well-known is the Gower (1971) similarity coefficient expressed as a dissimilarity measure (Ricaud et al., 2010; Paul et al., 2013; Stojanowski and Hubbard 2017; Rathmann et al. 2019, 2022; Kharobi et al., 2021; Mardini et al., 2023). It can process mixed data by calculating distances variable by variable, which are then scaled and averaged to arrive at an overall distance. Missing values are handled by simply not contributing numerically to the calculation of the overall distance. Although appealing, the main disadvantage is that it assumes complete independence among variables, which is problematic when analysing highly integrated skeletal features. Practitioners often circumvented this problem by submitting the continuous portion of the mixed data (conventionally considered to be the most correlated) to a principal component analysis (PCA) to transform the variables into uncorrelated PCs which are then used together with the discontinuous data for Gower distance analysis (Paul et al., 2013; Stojanowski and Hubbard 2017; Rathmann et al. 2019, 2022; Mardini et al., 2023). However, this strategy is not fully satisfying because it only accounts for correlations in the continuous but not in the discontinuous variables. Moreover, conventional PCA requires complete data for all individuals without any missing values. Rathmann et al. (2022) and Mardini et al. (2023) used *k*-Nearest Neighbor (*k*NN) imputation prior to Gower distance analysis to predict missing continuous values, but *k*NN and other imputation techniques usually require large datasets with many complete individuals as reference cases (Kenyhercz and Passalacqua 2016; Wissler et al., 2022), and this may not be the case when dealing with small and fragmented archaeological datasets where most, if not all, individuals comprise missing values. Theoretically, this issue could be addressed by including larger external samples with better preserved individuals, but this may introduce spatiotemporal bias.

Here, we introduce a flexible software tool named FLEXDIST for estimating inter-individual distances from correlated, mixed, fragmented, and high-dimensional data. FLEXDIST is designed to provide an effective and user-friendly alternative to the Gower distance approach, bypassing the need for excessive data pre-processing steps and external samples. Conceptually, the procedure involves four steps: First, missing values in individuals with only partially observed data are replaced with randomly generated values using a multiple imputation approach, resulting in a large number of differentially imputed datasets. Second,

each imputed dataset is submitted to a mixed data PCA for estimating uncorrelated PCs, which are then used for arriving at an inter-individual Mahalanobis-type distance matrix. Third, the various distance matrices are combined for constructing a median pairwise distance matrix and confidence intervals reflecting the uncertainty about missing values. Fourth and finally, the first two PCs that explain most of the variation across individuals are visualised in a two-dimensional scatterplot, where each individual is displayed as a centroid estimate of the various imputed duplicates of that individual and a confidence ellipse around the centroid. Although none of these technical procedures are entirely new, their combination into a single software tool dedicated to bio-distance research is new to our knowledge. We demonstrate the performance of FLEXDIST in a simulation framework and compared its performance against the Gower distance approach.

We then apply FLEXDIST to a biodistance dataset collected from human skeletal remains in Southwest Germany, with the aim of investigating the regional population history across a time transect spanning the Final Neolithic to Early Iron Age (2900-450 BC). Archaeological, anthropological, isotopic, and genetic research, in particular, revealed that the prehistory of Central Europe during the third to first millennia BC oversaw highly dynamic interactions of diverse societies, involving several migration, admixture, and turnover events (Menk 1979; Vander Linden 2006; Desideri 2011; Desideri et al., 2012; Furholt 2014; Allentoft et al., 2015; Haak et al., 2015; Sjögren et al., 2016; Szécsényi-Nagy et al., 2017; Mathieson et al., 2018; Olalde et al., 2018; Brunel et al., 2020; Papac et al., 2021; Fischer et al., 2022). Much of our current understanding is built upon studies with supra-regional and pan-European sampling strategies that focus on long-term population trends. Although important, these studies cannot fully uncover the complex role of individuals within these processes, which have been demonstrated to vary subtly from one regional setting to another (Czarnetzki 1984; Desideri 2011; Kreutz 2011; Irrgeher et al., 2012; Oelze et al., 2012; Knipper et al., 2017; Mittnik et al., 2019; Furtwängler et al., 2020; Sjögren et al., 2020; Papac et al., 2021). Consequently, there is a need for further research with an emphasis on regional, high-resolution temporal transects in order to fill geographical and temporal sampling gaps. Our analysis provides the first systemic diachronic regional comparison of human skeletal remains from Southwest Germany associated with the Corded Ware complex, Neckar group, and Hallstatt culture.

2. Materials and methods

2.1. Introducing FLEXDIST

Conceptually, FLEXDIST involves the following steps: First, missing values in individuals with only partially observed data are replaced with randomly generated values. Several different values are generated for each missing entry, leading to a set of differentially imputed datasets. The variation across imputed dataset reflects the uncertainty about the missing values. The randomly generated values are sampled from predictive kernel density estimates derived from the distributions of the observed data. Sampling from kernel density estimates ensures that more probable values are more likely to be drawn (and less probable values less likely) and that the sampled values cannot be lower or higher than the minimum or maximum values in the observed data. The number of imputed datasets that should be generated is a trade-off between analytical precision and computational time. The more iterations, the better, and we recommend running at least 1000 iterations in order to ensure stable uncertainty estimates about the missing values.

As an optional step, the continuous variable portion of the data is converted into scale-free shape variables by dividing each measurement by the geometric mean for all measurements in each individual (Jungers et al., 1995). This procedure reduces the effect of size and sexual dimorphism on the generated inter-individual relationship structure.

Then, each imputed dataset is submitted to a mixed data PCA to

estimate a set of uncorrelated PCs. Mixed data PCA can be seen as a compromise between a conventional PCA for continuous variables and a multiple correspondence analysis (MCA) for discontinuous variables (Hill and Smith 1976). Discontinuous variables are transformed into dummy variables and are concatenated with the continuous variables. All variables are then standardised to give the same weight to each variable. Continuous variables are standardised by subtracting the column mean and dividing them by the standard deviation. Each dummy variable is standardised by dividing it by the squared root of the proportion of objects taking the associated discontinuous category. Lastly, a conventional PCA is performed on the concatenated and standardised dataset. If the dataset contains only continuous variables, this procedure is equivalent to a conventional PCA. If the dataset includes only discontinuous variables, this is equivalent to a conventional MCA.

In the next step, the uncorrelated PCs estimated for each imputed dataset are again standardised (by subtracting the column mean and dividing it by the standard deviation), and the PC scores are used as new variables for estimating a matrix of pairwise Euclidean distances across individuals. These distances are equivalent to inter-individual Mahalanobis-type distances. In high-dimensional datasets, only the first PCs that together explain at least 90% of the variation are used. The Mahalanobis-type distance matrices estimated from each imputed dataset are then organised in a three-dimensional data array (FLEXDIST_{array}), summarising the different distance matrices for the various imputation iterations. Additionally, three summary matrices are computed: The first one reports the median of the distribution of pairwise distance values (FLEXDIST_{median}), whereas the second and third report the upper and lower bounds of a 95% confidence interval for each pairwise comparison reflecting the uncertainty about missing values (FLEXDIST_{upper} and FLEXDIST_{lower}).

Finally, the results are visualised in a two-dimensional PCA plot (FLEXDIST_{plot}), illustrating in a visually intuitive way the relatedness among individuals taking into account the uncertainties resulting from missing data. For this, a mixed data PCA is estimated using a dataset where missing entries are replaced by the median values of the distribution of all randomly generated values in the various imputed datasets. The estimated PCA space is considered as central reference configuration. Then, all individuals in each imputed dataset are projected as supplementary individuals onto the PCA space of the reference configuration. Individuals without any missing values are projected exactly on their corresponding point on the reference configuration, whereas individuals with missing values are projected around their corresponding reference point. To ease display, all points belonging to the same individual are visualised as a single centroid estimate and a 95% confidence ellipse around the centroid. The size of the confidence ellipse increases with increasing number of missing values.

2.2. Simulation study

We conducted a simulation study to explore the relative performance of FLEXDIST compared against the Gower distance on datasets with varying degree of quality. We focused on four different scenarios: a low-dimensional data case with more individuals (100) than variables (20), and a high-dimensional data case with more variables (200) than individuals (100), one time with few missing values (10%) and one time with many missing values (50%). Variables were randomly chosen to be continuous, ordinal, nominal, or any mixture thereof, with different correlation levels ranging from weak to strong. For each of the four scenarios, we created 100 simulated datasets, for a total of 400. When simulating datasets, we followed Nikita (2015) and first generated artificial correlated continuous variables drawn from a multivariate normal distribution. Continuous variables were then categorised into mixed variables using the mean as threshold for transformation into nominal data, and the first, second, and third quartile as thresholds for transformation into four-rank ordinal data. Missing values were added per individual completely at random affecting all variables.

For each simulated dataset, we estimated FLEXDIST (in the form of FLEXDIST_{median}) and the Gower distance (following the protocols of Rathmann et al. (2022) and Mardini et al. (2023) where the continuous variables of the mixed data are transformed into PCs after imputing missing values with *k*NN). The results of FLEXDIST and the Gower distance were then compared to a benchmark containing information about the true distance structure. Similar to the procedures outlined in Nikita (2015), this benchmark was defined as a Mahalanobis distance matrix calculated over the un-categorised continuous variables without missing values. Pearson correlations were used to measure the agreement between the benchmark and the results obtained with FLEXDIST and the Gower distance. Results were visualised using violin plots.

2.3. Data collection

We then applied FLEXDIST to a biodistance dataset collected from 144 human skeletal remains retrieved from six archaeological locations in the upper and middle Neckar river and Tauber valley regions in the state of Baden-Württemberg, Southwest Germany (Fig. 1). The sites date to the Final Neolithic (ca. 2900-2000 BC), Early Bronze Age (ca. 2300-1600 BC), and Early Iron Age (ca. 750-450 BC), and are associated with the Corded Ware complex, Neckar group, and Hallstatt culture, respectively. Site and sample descriptions can be found in Appendix A.1. Summary information for the studied samples is provided in Table 1.

We used dental morphological features for biodistance analysis as they are considered to be heritable, selectively neutral, and an ideal data source for inferring genetic relatedness (Rathmann et al., 2017; Scott et al., 2018; Irish et al., 2020; Rathmann and Reyes-Centeno, 2020). Moreover, teeth are among the best-preserved elements in the skeletal record as they are more resistant to taphonomic processes than bone (Scott et al., 2018). Furthermore, teeth develop early during ontogeny and their form remains unchanged, except by wear or pathology. Two types of dental data were collected: continuous data (also called “metrics”) and discontinuous data (also called “non-metric traits”).

The continuous data comprises 88 variables of the permanent dentition, consisting of maximum length (mesiodistal), width

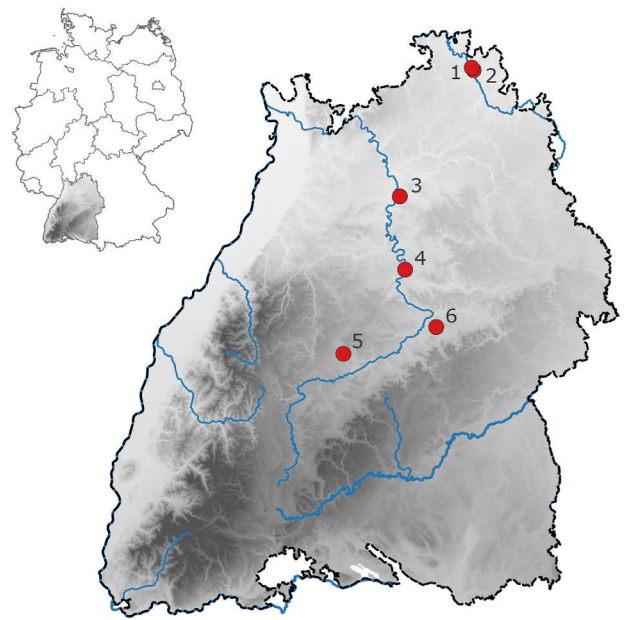


Fig. 1. Map of Baden-Württemberg (Southwest Germany) showing the geographic locations of the human skeletal samples analysed in this study: (1) Tauberbischofsheim (Final Neolithic); (2) Tauberbischofsheim (Early Iron Age); (3) Heilbronn (Final Neolithic); (4) Remseck-Aldingen (Early Bronze Age); (5) Ammerbuch-Reusten (Early Bronze Age); (6) Kirchheim unter Teck (Early Bronze Age).

Table 1

Summary of skeletal samples used in this study.

Sample name (time period in parentheses) ^a	Archaeological site	Cultural affiliation	Geographic origin	Radiocarbon date	n (total number) ^b	n (used for FLEXDIST) ^c
Heilbronn (FN)	Kirschengartenstraße	Corded Ware complex	Middle Neckar	2863-2471/2299 cal BC	23	13 (3/4/2/4)
Tauberbischofsheim (FN)	Impfingen, Rebhuhn	Corded Ware complex	Tauber valley	2622-1885/1624 cal BC	29	7 (2/-/1/4)
	Kirchelberg/Acker NOE West	Corded Ware complex	Tauber valley	2847-2031 cal BC	7	3 (1/-/-/2)
	Gärtnererei Scheuermann	Corded Ware complex	Tauber valley	3007-2494 cal BC	1	-
Remseck-Aldingen (EBA)	Halden II	Neckar group	Middle Neckar	2276-1743 cal BC	26	5 (2/-/-/3)
Ammerbuch-Reusten (EBA)	Stützbrunnen	Neckar group	Upper Neckar	1870-1519 cal BC	25	11 (1/1/-/9)
	Grüniger	Neckar group	Upper Neckar	1751-1511 cal BC	4	1 (-/1/-/-/)
	Kirchheim unter Teck (EBA)	Stuttgarter Straße	Neckar group	NA	1	-
Tauberbischofsheim (EIA)	Impfingen, Rebhuhn	Hallstatt culture	Tauber valley	NA	28	24 (4/10/1/9)

^a Abbreviations: FN = Final Neolithic, EBA = Early Bronze Age, EIA = Early Iron Age.

^b Total number of skeletons for which at least one dental feature was recorded.

^c Subset of skeletons submitted to FLEXDIST analyses (in parentheses number of adult males/adult females/adults of unknown sex/subadults).

(buccolingual), and diagonal (mesiobuccal-distolingual and mesiolingual-distobuccal) diameters at the tooth crown and cement-enamel junction. Only left teeth were measured, but when a tooth was missing, damaged, or affected by wear or pathology, the right antimer was used. Mesiodistal and buccolingual crown diameters were recorded following the methods by Mayhall (1992) and Buikstra and Ubelaker (1994). All other diameters were recorded following the procedures by Hillson et al. (2005). All measurements were taken with a Mitutoyo pointed blade digital sliding calliper with 0.01 mm accuracy. When analysing dental dimensions, studies often focus on polar teeth as they are assumed to be the most genetically stable (Pilloud and Larsen 2011; Sciuili and Cook 2016; Rathmann et al., 2022; Mardini et al., 2023). In this study we pursued an alternative standard approach by analysing all available measurements (Cucina et al., 1999; Hanihara and Ishida 2005; Bernal et al., 2010; Paul et al., 2013; Prevedorou and Stojanowski 2017) in an effort to maximise genomic coverage as pervasive integration through pleiotropy limits independent genomic information preserved in dental dimensions (Stojanowski et al., 2017).

The discontinuous data consists of 111 variables of the permanent dentition, comprising nominal and ordinal trait expression scores of crown, root and jawbone variants. Trait recording followed the reference standards of the Arizona State University Dental Anthropology System (ASUDAS) (Turner II et al., 1991; Scott and Irish 2017). Although we recorded ASUDAS traits on all teeth, we followed the standard protocol and used only traits on key teeth for further analysis, as morphological expressions on key teeth are considered most stable in terms of development and evolution (Scott and Irish 2017; Scott et al., 2018), and have been demonstrated to be less affected by pleiotropic effects (Stojanowski et al., 2018, 2019). To capture an individual's maximum genetic potential, the individual count method was used; if both antimeres were present, the side with the highest level of expression was scored (Scott and Irish 2017). Many ASUDAS studies dichotomise ordinal-scale trait expression scores into simplified categories of absence or presence, primarily to ease statistical analysis, however, this procedure also reduces information about trait expressivity. Thus, following Stojanowski and Hubbard (2017) and Paul and Stojanowski (2017), ordinal data were not dichotomised to retain as much variation as possible for the purpose of detecting small-scale inter-individual relationships.

Furthermore, age and sex were determined using standard osteological techniques, as detailed in Appendix A.2.

2.4. Data pre-processing

When analysing dental data, we follow the widely-held assumption that biodistance analyses based on a larger number of morphological

variants are generally more reliable than those based on only a few variants (Scott and Irish 2017; Stojanowski and Hubbard 2017; Scott et al., 2018). This has been explicitly demonstrated for example by Rathmann and Reyes-Centeno (2020) in the context of ASUDAS traits, who found that increasing the number of traits generally improves the capture of underlying genomic variation. While the best performance is achieved when using specific combinations of highly diagnostic traits, utilising at least 16 of any of the ASUDAS traits (regardless of which ones are chosen) significantly captures genomic variation across populations.

Before submitting the dataset to FLEXDIST, we performed several standard data pre-processing and quality control procedures commonly applied in individual-level biodistance research (Pilloud and Larsen 2011; Paul et al., 2013; Rathmann et al. 2019, 2022; Mardini et al., 2023): First, the data collector (S.L.) quantified the level of intra-observer error by recording the Final Neolithic individuals from the Tauberbischofsheim site ($n = 37$) twice, with an approximate interval of three months. Dental metrics from the two sessions were compared using paired Student *t* tests, and dental non-metric traits were compared using Cohen's Kappa tests. None of the comparisons was statistically significant, indicating that intra-observer error is negligible (Appendix B, Table B.1 and B.2).

We then tested for morphological differences that may result from sexual dimorphism. For this, 53 sex determined individuals were used to calculate Student's *t*-test for dental metric variables, Fisher's Exact test for nominal variables, and Mann-Whitney *U* test for ordinal variables. We found that 25% of the metric variables (22 of 88) and 5.5% of the non-metric variables (3 of 54) showed significant differences between sexes (Appendix B, Table B.3 and B.4). Hence, we used a scaling-approach to mitigate sex-specific size-effects on metric variables (see above) while sexual dimorphism in non-metric variables was removed by dropping affected traits from analysis (i.e., Enamel Extension UM1, Premolar Accessory Ridge UP2, Rocker Jaw).

When dental non-metric traits were collected on more than one possible key tooth (e.g., Anterior Fovea on LM1 and LM2) (Scott and Irish 2017), we following standard ASUDAS practices and used the key tooth exhibiting the highest number of individuals scored. Subsequently the following traits were dropped from analysis: Canine Distal Accessory Ridge UC, Anterior Fovea LM1, Reduced/Pegged/Missing UM3, Distal Trigonid Crest LM2, and Mid Trigonid Crest LM2.

Although FLEXDIST allows for missing values, we feel that excessive amounts of missing entries should be minimised to avoid comparing individuals who share no or very little data. Therefore, we first removed dental metrics of third molars as they are often congenitally absent. Then, we dropped variables and individuals with more than 50% missing values in a stepwise manner. Finally, non-metric dental variables that exhibit no variability between individuals were omitted.

These pre-processing steps reduced the original sample of 144 individuals and 199 variables (88 dental metrics and 111 dental non-metric traits), with an overall percentage of ~60% missing values, to a final sample of 64 individuals and 85 variables (56 dental metrics, and 29 dental non-metric traits), with an overall percentage of ~26% missing values. Due to poor preservation and limited sample size for the site of Kirchheim unter Teck ($n = 1$) the sample had to be excluded after data pre-processing. Summary information about the dental metric and non-metric variables used for FLEXDIST analysis are shown in Tables 2 and 3. Summary information broken down by site are provided in Appendix B (Table B.5 and B.6).

Finally, FLEXDIST requires the nominal and ordinal trait variables to be coded as non-negative integers differing by one. Thus, trait variables missing some grades along the grade expression scale in our final dataset were re-coded (e.g., 0, 1, 4, 7 was re-coded as 0, 1, 2, 3). Although this procedure removes some information about trait expressivity in ordinal-scale variables, the general relative ordering of expression grades is retained. Re-coding was performed for the following six traits: Shoveling UI1, Canine Mesial Ridge UC, Upper Lateral Incisor Variants UI2, Cusp 7 LM1, Enamel Extension LM1, and Reduced/Pegged/Missing LM3. Ordinal-scale variables represented by only two grades (i.e., 0 and 1) were treated as nominal-scale variables. This affected the following five traits: Mandibular Torus, Palatine Torus, Parastyle UM1, Protostylid LM1, Root Number UP1.

We visualised the correlation structure of the final pre-processed dataset by estimating a heterogeneous correlation matrix with Pearson correlations for continuous variables, polychoric correlations for ordinal variables, tetrachoric correlations for nominal variables, and polyserial or biserial correlations for mixed variables (Fig. 2). Overall, there is a high amount of integration within dental continuous variables, while there is general independence within dental discontinuous variables as well as between continuous and discontinuous variables.

All calculations were performed in R 4.0.2 (R Core Team 2022) using various packages, most of them detailed in Rathmann et al. (2022). The mixed data PCA in FLEXDIST utilizes the *dudi.mix* function implemented in the *ade4* package (Dray and Dufour 2007). For simulating data, we used the *rcormmatrix* function in the *clusterGeneration* package (Qiu and Joe 2020).

3. Results and discussion

3.1. Evaluating the performance of FLEXDIST in comparison to Gower's distance

Fig. 3 visualises the performance of FLEXDIST (in the form of $FLEXDIST_{median}$) compared to Gower's distance (with continuous variables transformed into PCs after imputing missing values with *k*NN) in simulated datasets with different compositions of variables randomly chosen to be continuous, ordinal, nominal, or any mixture thereof. Overall, FLEXDIST outperformed Gower's distance in most simulated data scenarios, regardless of the percentage of missing values and the dimensionality of the data. This behaviour is expected because FLEXDIST takes correlations within and between continuous and discontinuous variables into account, whereas Gower's distance only accounts for correlations in the continuous variables but not in the discontinuous variables. Theoretically, this problem could be circumvented by identifying and removing single highly correlated discontinuous variables prior to Gower distance analysis (Rathmann et al., 2019; Maaranen et al., 2022), but this strategy results in data loss and is therefore not fully satisfying. Thus, with FLEXDIST, we provide not only an effective but also a more user-friendly alternative to Gower's distance, as it eliminates the need for additional data pre-processing steps inherent to Gower's distance approach, such as removing correlated discontinuous variables, imputing missing continuous values, and transforming continuous variables into PCs.

We note that in some simulations the performance of FLEXDIST and

Table 2
Summary statistics of the 56 dental continuous variables.

Dental measurement	Number of individuals measured	Mean	Standard deviation
UI1 BL-CR	43	7.09	0.42
UI1 BL-CE	44	6.30	0.44
UI1 MD-CE	41	6.50	0.49
UI2 BL-CR	41	6.31	0.40
UI2 BL-CE	39	5.75	0.40
UI2 MD-CE	39	4.89	0.45
UC BL-CR	52	8.13	0.52
UC BL-CE	47	7.61	0.53
UC MD-CE	37	5.44	0.39
UP1 BL-CR	59	8.82	0.60
UP1 BL-CE	52	8.00	0.59
UP1 MD-CE	37	4.33	0.71
UP2 BL-CR	57	9.01	0.61
UP2 BL-CE	52	8.07	0.63
UP2 MD-CE	40	4.51	0.26
UM1 BL-CR	59	11.54	0.61
UM1 MBDL-CR	57	12.52	0.61
UM1 MLDB-CR	57	11.28	0.55
UM1 BL-CE	40	9.88	0.70
UM1 MD-CE	41	7.81	0.48
UM1 MBDL-CE	50	11.35	0.66
UM1 MLDB-CE	51	10.01	0.59
UM2 BL-CR	60	11.41	0.73
UM2 MBDL-CR	55	11.56	0.79
UM2 MLDB-CR	61	10.34	0.64
UM2 BL-CE	54	9.88	0.56
UM2 MD-CE	34	7.19	0.58
UM2 MBDL-CE	46	10.89	0.75
UM2 MLDB-CE	44	9.43	0.68
LI1 BL-CR	44	5.78	0.36
LI1 BL-CE	43	5.49	0.27
LI1 MD-CE	34	3.46	0.18
LI2 BL-CR	45	6.21	0.30
LI2 BL-CE	51	5.95	0.33
LI2 MD-CE	44	3.86	0.30
LC BL-CR	46	7.64	0.46
LC BL-CE	43	7.53	0.46
LC MD-CE	33	5.08	0.37
LP1 BL-CR	53	7.63	0.48
LP1 BL-CE	44	6.64	0.50
LP1 MD-CE	41	4.65	0.28
LP2 BL-CR	51	8.12	0.58
LP2 BL-CE	38	7.03	0.45
LP2 MD-CE	37	4.92	0.25
LM1 BL-CR	58	10.61	0.54
LM1 MBDL-CR	57	11.84	0.56
LM1 MLDB-CR	54	11.57	0.56
LM1 MD-CE	36	8.89	0.53
LM1 MBDL-CE	39	10.65	0.61
LM1 MLDB-CE	41	9.90	0.42
LM2 BL-CR	55	10.02	0.57
LM2 MBDL-CR	50	11.16	0.75
LM2 MLDB-CR	55	11.07	0.72
LM2 MD-CE	41	8.81	0.62
LM2 MBDL-CE	38	9.94	0.70
LM2 MLDB-CE	43	9.85	0.73

Abbreviations: BL, maximum buccolingual; CE, cervical; CR, crown; LC, lower canine; LI1, lower first incisor; LI2, lower second incisor; LM1, lower first molar; LM2, lower second molar; LP1, lower first premolar; LP2, lower second premolar; MD, maximum mesiodistal; MBDL, maximum mesiobuccal-distolingual; MLDB, maximum mesiolingual-distobuccal; UC, upper canine; UI1, upper first incisor; UI2, upper second incisor; UM1, upper first molar; UM2, upper second molar; UP1, upper first premolar; UP2, upper second premolar.

Gower's distance was similar. An examination of these cases revealed that they occur when analysing continuous data only. This behaviour is expected because in such cases both approaches simplify to a conventional PCA, with the only difference being the way in which continuous variables are imputed (multiple imputation in FLEXDIST, and *k*NN in Gower's distance) and the manner in which inter-individual distances are generated from the PCs (Euclidean distance in FLEXDIST, and range-

Table 3
Summary information about the 29 dental discontinuous variables.

Trait	Grade										
	Scale	n	0	1	2	3	4	5	6	7	
Labial Convexity UI1	Ordinal	45	55.6	35.6	8.9	0.0	0.0	0.0			
Shoveling UI1	Ordinal	41	7.3	36.6	41.5	12.2	0.0	2.4	0.0	0.0	
Double-Shoveling UI1	Ordinal	46	78.3	13.0	4.3	4.3	0.0	0.0	0.0		
Interruption Grooves UI2 ^a	Nominal	47	61.7	14.9	12.8	6.4	4.3				
Tuberculum Dentale UI2	Ordinal	44	40.9	9.1	15.9	18.2	2.3	6.8	6.8		
Canine Mesial Ridge UC	Ordinal	51	94.1	0.0	3.9	2.0					
Upper Premolar Accessory Cusps UP1	Nominal	59	91.5	1.7	6.8	0.0					
Premolar Odontome P1-2	Nominal	64	92.2	7.8							
Metacone UM3 ^b	Ordinal	44	0.0	0.0	0.0	18.2	68.2	13.6	0.0		
Hypocone UM2	Ordinal	62	6.5	14.5	11.3	30.6	30.6	6.5	0.0		
Bifurcated Hypocone UM2	Nominal	61	96.7	3.3							
Cusp 5 UM1	Ordinal	40	62.5	12.5	7.5	17.5	0.0	0.0			
Carabelli's Cusp UM1	Ordinal	48	56.3	6.3	8.3	6.3	12.5	6.3	2.1	2.1	
Parastyle UM1	Ordinal	62	95.2	4.8	0.0	0.0	0.0	0.0	0.0		
Root Number UP1	Ordinal	37		56.8	43.2	0.0					
Root Number UM2	Ordinal	41		7.3	19.5	73.2					
Upper Lateral Incisor Variants UI2 ^c	Nominal	54	94.4	1.9	0.0	3.7	0.0	0.0	0.0		
Palatine Torus	Ordinal	34	76.5	23.5	0.0	0.0	0.0				
Premolar Lingual Cusp Number LP2	Ordinal	50	0.0	46.0	48.0	6.0					
Anterior Fovea LM2	Ordinal	49	28.6	18.4	34.7	16.3	2.0				
Groove Pattern LM2 ^d	Nominal	60	15.0	80.0	5.0						
Protostylid LM1	Ordinal	62	53.2	46.8	0.0	0.0	0.0	0.0	0.0	0.0	
Hypoconulid LM2	Ordinal	35	80.0	2.9	2.9	5.7	8.6	0.0			
Cusp 6 LM1	Ordinal	32	81.3	6.3	12.5	0.0	0.0	0.0			
Cusp 7 LM1 ^e	Ordinal	59	96.6	1.7	0.0	0.0	1.7	0.0			
Enamel Extension LM1	Ordinal	61	70.5	27.9	0.0	1.6					
Root Number LC ^f	Nominal	37		91.9	8.1						
Reduced/Pegged/Missing LM3	Nominal	50	80.0	0.0	0.0	20.0					
Mandibular Torus	Ordinal	49	95.9	4.1	0.0	0.0	0.0				

Dental non-metric trait names follow the ASUDAS and abbreviations denote tooth scored: LC, lower canine; LM1, lower first molar; LM2, lower second molar; LM3, lower third molar; LP2, lower second premolar; P1-2, first and second premolars; UC, upper canine; UI1, upper first incisor; UI2, upper second incisor; UM1, upper first molar; UM2, upper second molar; UM3, upper third molar; UP1, upper first premolar.

^a Corresponding to Scott and Irish (2017) Interruption Grooves 0 = 0, M = 1, D = 2, MD = 3, med. = 4.

^b Corresponding to Scott and Irish (2017) Metacone 0 = 0, 1 = 1, 2 = 2, 3 = 3, 3.5 = 4, 4 = 5, 5 = 6.

^c Corresponding to Scott and Irish (2017) Lateral Incisor Variants 0 = 0, 1 = 1, 2 = 3, 3 = 2, 4 = 4, 5 = 5, 6 = 6.

^d Corresponding to Scott and Irish (2017) Groove Pattern Y = 0, X = 1, + = 2.

^e Corresponding to Scott and Irish (2017) Cusp 7 0 = 0, 1 = 1, 1A = 5, 2 = 2, 3 = 3, 4 = 4.

^f Corresponding to Scott and Irish (2017) Lower Canine Root Number 0 = 1, 1 = 2.

scaled Manhattan distance in Gower's distance). Thus, when using continuous data only, both approaches are equally useful, though one may wish to apply a different analytical approach than Gower's distance in such cases anyway.

As expected, the performance of both approaches substantially decreases when the percentage of missing values increases. This result is in agreement with previous research on the effect of missing data on bio-distance analyses, reporting that distances based on imputed and complete data increasingly deviate with increasing amounts of missing values (Kenyhercz and Passalacqua 2016). One strength of FLEXDIST is, however, that it calculates not only the point estimate FLEXDIST_{median} used for assessing overall performance in our simulation framework, but also an 95% confidence interval to report the uncertainty resulting from incomplete cases (FLEXDIST_{upper} and FLEXDIST_{lower}).

Future research should investigate the performance of FLEXDIST and Gower's distance in comparison to methods used outside the field of biological anthropology, in particular ecology, psychology, and health sciences. Additional simulation work is needed to explore the effects of the structure of missing values in the data (i.e., missing completely at random, missing at random, missing not at random) (Kenyhercz et al., 2019; Wissler et al., 2022) and modularity within and between the different variable scales, for example by simulating data from covariance structures estimated from empirical anthropological data (Nikita 2015).

3.2. Applying FLEXDIST to investigate population history in Southwest Germany

Given that FLEXDIST is able to recover information about inter-individual relationships in simulated data, we applied the method to a dental morphological dataset collected from ancient human remains retrieved from five Final Neolithic to Early Iron Age (2900-450 BC) locations across Southwest Germany. The resulting summary matrices FLEXDIST_{median}, FLEXDIST_{upper}, and FLEXDIST_{lower} are provided in Appendix B (Tables B.7 to B.9). Fig. 4 visualises the PC plot FLEXDIST_{plot}, illustrating the relatedness among individuals (dots) taking into account the uncertainties resulting from missing data (confidence ellipses). We uncover a high degree of biological resemblance across all sampled individuals, and a large amount of overlap between individuals and archaeological locations. Despite differences in material culture between the Final Neolithic, Early Bronze Age, and Early Iron Age periods, no major biological shifts are discernible, indicating population continuity through time in Southwest Germany. Dental bio-distance analyses from Italy also indicate a high level of similarity from the Neolithic to Early Bronze Age, excluding substantial population movement (Cucina et al., 1999). Similar results in the same region clearly separate these time periods from earlier pre-Neolithic and to lesser extent from later Iron Age samples (Coppa et al., 2007). The results of these dental analyses are supported by aDNA findings in Central Europe, suggesting genetic continuity after a turnover event at the beginning of the Final Neolithic (Allentoft et al., 2015; Haak et al., 2015; Olalde et al., 2018; Brunel et al., 2020; Fischer et al., 2022).

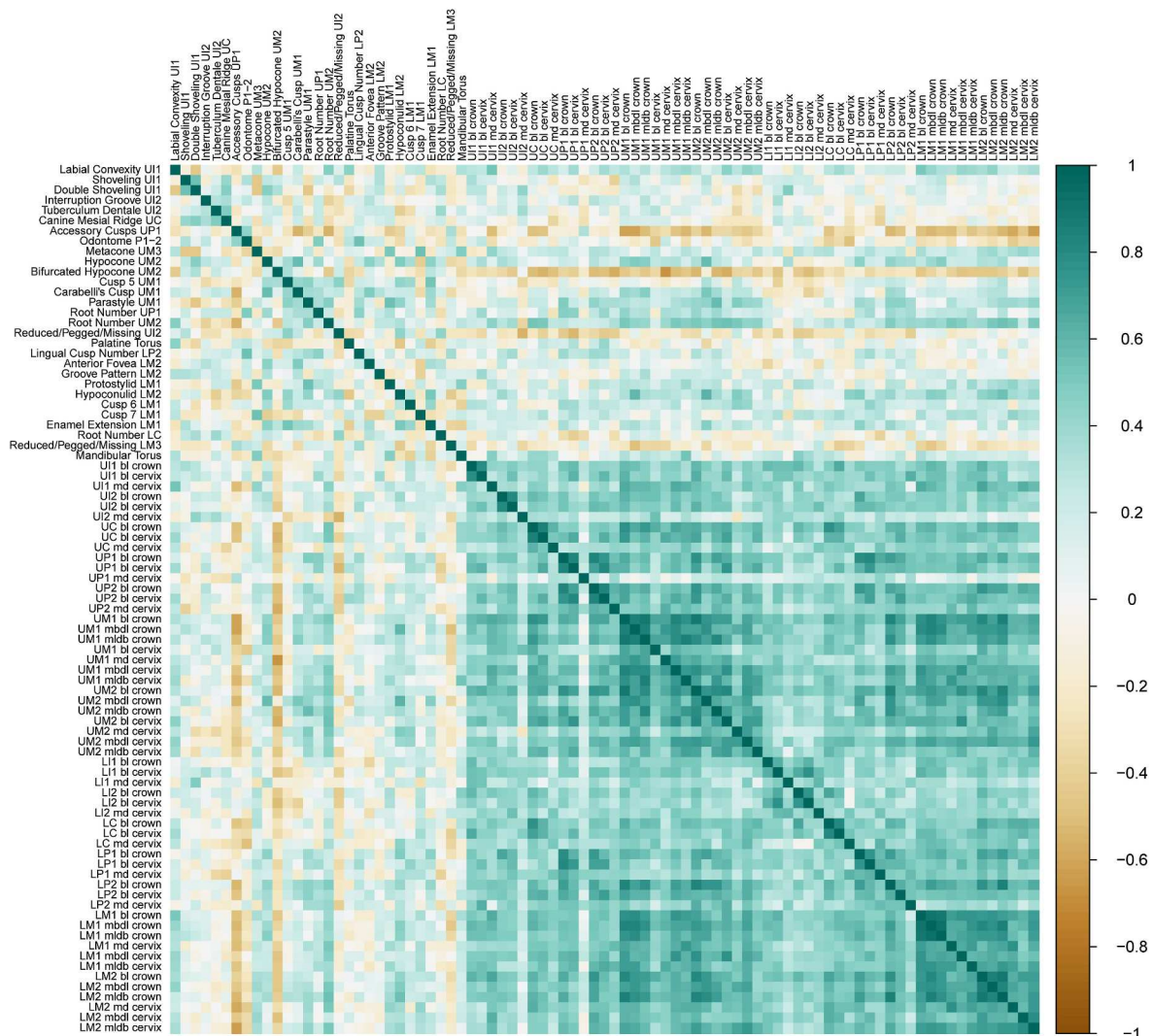


Fig. 2. Correlations among dental continuous and discontinuous variables. For variable names and abbreviations, see Tables 2 and 3

Fig. 5 visualises FLEXPLOT split into five individual plots, corresponding to the five archaeological locations, to ease visual interpretability. The figure also provides a summary of available osteological age and sex determinations. Most individuals within locations tend to overlap in PC space when considering the uncertainties resulting from missing data, with the exception of four individuals that appear slightly more divergent: HK_15.1 in Heilbronn (FN), TK_1.3 in Tauberbischofsheim (FN), RH_15.1 in Remseck-Aldingen (EBA), and TI_169 in Tauberbischofsheim (EIA). Interestingly, all four individuals were osteologically determined to be subadult or in transition to adulthood. This phenomenon was described in previous aDNA and isotope studies on Final Neolithic, Early Bronze Age, and Iron Age Central Europe and might indicate movement during childhood (Knipper et al., 2017; Mittnik et al., 2019), perhaps related to the practice of exchanging foster children within and across families (Müller-Scheeßel et al., 2015; Sjögren et al., 2020). Notably, the burial of HK_15.1 is also atypically oriented in a northeast-to-southwest direction, which contrasts with most other graves in Heilbronn following primarily a west-to-east/east-to-west orientation. RH_15.1 has been osteologically assigned to be male, while the sexes of HK_15.1, TK_1.3, and TI_169 are indeterminate, but the burial position of HK_15.1 is typical for females in the Corded Ware complex (i.e., lying on the left side in a crouched position).

Fig. 5 indicates different levels of intra-site variation, albeit

challenging to assess visually as the first two PCs explain only 13% of total variation. We therefore formally quantified intra-site variation as the average distance of each individual to the respective group centre, accounting for missing value uncertainty by using the information stored in FLEXPLOT_array (see Appendix A.3 for further computational details). Results are displayed with violin plots in Fig. 6. The Final Neolithic site of Heilbronn quantified as most heterogeneous and the Early Bronze Age site of Remseck-Aldingen as the most homogeneous. The overall decrease in intra-site variation from Final Neolithic to the Early Bronze Age is in line with aDNA studies reporting that the Central European gene pool from the Late Neolithic period onwards, which can be modelled as a tree-way mixture between Mesolithic hunter-gatherers, early Neolithic farmers, and Steppe pastoralists, gradually loses its Steppe pastoralists ancestry component, accompanied by an increase of early Neolithic farmer ancestry, resulting in a homogenisation and decreased differentiation in ancestry over time (Mittnik et al., 2019; Furtwängler et al., 2020; Patterson et al., 2022). A possible explanation for the increase of early Neolithic farmer ancestry is continuous admixture with coexisting, isolated groups who experienced less gene flow from Steppe pastoralists (Mittnik et al., 2019), and we hypothesise that the low-variation site Remseck-Aldingen could be one of those candidate populations. Notably, the north-to-south/south-to-north burial orientation of most individuals from Remseck-Aldingen is uncommon in the Neckar Group and rather known from other regions in

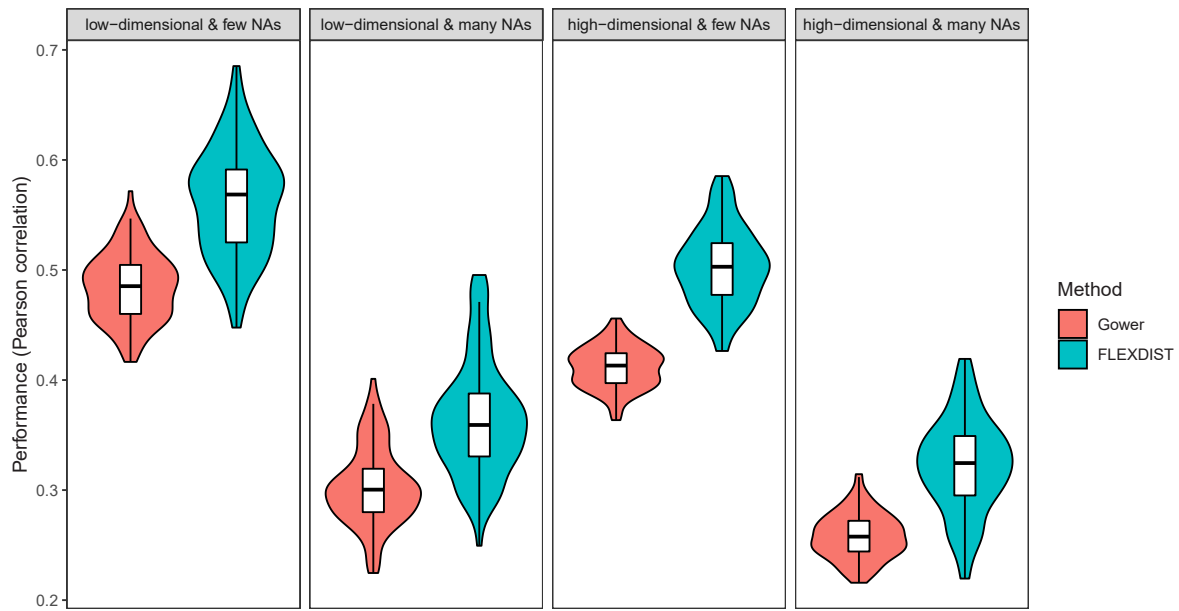


Fig. 3. Violin plots visualising the performance of FLEXDIST and Gower’s distance in simulated datasets with randomly generated mixed variables. Depicted are four different scenarios: low-dimensional data (100 individuals and 20 variables) and high-dimensional data (100 individuals, 200 variables), one time with few missing values (10%) and one time with many (50%) missing values (NAs).

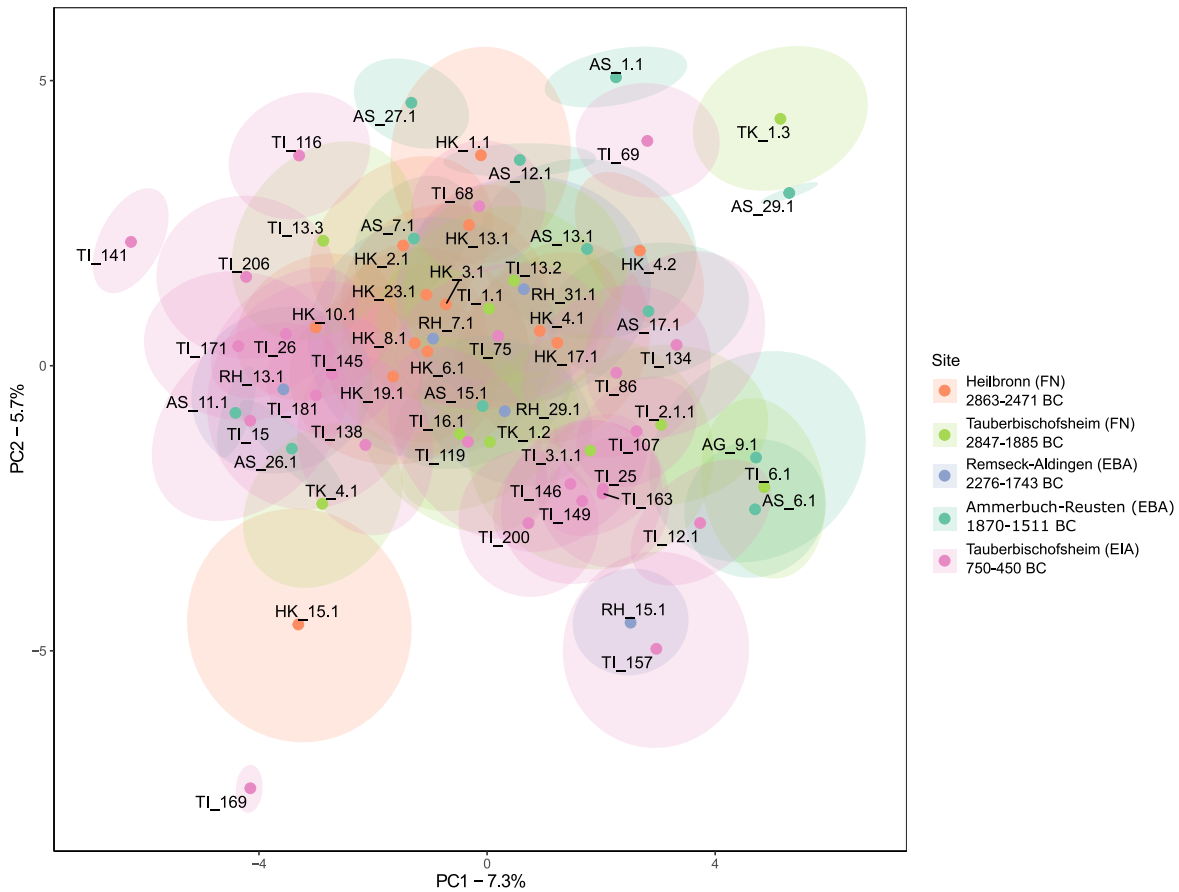


Fig. 4. PC plot showing relationships between Final Neolithic to Early Iron Age human remains from Southwest Germany estimated with FLEXDIST. Dots indicate an individual’s centroid estimate, surrounded by a 95% confidence ellipse reporting uncertainty resulting from missing data.

Central Europe. The observed increase of intra-site variation from the Early Bronze Age to Early Iron Age is in agreement with aDNA analyses reporting high degrees of variation during the European Iron Age,

perhaps as a result of increased mobility and different spatial degrees of admixture across Western Eurasia (Loog et al., 2017; Stolarek et al., 2018; Brunel et al., 2020; Feldman et al., 2021; Fischer et al., 2022).

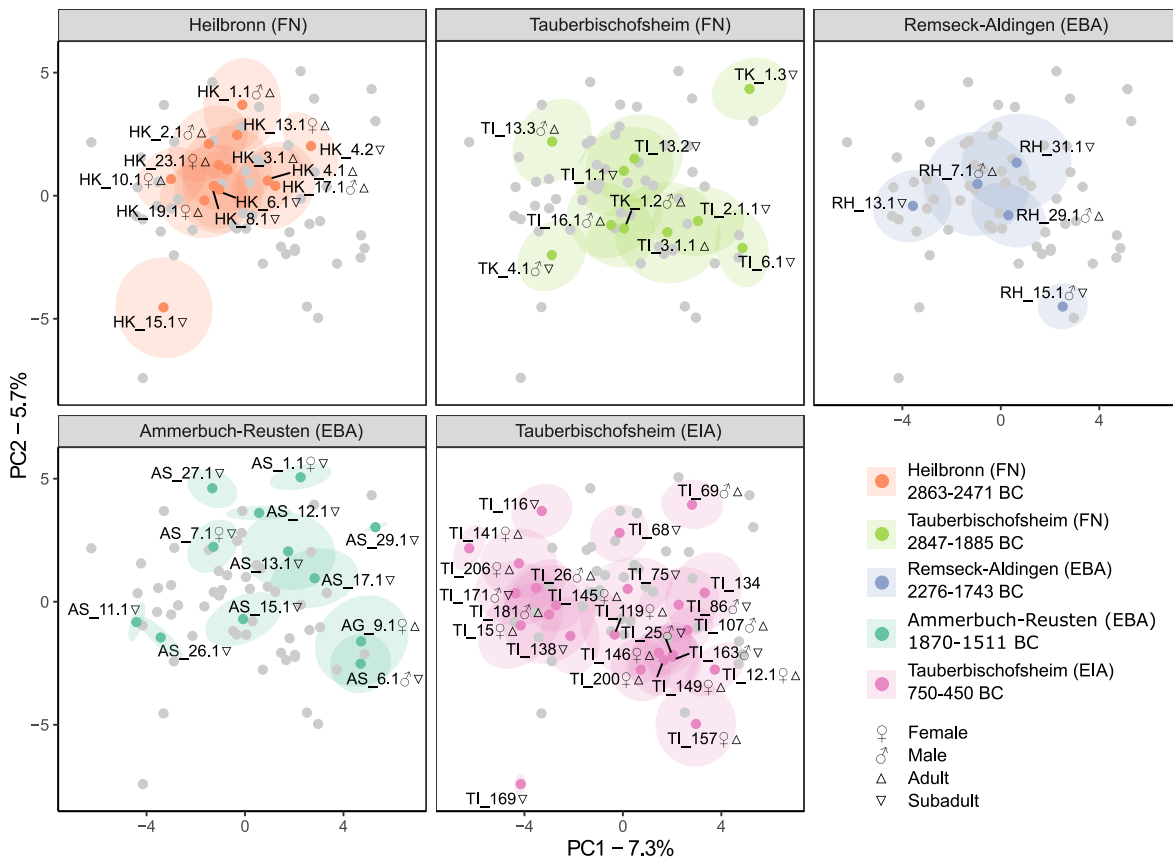


Fig. 5. PC plot showing relationships between Final Neolithic to Early Iron Age human remains from Southwest Germany estimated with FLEXDIST and broken down by site. Dots indicate an individual's centroid estimate, surrounded by a 95% confidence ellipse reporting uncertainty resulting from missing data. The figure also provides a summary of available osteological age and sex determinations.

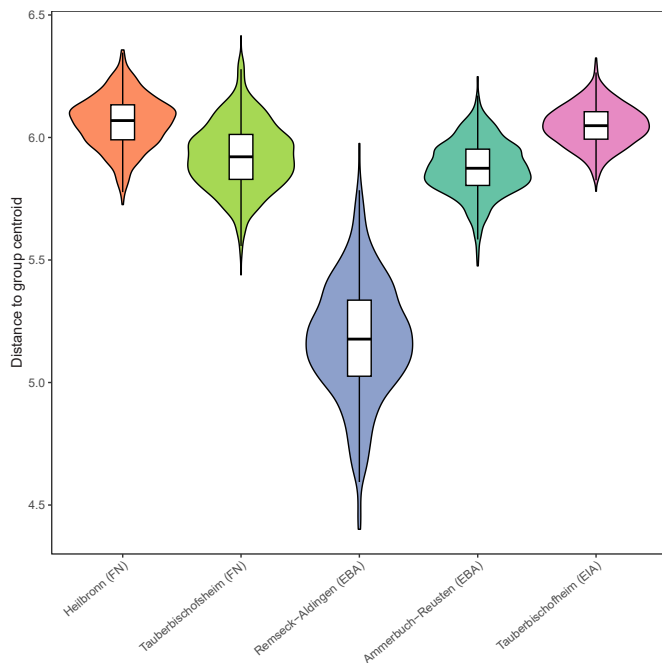


Fig. 6. Violin plots displaying intra-site variation. Sites are order by chronological age (from left to right).

Nevertheless, we caution that our overall small number of sites and sample sizes hamper sound conclusions about intra-site variation and diachronic trends until further samples are accessible for study.

Finally, although a vast body of literature demonstrated the utility of dental morphology for detecting inter-individual patterns in small-scale archaeological contexts (Alt and Vach 1995; Shimada et al., 2004; Stojanowski and Schillaci 2006; Maaranen et al., 2022), recent validation work pairing tooth morphology with genomic data demonstrated that biodistance studies tend to be most effective on global to continental scales (Rathmann et al., 2017; Irish et al., 2020; Rathmann and Reyes-Centeno, 2020) and increasingly less effective on regional to local scales (Hubbard et al., 2015; Paul and Stojanowski 2017; Stojanowski and Hubbard 2017). To increase the knowledge gained from dental morphology, we followed the recommendation to use a large set of variables (Scott and Irish 2017; Stojanowski and Hubbard 2017; Scott et al., 2018; Rathmann and Reyes-Centeno, 2020) and combine continuous with discontinuous data scales in a single analysis (Lease and Sciulli 2005). We therefore think our approach is adequately capturing subtle genetic inter-individual relationships among geographically proximate samples. Nevertheless, more validation work on paired morphological and genomic data from the same set of individuals is needed to systematically test how closely dental continuous and discontinuous variation approximates underlying genotypic variation in small-scale biodistance analyses, and how the choice of variables affects the results. Therefore, in agreement with Stojanowski and Hubbard (2017), we caution that our results should not be overestimated, even though they are in broad agreement with previous archaeological, genomic, and isotopic studies. Future research should focus on including additional samples, increasing sample sizes, incorporating additional dental variables, and striving for finer chronological resolution,

ultimately allowing for more refined inferences about population history in Southwest Germany.

4. Conclusion

We introduced a new software tool named FLEXDIST for estimating inter-individual Mahalanobis-type distances from fragmented and heterogeneous datasets commonly characterising biodistance investigations of archaeological skeletal remains. Similar to the conventional inter-individual Mahalanobis distance, FLEXDIST takes correlations among variables into account but has the advantage of working with multiple variable scales (nominal, ordinal, continuous, or any mixture thereof), allowing for missing values, and handling high-dimensional data. Using a simulation framework, we demonstrated the performance of FLEXDIST compared to the Gower distance and showed that FLEXDIST outperformed the Gower distance in most simulated data cases. By applying FLEXDIST to a newly collected dental dataset from archaeological human remains retrieved from Final Neolithic to Early Iron Age Southwest Germany, we were able to provide first insights into the population history of a regional context lacking systematic diachronic biodistance investigation. In agreement with previous archaeological, genomic, and isotopic studies from neighbouring regions, we found evidence for population continuity, movement during childhood, and alternating levels of variability through time. Our investigation thereby adds to an increasing number of studies in other Central European areas aiming at reconstructing past population dynamics not only on a supra-regional level but also in small-scale settings. We anticipate that our FLEXDIST method may be useful for future biodistance investigations and applicable to a wide range of biological and cultural datasets across different areas of archaeological research, for example, to assess biological similarities among faunal remains or technological similarities among lithic artifacts.

Author contributions

Hannes Rathmann: Methodology, Software, Formal analysis, Investigation, Validation, Writing – original draft, Writing – review & editing, Resources. **Stephanie Lismann:** Data collection, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Michael Francken:** Resources, Writing – review & editing. **André Spatzier:** Resources, Conceptualisation, Project administration, Writing – review & editing.

Data availability

All raw data and the fully automated R code for performing FLEXDIST are publicly available online at the Zenodo repository (<https://doi.org/10.5281/zenodo.7869075>).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jas.2023.105802>.

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Appendix A: Supplementary Information

Estimating inter-individual Mahalanobis distances from mixed incomplete high-dimensional data:
Application to human skeletal remains from 3rd to 1st millennia BC Southwest Germany

Hannes Rathmann, Stephanie Lismann, Michael Francken, André Spatzier

1. Sample description

Final Neolithic site of Heilbronn (Corded Ware complex)

We analysed 23 human skeletons with preserved dentitions from the Final Neolithic cemetery of Heilbronn Kirschengartenstraße in the middle Neckar region (GPS: 9° 13.6385' E, 49° 9.5459' N). The cemetery was excavated in 2016 and 2018/2019 and comprises 22 single burials and two double burials, resulting in a total of 26 individuals (Garcia and Neth, 2019). It is the first larger Corded Ware cemetery discovered in the middle Neckar region. The burials are oriented east-west in a crouched position lying on their left (females) or right (males) side facing towards the south, in line with the gender differentiating funerary customs of the Corded Ware complex. Two, perhaps three, exceptions are oriented along the southeast-northwest axis. The burials contain typical Corded Ware grave goods such as decorated beakers, stone axes, and arrowheads. Three AMS radiocarbon dates obtained from human bone samples range between 2863 and 2471 cal BC, with a fourth date range falling between 2471 and 2299 cal BC (95.4% probability). Among the 23 individuals analysed in this study, 14 were determined to be adults (five males, five females, and four of unknown sex), while nine were classified as subadults.

Final Neolithic site of Tauberbischofsheim (Corded Ware complex)

We analysed 37 human skeletons with preserved dentitions from three Final Neolithic sites in and near Tauberbischofsheim in the Tauber valley. Due to the close geographic proximity (less than 2 km) and similarity in material culture, we chose to combine the three sites into one composite sample.

Twenty-nine individuals originate from the site of Impfingen/Rebhuhn (GPS: 9° 39.6899' E, 49° 39.0760' N). The cemetery was discovered in 1928 and excavated between 1970 and 1973 and comprises 22 Corded Ware graves, including several double and multiple burials, resulting in a total of at least 40 inhumations (Dresely, 2004). Construction work and farming activity restricted the full excavation of the site. Additionally, the later necropolis of the Hallstatt culture may have destroyed earlier Corded Ware features. As a result, the 40 inhumations may only represent a part of the Final Neolithic cemetery. The individuals were buried in a crouched position according to the Corded Ware bipolar gender differentiation funerary customs, with males lying on the right body side and females on the left, and oriented along the northeast-southwest axis, as it is typical for the Tauber valley Corded Ware group. Various grave goods, including Corded Ware ceramics, stone and bone tools, were found. Six radiocarbon dates obtained from human bone samples range between 2622 and 1885/1624 cal BC (95.4% probability). One sample indicates a prolonged existence of the Corded Ware culture into the developed Early Bronze Age. However, it should be noted that these are old radiocarbon dates with a large standard deviation; they should be interpreted with caution. Among the 29 individuals analysed, ten are adults (seven males, two females, and one of unknown sex), 15 are subadults, one individual is in transition to adulthood, and three are isolated teeth of unknown age and sex.

Seven individuals originate from the site of Kirchelberg/Acker Noe West (GPS: 9° 39.9400' E, 49° 38.1602' N). The Corded Ware graves were excavated in 1968/1969 and consist of three single burials, one double burial, and one multiple burial, comprising at least nine individuals in total (Dresely, 2004). The individuals were buried in a crouched position according to the Corded Ware bipolar gender differentiation rules in right- and left-sided body posture and oriented along the northeast-southwest axis. Younger features probably destroyed parts of the Final Neolithic burial ground. Grave goods include ceramics, bone, and stone artefacts. Two radiocarbon dates from human bone samples range between 2847 and 2031 cal BC (95.4% probability); again, as noted above for the Impfingen/Rebhuhn cemetery, the old date with large standard deviation should be interpreted with care. Among the seven individuals, one is determined to be adult male and five were determined to be subadults, one individual was only represented by teeth preventing ageing and sexing.

One individual originates from the Gärtnerei Scheuermann site (GPS: 9° 39.9855' E, 49° 37.9452' N). The Corded Ware complex site was excavated in 1971 and consists of one single and one double burial, comprising at least three individuals (Dresely, 2004). Grave goods include ceramics, bone, and stone artefacts. One radiocarbon date with large standard deviation ranges between 3007 and 2494 cal BC (95.4% probability). The individual used for analysis was determined to be an adult male.

Early Bronze Age site of Remseck-Aldingen (Neckar group)

We analysed 26 human skeletons with preserved dentitions from the Early Bronze Age site of Remseck-Aldingen Halden II in the middle Neckar region (GPS: 9° 15.4387' E, 48° 52.3251' N). The cemetery was uncovered in 1987 likely to full extent, comprising 33 single graves and one multiple burial, totalling 37 individuals (Krause, 1988). Most graves contained stone beddings or stone constructions, in a few cases suggesting that the individuals had been buried in wooden coffins, perhaps made of tree trunks. While reflecting the burial custom typical for the Neckar group in terms of grave construction and crouched body posture, with males left-sided and females right-sided reflecting bipolar gender differentiation rules, the orientation of most individuals along the north-south axis is atypical for the Neckar region. Several graves contained bronze and bone artifacts, mostly adornments. Four AMS radiocarbon dates obtained from bone samples range between 2276 and 1743 cal BC (95.4% probability). Of the 26 individuals analysed in this study, nine are adults (four males, one female, and four of unknown sex), 14 are subadults, and three individuals are in transition to adulthood.

Early Bronze Age site of Ammerbuch-Reusten (Neckar group)

We analysed 29 human skeletons with preserved dentitions from the Early Bronze Age cemetery of Ammerbuch-Reusten in the upper Neckar region, originating from two parts of the cemetery. Due to the close geographic proximity (less than 200 m), we chose to combine the two cemetery plots into one composite sample.

Twenty-five individuals originate from the Stützbrunnen cemetery plot (GPS: 8° 54.7490' E, 48° 32.6655' N), which were excavated in 2000. Preservation suggests that the original number of inhumations may have been higher (Bofinger and Hald, 2000). The individuals were buried in a crouched position on their left and right body side, with most of them oriented along the northeast-southwest and west-east axis facing towards southeast and south respectively. Regarding body orientation and gender differentiation, a considerable number of exceptions from the common Early Bronze Age funerary practises of the Neckar region (as outlined above for the Remseck-Aldingen cemetery) can be observed. In some cases, the common burial rule seems to be inverted. In addition, the absence of stone constructions within graves and the lack of grave goods are remarkable. Only one bronze arm ring was found in a burial attributed to a juvenile, while green stains on skeletal remains from another burial indicate a second bronze object. Seven AMS radiocarbon samples obtained from human skeletal remains range between 1870 and 1519 cal BC (95.4% probability). Of the 25 individuals analysed in this study, nine are adults (four males, two females, and three of unknown sex), 14 are subadults, two individuals are in transition to adulthood.

Four individuals originate from the Grüninger cemetery plot (GPS: 8° 54.5839' E, 48° 32.6617' N). The graves were excavated in 2020/2021 and comprises a total of four inhumations in single burials. A woman's burial contained a small lock ring, which is the first gold artefact found in a closed context of the Early Bronze Age in Southwest Germany (Krauß et al., 2021). Another individual was equipped with a bronze arm ring. AMS radiocarbon samples from human bone date from 1751 to 1511 cal BC (95.4% probability). Of the four individuals analysed in this study, one is an adult female, one is a subadult, and two are isolated teeth of unknown age and sex.

Early Bronze Age site of Kirchheim unter Teck (Neckar group)

We analysed one human skeleton with preserved dentition from the Early Bronze Age site of Kirchheim unter Teck in the middle Neckar region, originating from the site of Stuttgarter Straße (GPS: 9° 26.1594' E, 48° 39.2153' N). Three single graves containing inhumations in a left-sided crouched position, oriented northeast-southwest, were excavated in 1937 (Lau, 1950, pp. 212-213). The graves contained two daggers, an arm spiral, and a pin, all made of bronze and dating to the younger phase of the Early Bronze Age. Today, only the skeletal remains and finds of one grave are available. The individual was analysed in this study and determined to be an adult male.

Early Iron Age site of Tauberbischofsheim (Hallstatt culture)

We analysed 28 human skeletons with preserved dentitions from the site of Tauberbischofsheim in the Tauber valley region, dating to the Early Iron Age and originating from the cemetery of Impfingen/Rebhuhn (GPS: 9° 39.6899' E, 49° 39.0760' N). The tumulus cemetery was initially discovered in the early 1960s and 1970s, with the majority of the excavation taking place in 1973. After the discovery of another grave in 1983, the cemetery now comprises more than 216 graves (Baitinger, 1999). However, due to the presence of buildings and farming activities, the site was not fully excavated, resulting in some areas remaining unexplored or destroyed. Unfortunately, the catalogue of the finds is unpublished. The burials mostly consist of inhumations, with skeletal remains laid out on the back and oriented south-north, often surrounded by stone circles and occasionally with traces of wooden

chambers. Additionally, a moderate number of cremations were also found. The tumulus burials and grave goods are typical for the Early Iron Age Hallstatt culture. The graves were mainly equipped with ceramic sets of typical Hallstatt vessels and bronze jewellery and attire, complemented by other items and iron objects, dating the site to the Hallstatt period (750-450 BC). Out of the 28 individuals analysed in this study, 15 were determined to be adults (four males, ten females, and one individual of unknown sex), while 13 were identified as subadults.

2. Skeletal Age and sex determinations

Skeletal age-at-death and sex were determined using standard osteological techniques. Subadult age-at-death was determined using skeletal and dental development based on AlQahtani et al. (2010), Scheuer et al. (2010), Stloukal and Hanáková (1978), and Ubelaker (1989). Adult age-at-death was estimated using cranial suture closure, auricular surface and pubic symphysis morphology, sternal rib end morphology, and dental attrition based on Brooks and Suchey (1990), Brothwell (1981), Buckberry and Chamberlain (2002), Işcan et al. (1984), Mann et al. (1991), and Vallois (1937). The sex of subadult individuals was estimated using the mandible and ilium following Schutkowski (1993), however, these estimates should be interpreted with caution as subadult sex estimation is prone to errors. Sex determinations of adult individuals were based on cranial and pelvic morphology according to Ferembach et al. (1979) and Phenice (1969). The age and sex of the Late Neolithic individuals from the site of Tauberbischofsheim have already been analysed by Dresely (2004), and the results were adopted in the present study as the osteological methods used are identical. This ensures that the estimated results are comparable.

3. Quantifying intra-site variation

To explicitly quantify the variation within each site, we made use of the 1,000 different inter-individual Mahalanobis-type distance matrices from the various imputation iterations stored in `FLEXDISTarray`. For each matrix, we first estimated the spatial median centres of each group, and then estimated the distance of each individual to the respective group centre. Next, for each group we estimated the mean of the individual distance-to-group-centre values to arrive at an estimator of average dispersion per group. A high value indicates overall heterogeneity, whereas a lower value indicates overall homogeneity. Performing this procedure for all 1,000 matrices resulted in a distribution of 1,000 average dispersion estimates per group. The width of the distributions for a particular group reflects uncertainty resulting from incomplete individuals and sample size, whereas differences in distributions between groups reflect differences in dispersion. Distance-to-group-centre calculations were performed with the `betadisper` function implemented in the R package `vegan` (Oksanen et al. 2020). The distributions were visualised using violin plots using the R package `ggplot2` (Wickham 2016).

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Appendix B

Study II

Reconstructing Life History

New Palaeodemographic Insights into Final Neolithic and Early Bronze Age Populations in
Southwest Germany

Stephanie Lismann, Michael Francken, Katerina Harvati, Martin Bartelheim, André Spatzier

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Stephanie Lismann · Michael Francken · Katerina Harvati
Martin Bartelheim · André Spatzier

Reconstructing Life History

New Palaeodemographic Insights into Final Neolithic and Early Bronze Age Populations in Southwest Germany

Abstract

During the third to mid-second millennia BC in Europe, human culture witnessed dramatic changes. Various studies indicate that this sociocultural shift had complex and regionally variable biological impacts. Hence, palaeodemographic analyses of age-at-death and sex from human skeletal remains provide valuable insights into life span and mortality. This study reconstructs the demographic profile of 322 Final Neolithic (Corded Ware culture) and Early Bronze Age (Neckar group) individuals from 17 sites in Baden-Württemberg (Southwest Germany) by using life tables. The results indicate diachronic changes in mortality and life expectancy of infant individuals, and juvenile and adult females accompanied by regional variations. This suggests generally improving living conditions from the Final Neolithic to the Early Bronze Age, except for increased mortality in Early Bronze Age juveniles potentially related to adolescent pregnancies.

Keywords

Southwest Germany / Final Neolithic / Early Bronze Age / palaeodemography / anthropology

Over the past two decades, research in archaeology, genetics and isotopes has made it clear that the third to mid-second millennia BC were highly dynamic regarding population development and social interaction. In Central Europe, the cultural complexes of the Corded Ware (ca. 2900–2100 BC) and the Bell Beaker (ca. 2750–2000 BC) spread during the Final Neolithic. Both constituted a substratum of which several

later cultures and regional groups emerged during the Early Bronze Age (ca. 2300–1600 BC). Multiple developments between ca. 2900 and 1600 BC have been identified, which were propelled by pan-European (and, on a more global scale, pan-Eurasian) mobility and spread of new cultural phenomena and ideologies. On a regional scale, new cultural and social influences were assimilated and adapted by lo-

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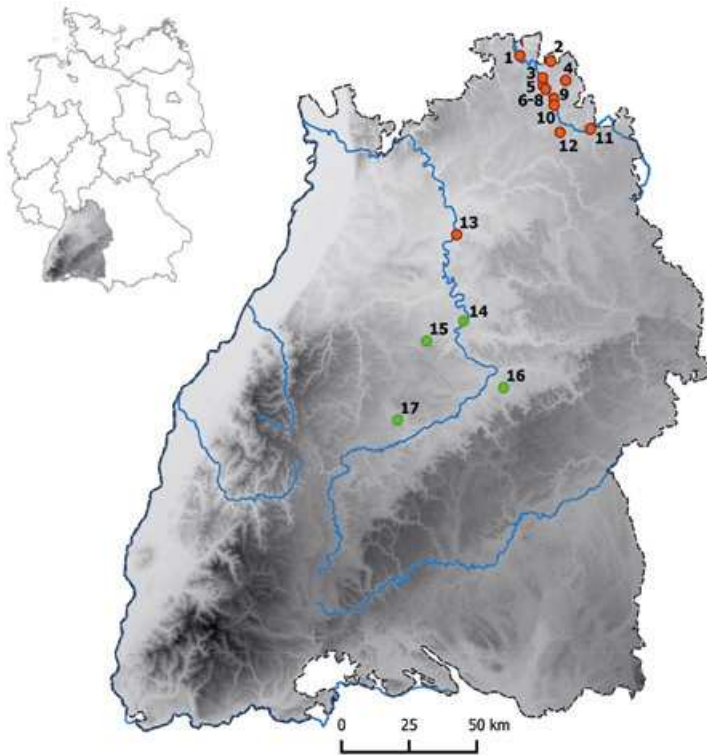


Fig. 1 Map of Baden-Württemberg (Southwest Germany) showing the geographic locations of the human skeletal remains analysed in this study. Final Neolithic sites are indicated in orange, Early Bronze Age sites in green: **1** Wertheim-Reicholzheim. – **2** Werbach-Wenkheim. – **3** Tauberbischofsheim-Impfingen. – **4** Grünsfeld-Krensheim. – **5** Tauberbischofsheim-Dittigheim. – **6-8** Tauberbischofsheim (three sites). – **9** Lauda-Königshofen/Gerlachsheim. – **10** Lauda-Königshofen. – **11** Weikersheim. – **12** Bad Mergentheim-Althausen (I–12 Main-Tauber-Kreis/DE). – **13** Heilbronn (DE). – **14** Remseck-Aldingen (Lkr. Ludwigsburg/DE). – **15** Gerlingen (Lkr. Ludwigsburg/DE). – **16** Kirchheim unter Teck (Lkr. Esslingen/DE). – **17** Ammerbuch-Reusten (Lkr. Tübingen/DE). – (Image A. Spatzier/S. Lismann; map: USGS 30 ARC-second Global Elevation Data, GTOPO30, DOI: [10.5065/A1Z4-EE71](https://doi.org/10.5065/A1Z4-EE71); OpenStreetMap contributors, www.openstreetmap.org).

cal communities to different degrees (Furholt 2014; 2021; Furtwängler et al. 2020; Haak et al. 2015; Heyd 2023; Knipper et al. 2017; Vander Linden 2006; Wentink 2020).

One key to comprehending cultural development and social changes is by examining the human bones. To which extent the cultural change was accompanied by variations in the biology of the populations has been investigated by several studies concerning Central Europe (e. g., Allentoft et al. 2015; Sjögren et al. 2016; Hubensack et al. 2018; Nicklisch 2017). Genetic and isotope studies observed different mobility patterns ranging from age- and sex-specific mobility (Knipper et al. 2017; Mittnik et al. 2019; Sjögren et al. 2016) to a local population without individual mobility (Oelze et al. 2012) in Southern Germany. In Central Germany, both varying degrees of genetic origin and composition resulting from rapid DNA changes (Brandt et al. 2013), and rather residential communities with low mobility (Knipper et al. 2016) are indicated. Therefore, even within geographically and chronologically defined groups local differences are discernible.

Palaeodemographic estimates are one approach to describe the life history of past populations and link biological with cultural findings (Boldsen et al. 2022; DeWitte 2018; Eshed et al. 2004; Howell 1982). By constructing life tables, differences among groups in life course can be observed, including variation in age- and sex-specific mortality and life expectancy. This allows us to infer social, economic and health

statuses as they relate to life span (Boldsen et al. 2022; Colchero et al. 2016).

The region along the rivers Tauber and Neckar in Baden-Württemberg (Southwest Germany) is characterised by cultural groups of the Corded Ware complex, the Bell Beaker phenomenon and the so-called Neckar group during the Final Neolithic and the Early Bronze Age. The density of respective archaeological sites and micro-regional differences in the clustering of these cultural phenomena make it an interesting research area, particularly with respect to the study of the demographic segmentation of past populations.

Recent studies in Central Germany, Southeast Germany, Denmark and Sweden, the Czech Republic and Slovakia have demonstrated that the palaeoanthropological analysis of human remains can considerably improve the understanding of Final Neolithic and Early Bronze Age societies (Hubensack et al. 2018; Hukelova 2016; Nicklisch 2017; Staskiewicz 2018a; 2018b; Tornberg/Vandkilde 2025). Concerning Southwest Germany, and the Neckar- and Tauber regions specifically, valuable insights in Final Neolithic populations in the region of Tauberbischofsheim (Main-Tauber-Kreis/DE) have been yielded previously by Veit Dresely (2004) and Martin Trautmann (2012). However, systematic diachronic analyses for the Final Neolithic and the Early Bronze Age in this region, and in Southwest Germany generally, are still rare (Rathmann et al. 2023).

no.	location	site	time period	cultural affiliation	radiocarbon date	sample size ^a
1	Wertheim-Reicholzheim	In der Ecke	Final Neolithic	Corded Ware complex	NA	1 (1/-/-/-)
2	Werbach-Wenkheim	Wertheimer Weg	Final Neolithic	Corded Ware complex	NA	3 (2/-/-/1)
3	Tauberbischofsheim-Impfingen	Rebhuhn	Final Neolithic	Corded Ware complex	2622-1885, 1624 cal BC	42 (8/2/1/25)
4	Grünsfeld-Krensheim	Luxenäcker	Final Neolithic	Corded Ware complex	NA	1 (1/-/-/-)
5	Tauberbischofsheim-Dittigheim	Am Stadtschreiber	Final Neolithic	Corded Ware complex	2557-2393 cal BC	64 (11/7/5/36)
6	Tauberbischofsheim	Burgweg/ Kräutergarten	Final Neolithic	Corded Ware complex	NA	5 (2/1/1/1)
7	Tauberbischofsheim	Gärtnerei Scheuermann	Final Neolithic	Corded Ware complex	3007-2494 cal BC	3 (1/2/-/-)
8	Tauberbischofsheim	Kirchelberg/ Acker Noe West	Final Neolithic	Corded Ware complex	2847-2031 cal BC	9 (2/-/-/7)
9	Lauda-Königshofen/ Gerlachsheim	Flur	Final Neolithic	Corded Ware complex	NA	14 (2/1/1/10)
10	Lauda-Königshofen	Wöllerspfad	Final Neolithic	Corded Ware complex	NA	91 (15/13/3/58)
11	Weikersheim	Katholische Kirche	Final Neolithic	Corded Ware complex	NA	5 (-/-/1/1)
12	Bad Mergentheim-Althausen	Sportplatz neben Schule	Final Neolithic	Corded Ware complex	NA	4 (1/1/-/2)
13	Heilbronn	Kirschengarten- straße	Final Neolithic	Corded Ware complex	2863-2471, 2299 cal BC	24 (5/5/4/10)
14	Remseck-Aldingen	Halden II	Early Bronze Age	Neckar group	2276-1743 cal BC	33 (6/1/6/20)
15	Gerlingen	Seefeld	Early Bronze Age	Neckar group	NA	5 (2/-/-/2)
16	Kirchheim unter Teck	Stuttgarter Straße	Early Bronze Age	Neckar group	NA	1 (1/-/-/-)
17	Ammerbuch-Reusten	Stützbrunnen/ Grüninger	Early Bronze Age	Neckar group	1870-1511 cal BC	34 (3/4/7/20)

Tab. 1 Summary of the skeletal samples used in this study. –^a In parentheses number of adult males/adult females/adults of unknown sex/subadults. Individuals without age and sex identification are not listed in parentheses and excluded for analyses. – (Table S. Lismann).

In the present study, we analysed the skeletal remains of 322 individuals from 17 different sites from the third to mid-second millennia BC, belonging to the Corded Ware culture and the Neckar group in the Neckar- and Tauber regions of Southwest Germany. Unfortunately, the scarcity of Bell Beaker skeletal remains from this geographical area does not allow for valid conclusions on a demographic level, so they have been excluded from this study.

Life tables were calculated on the basis of our reconstructions of age-at-death and biological sex, to infer demographic population structures. We aim to reconstruct the demographic profile and detect potential inter- and intra-population differences through time related to the change from the Final Neolithic to the Early Bronze Age on a regional scale in northeastern and central Baden-Württemberg (Southwest Germany).

Materials and Methods

A total of 339 individuals were excavated at 17 sites in northeastern and central Baden-Württemberg (fig. 1; tab. 1). Of these, 322 were suitable for anthropological analysis and were included in our study. They belong to the Corded Ware complex (ca. 2900–

2100/1800 BC) of the Final Neolithic and the Neckar group (ca. 2200–1600 BC) of the Early Bronze Age in this region. The Final Neolithic sample totals 250 individuals (99 adults, 151 subadults, of which six are in transition to adulthood), and the Early Bronze Age

sample totals 72 individuals (30 adults, 42 subadults, of which six are in transition to adulthood). The sites are chronologically and geographically separated, with the Final Neolithic sites in the Tauber region, except for Heilbronn, and the Early Bronze Age sites in the middle Neckar region. Summary information for the studied sites is provided in **table 1**.

The Final Neolithic samples originate from 13 different sites, totalling 250 skeletons. Twelve Final Neolithic sites are situated in the Tauber valley, comprising three large and nine small burial sites. Tauberbischofsheim-Impfingen, Tauberwbischofsheim-Dittigheim and Lauda-Königshofen are larger cemeteries while at Bad-Mergentheim-Althausen, Grünsfeld-Krensheim, Lauda-Königshofen/Gerlachsheim, Tauberbischofsheim (three sites), Weikersheim, Werbach-Wenkheim and Wertheim-Reicholzheim only a few graves have been excavated (all Main-Tauber-Kreis/DE; Dresely 2004; Trautmann 2012; Ortolf 2014). In general, the individuals are buried in simple, rectangular to oval grave pits and in crouched positions predominantly oriented along the northeast-southwest axis or along the east-west axis. While the majority was buried according to the typical Corded Ware mortuary practises (e. g., Strahm 2002, 184) with females lying on their left and males on their right body side, the Tauber Valley Corded Ware group is characterised by a high percentage of »inverted« alignments, particularly men having been buried in left-sided position (Dresely 2004, 105–108. 113–114; Trautmann 2012, 276–277. 282–284; Ortolf 2014, 439–442. 446). Interestingly, the common Corded Ware bipolar differentiation according to sex generally seems to be inverted at Heilbronn, located in the northern part of the middle Neckar region: Aligned along the east-west

axis facing south, the individuals anthropologically determined as male had been buried in left-sided crouched body posture and those determined as female crouched on their right side, except for two women in left-sided position.

The Early Bronze Age samples come from the two larger cemeteries of Remseck-Aldingen (Lkr. Ludwigsburg/DE) and Ammerbuch-Reusten (Lkr. Tübingen/DE), and two sites where only a few graves are known, Kirchheim unter Teck (Lkr. Esslingen/DE) and Gerlingen (Lkr. Ludwigsburg/DE), totalling 72 skeletons. Remseck-Aldingen (Krause 1987; Keefer/Krause 1992, 42–49), Kirchheim unter Teck (Lau 1950, 212–213) and Gerlingen (Zürn 1975) reflect the typical Early Bronze Age burial customs in the Neckar region. These customs are characterised by bipolar gender differentiation in crouched body posture, with males on the left and females on the right, frequently buried – in addition to simple rectangular to oval pits – with packings, beddings or other constructions made of stone, in some cases suggesting wooden coffins (cf. Krause 1987, 138; Spatzier 2023, 169–170). The inhumations are mostly oriented along the northeast-southwest axis facing southeast, but frequently also aligned east-west facing south and north-south facing east. The latter orientation is particularly prevalent at Remseck-Aldingen, which may indicate a special significance of this cemetery within the region. The cemetery at Ammerbuch-Reusten (Bofinger et al. 2021; 2023), located in the southern part of the middle Neckar area, is of even greater interest: The absence of stone constructions within the graves and the lack of grave goods are unusual. Furthermore, a considerable number of exceptions from the common Early Bronze Age funerary practices described above can be observed with re-

x	D _x	d _x	l _x	q _x	L _x	T _x	e _x
0-4	59.50	23.80	100.00	0.24	440.50	1914.00	19.14
5-9	45.83	18.33	76.20	0.24	335.17	1473.50	19.34
10-14	22.83	9.13	57.87	0.16	266.50	1138.33	19.67
15-19	16.83	6.73	48.73	0.14	226.83	871.83	17.89
20-24	18.03	7.21	42.00	0.17	191.97	645.00	15.36
25-29	19.86	7.94	34.79	0.23	154.08	453.03	13.02
30-34	20.15	8.06	26.84	0.30	114.08	298.94	11.14
35-39	15.31	6.13	18.79	0.33	78.62	184.87	9.84
40-44	13.73	5.49	12.66	0.43	49.57	106.25	8.39
45-49	7.23	2.89	7.17	0.40	28.61	56.68	7.91
50-54	4.90	1.96	4.28	0.46	16.48	28.07	6.56
55-59	2.90	1.16	2.32	0.50	8.69	11.59	5.00
60+	2.90	1.16	1.16	1.00	2.90	2.90	2.50
Σ	250.00	100.00			1914.00		

Tab. 2 Abridged life table for the combined Final Neolithic sites. – (Table S. Lismann).

spect to body orientation and gender differentiation. In some cases, the prevailing burial customs appear to have been inverted (Spatzier 2023, 169).

For skeletal age-at-death and sex analysis, standard macroscopic techniques were used. Subadult age-at-death was determined using the individuals' dental (AlQahtani et al. 2010; Ubelaker 1989) and skeletal development (Scheuer et al. 2010; Stloukal/Hanáková 1978). Adult age-at-death estimation was based on cranial and maxillary suture closure (Mann et al. 1991; Vallois 1937), pelvic morphological variations in the pubic symphysis and auricular surface (Brooks/Suchey 1990; Buckberry/Chamberlain 2002), sternal rib end morphology (İşcan et al. 1984), and dental attrition (Brothwell 1981). Sex in subadults was estimated using the mandible and ilium (Schutkowski 1993). However, subadult sex estimation is prone to errors and should be interpreted with caution. Adult sex determination was based on cranial and pelvic morphology (Ferembach et al. 1979; Phenice 1969), and pelvic dimensions (Murail et al. 2005). The Final Neolithic data, except for Heilbronn, were adopted from Dresely (2004) and Trautmann (2012): since the ageing and sexing methods in that study were identical to ours, the results are assumed to be comparable.

To compare demographic inter- and intra-site population variation, life tables were calculated

(Acsádi/Nemeskéri 1970) based on the assumption that the skeletal samples reflect the composition of the once-living populations. For this, individuals were attributed to age categories in 5-year intervals. If an individual's age-at-death spanned more than one age category, it was equally distributed (e.g., an individual of 14–16 years was classified as 50 % 10–14 years and 50 % 15–19 years), as frequently practiced (Bocquet-Appel 2002, 638). To increase the sample size in the gender differentiated life tables, adult individuals with fewer diagnostic traits, who could not be assigned to sex securely, were nonetheless included in the respective sex categories (Final Neolithic: five males and four females; Early Bronze Age: one male and three females). Additional skeletal fragments in a grave without clear assignment to the buried individual, and individuals without age estimation ($n = 19$) were excluded from demographic analyses. Furthermore, life tables were not calculated for sites with low sample sizes. Instead, these individuals were included in the composite life tables for the Final Neolithic and the Early Bronze Age. Statistical comparisons of number of dead, mortality and life expectancy within and between the temporal periods were conducted by utilising Friedman rank sum test (*psych* package [Revelle 2024]) and Wilcoxon rank sum test in RStudio (Posit team 2024). For all analyses, statistical significance was set at $p < 0.05$.

Results

Tables 2 and 3 show the life tables for the combined Final Neolithic and Early Bronze Age sites, respectively. Site-specific life tables for the larger sites of Heilbronn, Lauda-Königshofen, Tauberbischofs-

heim-Dittigheim, Tauberbischofsheim-Impfingen, Ammerbuch-Reusten and Remseck-Aldingen can be found in the Appendix (Appendix, tab. A.1-6). Based on these, figure 2 shows the number of

x	D _x	d _x	l _x	q _x	L _x	T _x	e _x
0-4	12.00	16.67	100.00	0.17	458.33	2135.42	21.35
5-9	9.50	13.19	83.33	0.16	383.68	1677.08	20.13
10-14	6.50	9.03	70.14	0.13	328.13	1293.40	18.44
15-19	11.00	15.28	61.11	0.25	267.36	965.28	15.80
20-24	6.46	8.97	45.83	0.20	206.74	697.92	15.23
25-29	4.46	6.19	36.86	0.17	168.84	491.17	13.32
30-34	5.96	8.28	30.67	0.27	132.67	322.34	10.51
35-39	5.96	8.28	22.40	0.37	91.29	189.67	8.47
40-44	4.46	6.19	14.12	0.44	55.12	98.38	6.97
45-49	3.46	4.80	7.93	0.61	27.63	43.26	5.46
50-54	1.13	1.56	3.13	0.50	11.72	15.63	5.00
55-59	1.13	1.56	1.56	1.00	3.91	3.91	2.50
60+	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Σ	72.00	100.00			2135.42		

Tab. 3 Abridged life table for the combined Early Bronze Age sites. – (Table S. Lismann).

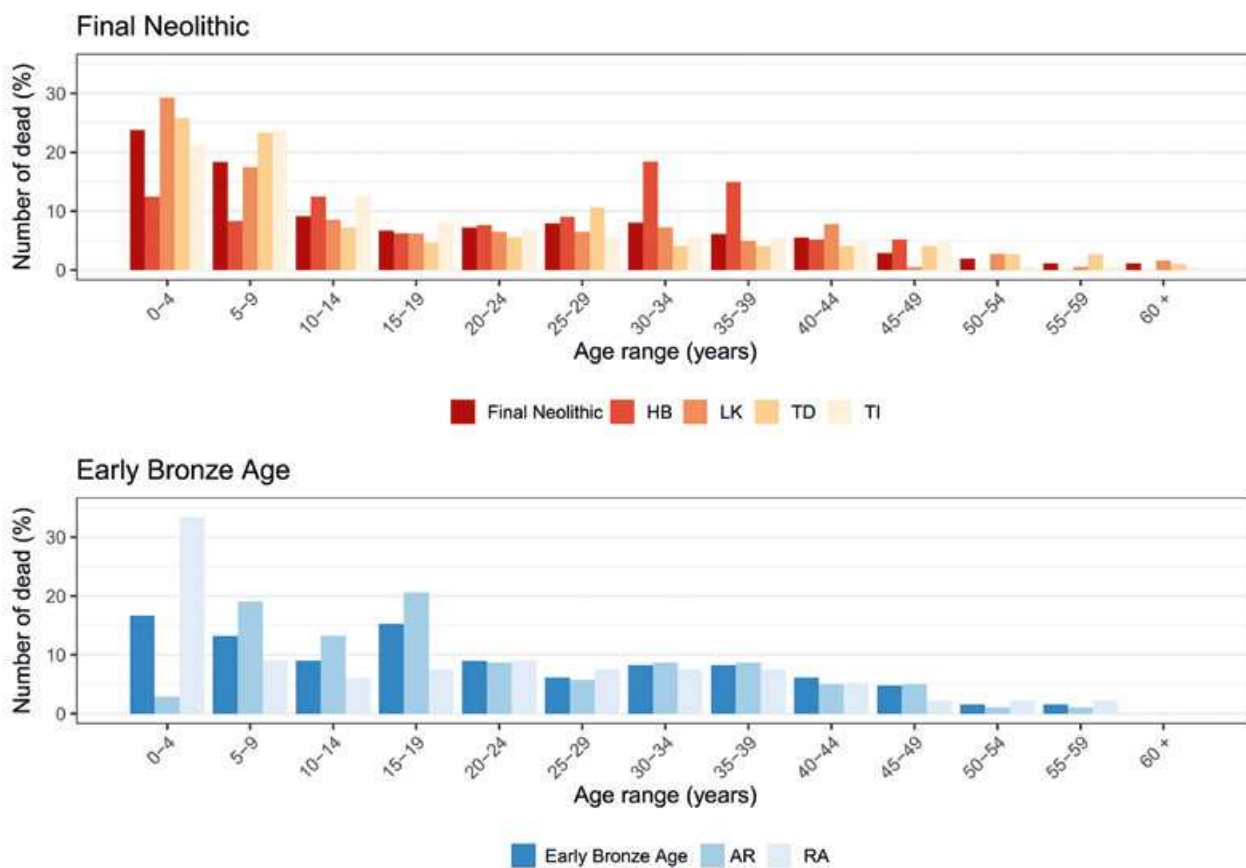


Fig. 2 Comparison of number of dead (d_x) in Final Neolithic and Early Bronze Age composite and single sites. Abbreviations: AR – Ammerbuch-Reusten; HB – Heilbronn; LK – Lauda-Königshofen; RA – Remseck-Aldingen; TD – Tauberbischofsheim-Dittigheim; TI – Tauberbischofsheim-Impfingen. – (Image S. Lismann).

dead (d_x), and **figure 3a-d** the mortality rate (q_x) and life expectancy (e_x) for combined and single sites. The examination of the life tables for the Final Neolithic and the Early Bronze Age demonstrate that, firstly, most of the individuals died before reaching adulthood, peaking at 0–4 years in both periods (**fig. 2**). Secondly, the mortality rate in the Final Neolithic was high during infancy, but subsequently decreased before increasing gradually from 20–24 years onwards (**fig. 3a**). The Early Bronze Age mortality followed a similar trend, but with a slightly lower rate during infancy and early adulthood. However, there is a prominent mortality peak at 15–19 years (**fig. 3c**). Finally, in both periods, life expectancy decreased with age, even though in the Final Neolithic life expectancy remains nearly constant until age 14 (**fig. 3b**) and the Early Bronze Age exhibits a small dip at 15–19 years (**fig. 3d**). Furthermore, the Early Bronze Age life expectancy is lower than in the Final Neolithic for all age categories with the exception of infancy (0–9 years). However, none of these differences are statistically significant. The fluctuating data after ages 40–44, both in mortality and

life expectancy, are probably statistical artifacts due to the low number of old individuals in the samples and were not considered for further interpretations.

However, when the individual Final Neolithic and Early Bronze Age sites are considered, some variation is detectable. Lauda-Königshofen, Tauberbischofsheim-Dittigheim and Tauberbischofsheim-Impfingen best approximate the Final Neolithic composite sample, despite some minor variations in mortality and life expectancy in Tauberbischofsheim-Dittigheim and Tauberbischofsheim-Impfingen. In contrast, Heilbronn highly deviates from the overall pattern, with a low number of dead during infancy (0–9 years) and an increased number of dead from middle adulthood (30–34 years) onwards, as also visible in elevated mortality and reduced life expectancy. Statistically significant differences are only observable in life expectancy in the site of Heilbronn when paired with Lauda-Königshofen and Tauberbischofsheim-Dittigheim (Friedman chi-squared = 16.238, $df = 3$, p -value = 0.001013; HB-LK: p -value = 0.03897915 and HB-TD p -value = 0.00831651). The Early Bronze Age sites of Ammerbuch-Reusten

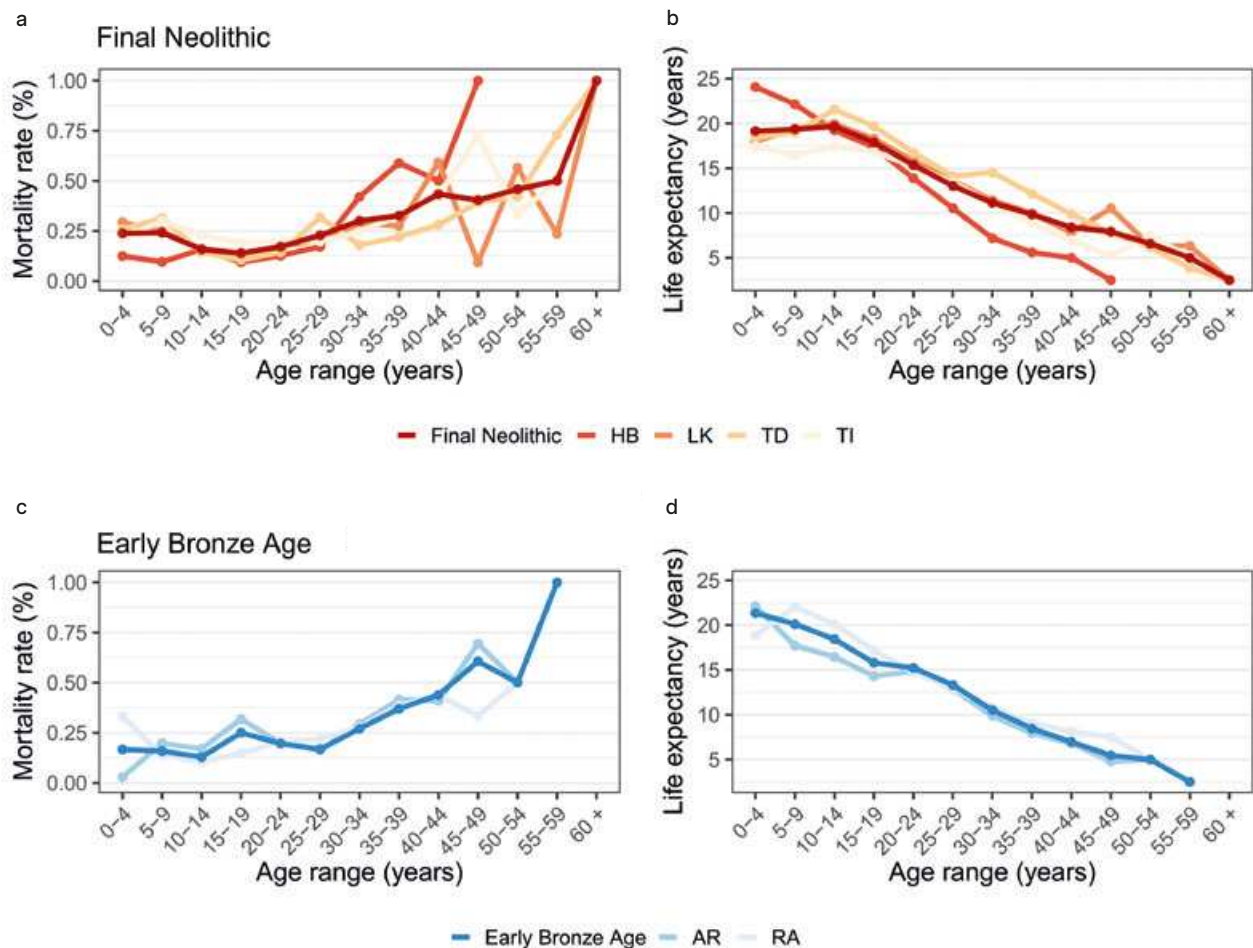


Fig. 3 Comparison of mortality rate (q_x) and life expectancy (e_x) in Final Neolithic (a-b) and Early Bronze Age (c-d) composite and single sites. Abbreviations: AR – Ammerbuch-Reusten; HB – Heilbronn; LK – Lauda-Königshofen; RA – Remseck-Aldingen; TD – Tauberbischofsheim-Dittigheim; TI – Tauberbischofsheim-Impfingen. – (Image S. Lismann).

and Remseck-Aldingen are nearly identical during adulthood, but opposing in the subadult age categories. In Ammerbuch-Reusten most of the individuals died between 5 and 19 years, whereas in Remseck-Aldingen, the majority died before age 5. This is also reflected in high mortality in 15–19-year-old individuals in Ammerbuch-Reusten, and 0–4-year-old individuals in Remseck-Aldingen. Even though life expectancy is initially higher in Ammerbuch-Reusten, it declines below that of Remseck-Aldingen during 5–19 years. No statistically significant differences are detectable for the Early Bronze Age. To outline possible sex related differences, the distribution of males (Final Neolithic: 93; Early Bronze Age: 25) and females (Final Neolithic: 63; Early Bronze Age: 19) was calculated. The related life tables of the male, female and unsexed Final Neolithic and Early Bronze Age composite sample can be found in the Appendix (Appendix, tab. A.7-12). Based on these, figure 4 shows the number of dead (d_x), and figure 5a-d the mortality rate (q_x) and life

expectancy (e_x) by sex for the two periods. Sex differentiated life tables reveal that: First, in the Final Neolithic, the number of dead is comparable for both sexes except for higher numbers of females at 0–4 years and 25–29 years, and of males at 5–9 years. Similarly, in the Early Bronze Age, the number of females is highest at 0–4 and 15–19 years, and compared to the females the number of males reaches higher values at 5–9 and 25–34 years. However, the majority of subadults could not be sexed. Second, after initial higher female mortality in the Final Neolithic, mortality rates are nearly equal in both sexes until 15–19 years. Subsequently, the mortality is constantly higher for females than for males. In the Early Bronze Age, female mortality is also higher at 0–4, but reaches a peak between 15 and 24 years. Male mortality is slightly increased during 25–34 years. Third, the Final Neolithic life expectancy for males is nearly constantly higher than for females until 40–44 years, which also yields significant results ($V = 0$, p -value = 0.005889). This also applies to

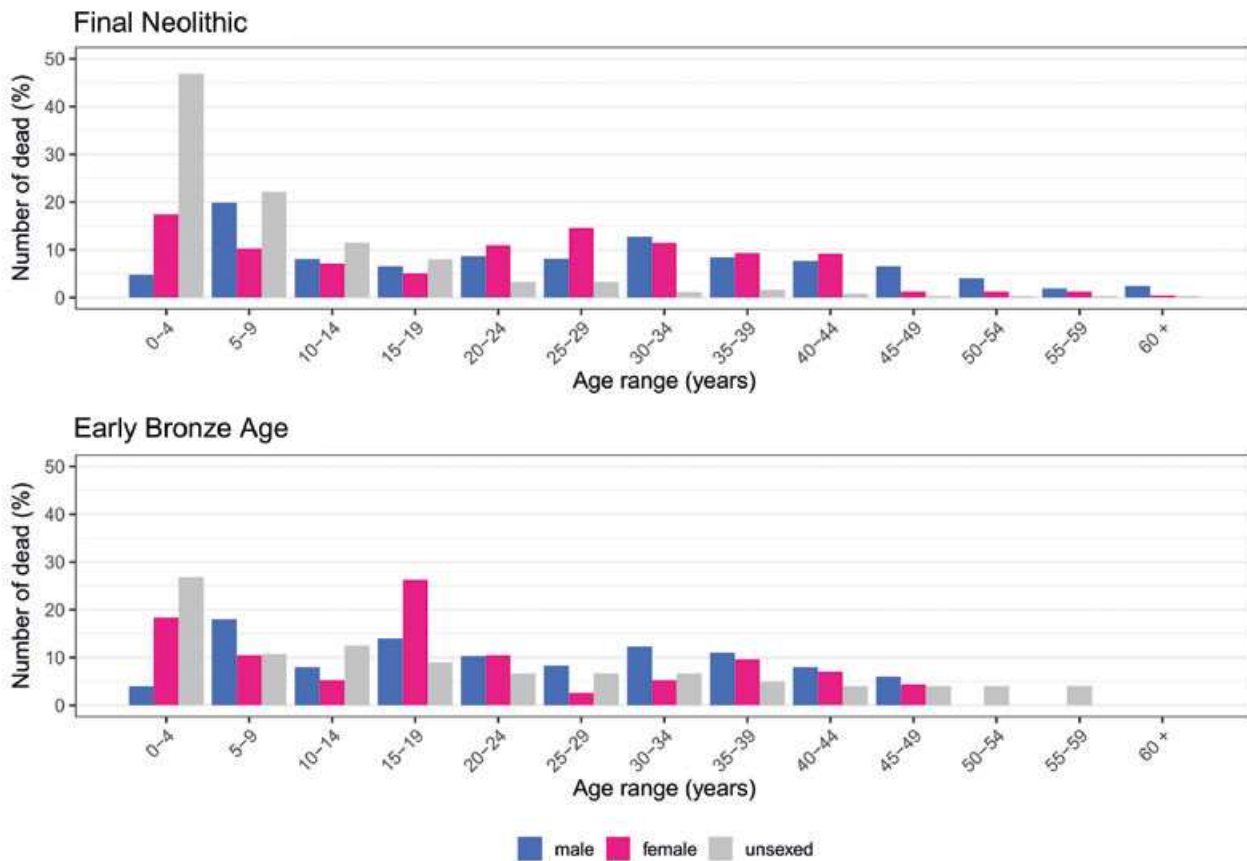


Fig. 4 Comparison of sex-specific number of dead (d.) in the Final Neolithic and Early Bronze Age composite sample. – (Image S. Lismann).

the Early Bronze Age until 20–24 years, after which age males and females show similar mortality levels. Further statistically significant results are also observable when male mortality and life expectancy are compared for both periods ($V = 0$, p -value =

0.03451 and $V = 55$, p -value = 0.005889, respectively). Nevertheless, the sex-specific life tables should be viewed cautiously, as only 62.4 % of the Final Neolithic and 61.1 % of the Early Bronze Age skeletons could be assigned to sex.

Discussion

Our study compares the demographic traits of age-at-death, mortality and life expectancy distributions through life tables in the Final Neolithic and the Early Bronze Age (ca. 2900–1600 BC) in Southwest Germany. The results indicate diachronic trends accompanied by local variations.

The composite samples differ mainly in the subadult age categories with varying mortality and life expectancy for infants in both periods and for older juveniles in the Early Bronze Age. However, the larger Early Bronze Age cemeteries of Ammerbuch-Reusten and Remseck-Aldingen greatly diverge in the number of dead in the subadult age categories, specifically at 0–4 years, making it difficult to draw secure conclusions based on the composite sample. The different sample sizes of the Early Bronze Age

infants probably introduce a bias that erroneously leads to lower values in the composite sample. Reasons for this could be the preservation of archaeological features and fragile skeletal remains, or burial practices that do not manifest in the archaeological record (Grosskopf 2023; Tornberg/Vandkilde 2025, 9. 13). This may particularly apply to the site of Ammerbuch-Reusten, because the integrity of the cemetery has been severely compromised by farming, potentially resulting in the near absence of 0–4-year-olds. In contrast, for Remseck-Aldingen the number of 0–4-year-olds approximates or even exceeds the values of the Final Neolithic sites and, therefore, can be considered as representative. Nevertheless, the demographic pattern of subadults in Remseck-Aldingen needs further consideration.

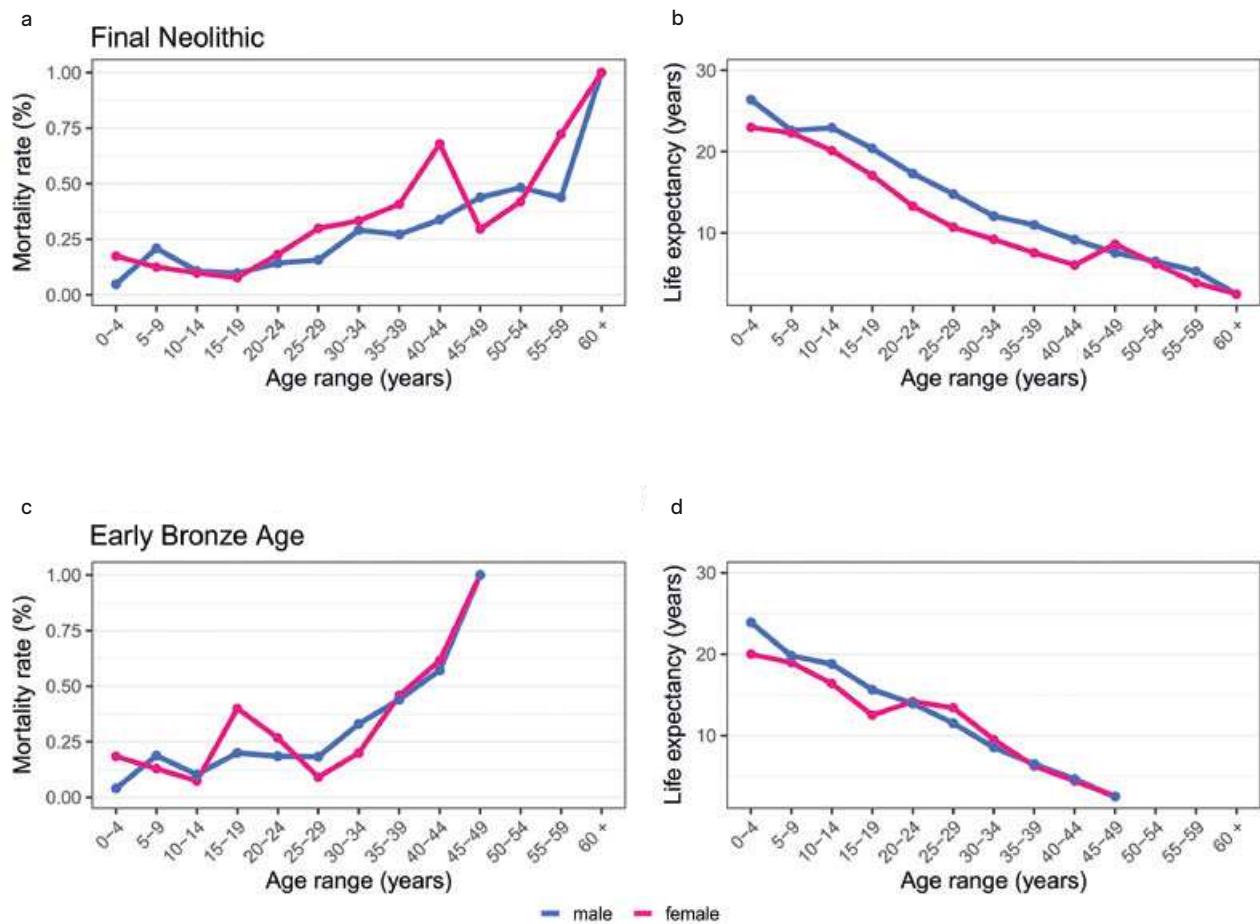


Fig. 5 Comparison of sex-specific mortality rate (q_x) and life expectancy (e_x) in the Final Neolithic (a-b) and Early Bronze Age (c-d) composite sample. – (Image S. Lismann).

In general, increased subadult mortality in the Corded Ware culture sites and the Early Bronze Age site of Ammerbuch-Reusten could indicate increased fertility and birth rates, and subsequent population growth (Boldsen et al. 2022, 134), as also suggested in Scandinavian Corded Ware cultures (Tornberg/Vandkilde 2025, 10 fig. 5; 13–14). However, this population growth trend does not apply to Remseck-Aldingen, since a concomitant higher number of older children and juveniles is not observable (cf. Chamberlain 2006, 64–65). Furthermore, the youngest age category (0–4 years) encompasses two critical stages of early life: birth and weaning. Since neonates (0–1 year) are not overly represented in Remseck-Aldingen (8.3 %; Final Neolithic 25.2 %), the increased mortality is based on high numbers of 2–4-year-olds, probably due to infectious diseases or stress during and after weaning. Even though the weaning behaviour did not change essentially throughout the Neolithic and the Early Bronze Age in Central Germany (Münster et al. 2018, 23), regional differences are observed (Münster et al. 2018, 24), which may apply to Remseck-Aldingen. Preliminary examinations of linear enamel hypoplasia indicate an ear-

lier occurrence of weaning in this site than in the other samples under study, presumably suggesting a higher stress level and mortality in infants. However, palaeopathological analyses are needed to test this hypothesis, which is currently conducted by us. Interestingly, Rathmann et al. (2023, 7. 9 fig. 6) found less biological variation in Remseck-Aldingen than in the other samples studied, and concluded that this site may represent an isolated population, which coincides with the »uncommon« orientation of the burials within the Neckar group. Their presumed isolation may have encouraged distinct cultural behaviours that, in combination with potential environmental factors (e. g., early weaning, limited access to nutritious weaning foods, disease, living conditions), had deleterious effects on child rearing, eventually distinguishing the Remseck-Aldingen population from those of other sites under study.

Moreover, late adolescence seems to offer more dangers for the people of the Early Bronze Age than for those of the Final Neolithic. Considering biological sex, it becomes evident that this spike mirrors increased female mortality emerging at 15–19 years during the Early Bronze Age. Combined with the

generally high female mortality rate in the subsequent age category at 20–24 years in both periods, this probably reflects more severe hazards of pregnancy and parturition for Early Bronze Age women. Interestingly, this trend only prevails in the site of Ammerbuch-Reusten, which is temporally and micro-regionally distinct from Remseck-Aldingen. Even though adolescent pregnancies seem to be more frequent in European Bronze Age societies (Pany-Kucera et al. 2020, 45; Rebay-Salisbury 2017, 174–176, 184; Rebay-Salisbury et al. 2018, 100–106), this is not a general trend. Peak female mortality presumably related to reproduction is reached in the Early Bronze Age between 30 and 40 years in Central Germany and between 20 and 30 years in Southeast Germany (Nicklisch 2017, 107 fig. 1.7; 108; Staskiewicz 2018a, 478 fig. 268; 480; 2018b, 514 fig. 293; 515). However, increased female mortality in late adolescence has also been discovered in Corded Ware cultures in Scandinavia (Tornberg/Vandkilde 2025, 10 fig. 5; 11). This could imply that the transition to womanhood was differently perceived, resulting in chronologically and regionally different marital ages and first pregnancies. However, as the development of parturition scars is highly variable and dependent on several conditions (Pany-Kucera et al. 2022a; 2022b; Waltenberger et al. 2022), biologically identifying pregnancies is not straightforward, especially in juveniles. Still, one inhumation of a possibly female juvenile individual at Ammerbuch-Reusten contained neonate skeletal remains, constituting a potential subadult pregnancy and mother-child burial. The lack of further such burials and the generally low number of very young subadults in Ammerbuch-Reusten could be related to the aforementioned reasons.

Furthermore, both time periods are characterised by more potentially female individuals in the youngest age category. Since diseases are largely sex-independent, it is possible that males were culturally more acknowledged, ultimately leading to higher parental investment in male offspring, with neglect or infanticide of female children (Trautmann 2012, 331, 334, 341, 344; Rebay-Salisbury et al. 2020, 265). Archaeological findings, however, do not indicate a preferred sex through burial traditions in the sites included in our analysis. Moreover, missing signs of sharp or blunt force trauma do not indicate violent acts against subadults. Having said this, it must be mentioned that the poor preservation, especially of cranial bones, hampers interpretations, and other causes of violent death that leave no skeletal traces cannot be excluded. Active or passive infanticide was also hypothesised by Trautmann (2012, 330–331). Another option is that the male birth rate declined

due to the poor living conditions of the mothers (Song 2012). Even though preliminary observations indicate high frequencies of pathological conditions, more detailed analyses are necessary to test this hypothesis. Nevertheless, the high number of unsexed subadults could introduce a data bias, as subadult morphological sexing techniques are error-prone (e. g., Leskovar et al. 2023; Vlak et al. 2008). We therefore caution to interpret these results with care.

Interestingly, Final Neolithic women consistently exhibit higher mortality rates and lower life expectancy than males, while in the Early Bronze Age they are equal for both sexes after the probable reproductive phase of females. This indicates ameliorating conditions for women from the Final Neolithic to the Early Bronze Age with cultural and social changes positively affecting female life circumstances. The results of Macintosh et al. (2014; 2016) support this hypothesis, demonstrating a stress-related reduction in body size, particularly among Final Neolithic women, and changes in female behaviour and labour division in the Early Bronze Age. Interestingly, this sexual dimorphic trend is not observable in Final Neolithic and Early Bronze Age Central Germany (Nicklisch 2017, 107 tab. 1.5), accentuating regional differences. It should be noted that the validity of this observation is limited due to the small number of sexed individuals in the Early Bronze Age samples under study.

The site of Heilbronn stands out with respect to the relative demographic uniformity of all other Final Neolithic sites. Keeping in mind that the small sample size compared to the other Final Neolithic sites could also introduce some error, a distinct pattern can be observed. The low number of infants and the high frequencies of individuals in middle adulthood preclude an attritional cemetery, which would reflect a pattern with high mortality during infancy, that decreases afterwards and again increases from adulthood onwards. Natural disasters or epidemics are also unlikely since these factors largely act independent of age, which contradicts the high number of middle-aged adults. Rather, this could indicate warfare or conflicts (Meyer et al. 2018; Fernández-Crespo et al. 2023; Fibiger et al. 2023). However, since both sexes are equally affected and evidence for trauma is lacking, this hypothesis also has limited plausibility. Even though the small number of infants could be explained by the reasons mentioned above, the pattern for adult individuals still remains to be explained in a satisfactory manner. Nevertheless, most intriguingly this observation coincides with the fact that individuals anthropologically determined as male had been buried on their left side and those determined as female almost exclusively

on their right side, seemingly reversing the common bipolar differentiation practises of the Corded Ware. An explanation might be mutually adoptive processes between Corded Ware and Bell Beaker that are visible in pottery styles and burial customs from 2480 cal BC onwards (Großmann 2016). However, of the four radiocarbon-dated graves from Heilbronn that exhibit the »inverted« gender scheme, three most probably fall into an earlier period, while only one dates after 2480 cal BC. In any case, the Heilbronn cemetery is certainly of particular importance to understand the multi-faceted manner of the complex social and cultural processes that occurred in Southwest Germany during the third millennium BC.

Finally, even though several studies have demonstrated the value of age and sex analyses to detect palaeodemographic trends in historic and prehistoric populations (e. g., Alesan et al. 1999; Eshed et al. 2004; Howell 1982; Nagaoka et al. 2006; Nicklisch 2017), it is an ongoing debate to which extend palaeodemographic analyses actually reflect the once-living population (Bocquet-Appel/Masset 1982; DeWitte/Stojanowski 2015; Wood et al. 1992; Wright/Yoder 2003). Insufficient sample size and inaccuracy in age and sex determination are particularly criti-

cised (Boldsen et al. 2022; DeWitte 2018). To circumvent these issues, we pooled sites of the same cultural complexes, as frequently practiced and suggested (Milner/Boldsen 2017, 33; Nicklisch 2017; Brewis et al. 1990). However, by simultaneously considering single-site samples, we are able to account for local conditions, and acknowledge the reduced statistical validity of these results. In addition, we have used various well-established ageing methods and therefore assume that the patterns in the age categories beyond 45 years in the present data reflect populations with reduced life expectancy (Alesan et al. 1999). Furthermore, the small number of Early Bronze Age sexed individuals and especially methodological limitations in sexing subadults cause biases; results are therefore only indicative. Despite these limitations, we believe that our analyses adequately represent demographic structures and they generally agree with studies in Austria, Scandinavia and Southeast Europe (Pany-Kucera et al. 2020; Rebay-Salisbury 2017; Rebay-Salisbury et al. 2018; Macintosh et al. 2014; 2016; Tornberg/Vandkilde 2025). To increase statistical validity and refine chronological and geographical coverage, future research should include additional sites and cultural complexes.

Conclusion

Our demographic analysis provides new valuable insights into the structure of Final Neolithic and Early Bronze Age populations in Southwest Germany. Cultural and social development during these periods affected the demographic profile of past populations in differing extents, and strict chronological conclusions are not generally valid, indicated by local deviations.

We found diachronic changes in mortality and life expectancy for infant individuals, as well as for juvenile and adult females. The higher mortality among Early Bronze Age female juveniles could potentially indicate adolescent pregnancies, probably as a consequence of changes in marital ages and social recognition of women. Nevertheless, Final Neolithic female individuals exhibit a constantly lower life expectancy than males, contrary to equal life expectancies of both sexes from middle adulthood

onwards in the Early Bronze Age. This may signal improving living conditions in the later period. Furthermore, even though female infanticide has been suggested in similar studies, DNA or peptide-based analyses are needed to corroborate the potential higher mortality in female infants. Finally, unusual mortality patterns and burial practices in the Corded Ware cemetery of Heilbronn still require detailed palaeopathological and archaeological analyses. Our findings demonstrate that even culturally and temporally defined groups are highly variable, and that analyses of individual sites are essential to detect and understand such variability. Ultimately, the results refine our knowledge of demographic development during the Final Neolithic and the Early Bronze Age and emphasize the importance of studies conducted at regional to micro-regional scales for these periods.

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Zusammenfassung

Résumé

Lebensgeschichte rekonstruieren. Neue paläodemografische Einblicke in endneolithische und frühbronzezeitliche Populationen Südwestdeutschlands

Während des dritten bis mittleren zweiten Jahrtausends v. Chr. erlebte die menschliche Kultur in Europa einen dramatischen Wandel. Verschiedene Studien zeigen, dass der soziokulturelle Wandel komplexe und regional unterschiedliche biologische Auswirkungen hatte. Daher liefern paläodemografische Analysen des Sterbealters und Geschlechts von menschlichen Skeletten wertvolle Einblicke in die Lebenserwartung und Sterblichkeit. In dieser Studie wird das demografische Profil von 322 Individuen des Endneolithikums (Schnurkeramik) und der Frühbronzezeit (Neckargruppe) aus 17 Fundstellen in Baden-Württemberg (Südwestdeutschland) anhand von Sterbetafeln rekonstruiert. Die Ergebnisse deuten auf diachrone Veränderungen der Sterblichkeit und Lebenserwartung von Kleinkindern sowie weiblichen Jugendlichen und erwachsenen Frauen, begleitet von regionalen Unterschieden. Dies weist auf generell verbesserte Lebensumstände vom Endneolithikum zur Frühbronzezeit, mit Ausnahme von erhöhter Sterblichkeit frühbronzezeitlicher junger Frauen, die möglicherweise auf Jugendschwangerschaften zurückzuführen ist.

Reconstruire l'histoire de la vie. Nouvelles perspectives paléodémographiques sur les populations du Néolithique final et de l'âge du Bronze ancien en Allemagne du Sud-Ouest

Au cours du troisième et du milieu du deuxième millénaire av. J.-C., la culture humaine en Europe a connu des changements spectaculaires. Plusieurs études montrent que ces changements socioculturels ont eu des répercussions biologiques complexes et différentes selon les régions. Par conséquent, les analyses paléodémographiques de l'âge au décès et du sexe des squelettes humains fournissent des informations précieuses sur l'espérance de vie et la mortalité. Dans cette étude, le profil démographique de 322 individus du Néolithique final (Céramique cordée) et du Bronze ancien (Groupe du Neckar) provenant de 17 sites du Bade-Wurtemberg, dans le sud-ouest de l'Allemagne, est reconstitué à partir de tables de mortalité. Les résultats indiquent des changements diachroniques de la mortalité et de l'espérance de vie des jeunes enfants, des adolescentes et des femmes adultes, accompagnés de différences régionales. Cela indique une amélioration générale des conditions de vie entre le Néolithique final et le Bronze ancien, à l'exception de la mortalité accrue des jeunes femmes du Bronze ancien, qui pourrait être due à des grossesses adolescentes.

Schlüsselwörter

Mots-clés

Südwestdeutschland / Endneolithikum / Frühbronzezeit / Paläodemografie / Anthropologie
Sud-Ouest de l'Allemagne / Néolithique final / Bronze ancien / paléodémographie / anthropologie

Appendix: Supplementary Life Tables

x	D _x	d _x	l _x	q _x	L _x	T _x	e _x
0-4	3.00	12.50	100.00	0.13	468.75	2406.25	24.06
5-9	2.00	8.33	87.50	0.10	416.67	1937.50	22.14
10-14	3.00	12.50	79.17	0.16	364.58	1520.83	19.21
15-19	1.50	6.25	66.67	0.09	317.71	1156.25	17.34
20-24	1.83	7.64	60.42	0.13	282.99	838.54	13.88
25-29	2.17	9.03	52.78	0.17	241.32	555.56	10.53
30-34	4.42	18.40	43.75	0.42	172.74	314.24	7.18
35-39	3.58	14.93	25.35	0.59	89.41	141.49	5.58
40-44	1.25	5.21	10.42	0.50	39.06	52.08	5.00
45-49	1.25	5.21	5.21	1.00	13.02	13.02	2.50
50-54	0.00	0.00	0.00	0.00	0.00	0.00	0.00
55-59	0.00	0.00	0.00	0.00	0.00	0.00	0.00
60+	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Σ	24.00	100.00			2406.25		

Tab. A.1 Abridged life table for Heilbronn. – (Table S. Lismann).

x	D _x	d _x	l _x	q _x	L _x	T _x	e _x
0-4	26.08	29.31	100.00	0.29	426.73	1797.75	17.98
5-9	15.58	17.51	70.69	0.25	309.69	1371.02	19.39
10-14	7.58	8.52	53.18	0.16	244.62	1061.33	19.96
15-19	5.55	6.24	44.66	0.14	207.72	816.71	18.29
20-24	5.80	6.52	38.43	0.17	175.84	608.99	15.85
25-29	5.80	6.52	31.91	0.20	143.26	433.15	13.57
30-34	6.44	7.24	25.39	0.29	108.87	289.89	11.42
35-39	4.44	4.99	18.15	0.27	78.29	181.02	9.97
40-44	6.94	7.80	13.16	0.59	46.31	102.73	7.80
45-49	0.44	0.50	5.36	0.09	25.56	56.42	10.52
50-54	2.44	2.74	4.86	0.56	17.46	30.86	6.34
55-59	0.44	0.50	2.12	0.23	9.35	13.40	6.33
60+	1.44	1.62	1.62	1.00	4.05	4.05	2.50
Σ	89.00	100.00			1797.75		

Tab. A.2 Abridged life table for Lauda-Königshofen. – (Table S. Lismann).

x	D _x	d _x	l _x	q _x	L _x	T _x	e _x
0-4	15.25	25.85	100.00	0.26	435.38	1843.22	18.43
5-9	13.75	23.31	74.15	0.31	312.50	1407.84	18.99
10-14	4.25	7.20	50.85	0.14	236.23	1095.34	21.54
15-19	2.75	4.66	43.64	0.11	206.57	859.11	19.68
20-24	3.28	5.56	38.98	0.14	181.03	652.54	16.74
25-29	6.28	10.64	33.43	0.32	140.54	471.52	14.11
30-34	2.42	4.10	22.79	0.18	103.68	330.98	14.52
35-39	2.42	4.10	18.68	0.22	83.17	227.30	12.17
40-44	2.42	4.10	14.58	0.28	62.65	144.14	9.88
45-49	2.42	4.10	10.48	0.39	42.14	81.48	7.78
50-54	1.59	2.69	6.38	0.42	25.15	39.35	6.17
55-59	1.59	2.69	3.69	0.73	11.70	14.19	3.85
60+	0.59	1.00	1.00	1.00	2.49	2.49	2.50
Σ	59.00	100.00			1843.22		

Tab. A.3 Abridged life table for Tauberbischofsheim-Dittigheim. – (Table S. Lismann).

x	D _x	d _x	l _x	q _x	L _x	T _x	e _x
0-4	7.67	21.30	100.00	0.21	446.76	1743.06	17.43
5-9	8.50	23.61	78.70	0.30	334.49	1296.30	16.47
10-14	4.50	12.50	55.09	0.23	244.21	961.81	17.46
15-19	2.93	8.15	42.59	0.19	192.59	717.59	16.85
20-24	2.46	6.84	34.44	0.20	155.13	525.00	15.24
25-29	1.96	5.45	27.61	0.20	124.42	369.87	13.40
30-34	1.96	5.45	22.16	0.25	97.18	245.45	11.08
35-39	1.96	5.45	16.71	0.33	69.95	148.26	8.87
40-44	1.71	4.75	11.27	0.42	44.44	78.32	6.95
45-49	1.71	4.75	6.51	0.73	20.68	33.87	5.20
50-54	0.21	0.59	1.76	0.33	7.33	13.19	7.50
55-59	0.21	0.59	1.17	0.50	4.40	5.86	5.00
60+	0.21	0.59	0.59	1.00	1.47	1.47	2.50
Σ	36.00	100.00			1743.06		

Tab. A.4 Abridged life table for Tauberbischofsheim-Impfingen. – (Table S. Lismann).

x	D _x	d _x	l _x	q _x	L _x	T _x	e _x
0-4	1.00	2.94	100.00	0.03	492.65	2213.24	22.13
5-9	6.50	19.12	97.06	0.20	437.50	1720.59	17.73
10-14	4.50	13.24	77.94	0.17	356.62	1283.09	16.46
15-19	7.00	20.59	64.71	0.32	272.06	926.47	14.32
20-24	2.96	8.70	44.12	0.20	198.84	654.41	14.83
25-29	1.96	5.76	35.42	0.16	162.68	455.58	12.86
30-34	2.96	8.70	29.66	0.29	126.53	292.89	9.88
35-39	2.96	8.70	20.96	0.42	83.03	166.36	7.94
40-44	1.71	5.02	12.25	0.41	48.71	83.33	6.80
45-49	1.71	5.02	7.23	0.69	23.59	34.62	4.79
50-54	0.38	1.10	2.21	0.50	8.27	11.03	5.00
55-59	0.38	1.10	1.10	1.00	2.76	2.76	2.50
60+	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Σ	34.00	100.00			2213.24		

Tab. A.5 Abridged life table for Ammerbuch-Reusten. – (Table S. Lismann).

x	D _x	d _x	l _x	q _x	L _x	T _x	e _x
0-4	11.00	33.33	100.00	0.33	416.67	1886.36	18.86
5-9	3.00	9.09	66.67	0.14	310.61	1469.70	22.05
10-14	2.00	6.06	57.58	0.11	272.73	1159.09	20.13
15-19	2.50	7.58	51.52	0.15	238.64	886.36	17.21
20-24	3.00	9.09	43.94	0.21	196.97	647.73	14.74
25-29	2.50	7.58	34.85	0.22	155.30	450.76	12.93
30-34	2.50	7.58	27.27	0.28	117.42	295.45	10.83
35-39	2.50	7.58	19.70	0.38	79.55	178.03	9.04
40-44	1.75	5.30	12.12	0.44	47.35	98.48	8.12
45-49	0.75	2.27	6.82	0.33	28.41	51.14	7.50
50-54	0.75	2.27	4.55	0.50	17.05	22.73	5.00
55-59	0.75	2.27	2.27	1.00	5.68	5.68	2.50
60+	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Σ	33.00	100.00			1886.36		

Tab. A.6 Abridged life table for Remseck-Aldingen. – (Table S. Lismann).

x	D _x	d _x	l _x	q _x	L _x	T _x	e _x
0-4	4.50	4.84	100.00	0.05	487.90	2639.78	26.40
5-9	18.50	19.89	95.16	0.21	426.08	2151.88	22.61
10-14	7.50	8.06	75.27	0.11	356.18	1725.81	22.93
15-19	6.10	6.56	67.20	0.10	319.62	1369.62	20.38
20-24	8.07	8.68	60.65	0.14	281.53	1050.00	17.31
25-29	7.57	8.14	51.97	0.16	239.47	768.47	14.79
30-34	11.86	12.75	43.82	0.29	187.24	529.00	12.07
35-39	7.86	8.45	31.07	0.27	134.24	341.76	11.00
40-44	7.11	7.64	22.62	0.34	94.01	207.52	9.17
45-49	6.11	6.57	14.98	0.44	58.48	113.51	7.58
50-54	3.77	4.06	8.41	0.48	31.92	55.03	6.54
55-59	1.77	1.91	4.35	0.44	17.00	23.11	5.31
60+	2.27	2.45	2.45	1.00	6.11	6.11	2.50
Σ	93.00	100.00			2639.78		

Tab. A.7 Abridged life table for Final Neolithic males. – (Table S. Lismann).

x	D _x	d _x	l _x	q _x	L _x	T _x	e _x
0-4	11.00	17.46	100.00	0.17	456.35	2297.62	22.98
5-9	6.50	10.32	82.54	0.13	386.90	1841.27	22.31
10-14	4.50	7.14	72.22	0.10	343.25	1454.37	20.14
15-19	3.20	5.08	65.08	0.08	312.70	1111.11	17.07
20-24	6.89	10.94	60.00	0.18	272.64	798.41	13.31
25-29	9.23	14.65	49.06	0.30	208.66	525.77	10.72
30-34	7.23	11.47	34.41	0.33	143.36	317.11	9.22
35-39	5.89	9.36	22.94	0.41	91.29	173.74	7.57
40-44	5.81	9.22	13.58	0.68	44.84	82.45	6.07
45-49	0.81	1.29	4.36	0.30	18.56	37.61	8.63
50-54	0.81	1.29	3.07	0.42	12.13	19.05	6.21
55-59	0.81	1.29	1.78	0.72	5.69	6.92	3.89
60+	0.31	0.49	0.49	1.00	1.23	1.23	2.50
Σ	63.00	100.00			2297.62		

Tab. A.8 Abridged life table for Final Neolithic females. – (Table S. Lismann).

x	D _x	d _x	l _x	q _x	L _x	T _x	e _x
0-4	44.00	46.81	100.00	0.47	382.98	938.83	9.39
5-9	20.83	22.16	53.19	0.42	210.55	555.85	10.45
10-14	10.83	11.52	31.03	0.37	126.33	345.30	11.13
15-19	7.53	8.01	19.50	0.41	77.48	218.97	11.23
20-24	3.06	3.26	11.49	0.28	49.31	141.49	12.31
25-29	3.06	3.26	8.23	0.40	33.02	92.18	11.20
30-34	1.06	1.13	4.98	0.23	22.06	59.16	11.89
35-39	1.56	1.66	3.85	0.43	15.09	37.10	9.64
40-44	0.81	0.86	2.19	0.39	8.78	22.02	10.07
45-49	0.31	0.33	1.32	0.25	5.79	13.24	10.00
50-54	0.31	0.33	0.99	0.33	4.14	7.45	7.50
55-59	0.31	0.33	0.66	0.50	2.48	3.31	5.00
60+	0.31	0.33	0.33	1.00	0.83	0.83	2.50
Σ	94.00	100.00			938.83		

Tab. A.9 Abridged life table for Final Neolithic unsexed individuals. – (Table S. Lismann).

x	D _x	d _x	l _x	q _x	L _x	T _x	e _x
0-4	1.00	4.00	100.00	0.04	490.00	2390.00	23.90
5-9	4.50	18.00	96.00	0.19	435.00	1900.00	19.79
10-14	2.00	8.00	78.00	0.10	370.00	1465.00	18.78
15-19	3.50	14.00	70.00	0.20	315.00	1095.00	15.64
20-24	2.58	10.33	56.00	0.18	254.17	780.00	13.93
25-29	2.08	8.33	45.67	0.18	207.50	525.83	11.51
30-34	3.08	12.33	37.33	0.33	155.83	318.33	8.53
35-39	2.75	11.00	25.00	0.44	97.50	162.50	6.50
40-44	2.00	8.00	14.00	0.57	50.00	65.00	4.64
45-49	1.50	6.00	6.00	1.00	15.00	15.00	2.50
50-54	0.00	0.00	0.00	0.00	0.00	0.00	0.00
55-59	0.00	0.00	0.00	0.00	0.00	0.00	0.00
60+	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Σ	25.00	100.00			2390.00		

Tab. A.10 Abridged life table for Early Bronze Age males. – (Table S. Lismann).

x	D_x	d_x	l_x	q_x	L_x	T_x	e_x
0-4	3.50	18.42	100.00	0.18	453.95	2000.00	20.00
5-9	2.00	10.53	81.58	0.13	381.58	1546.05	18.95
10-14	1.00	5.26	71.05	0.07	342.11	1164.47	16.39
15-19	5.00	26.32	65.79	0.40	263.16	822.37	12.50
20-24	2.00	10.53	39.47	0.27	171.05	559.21	14.17
25-29	0.50	2.63	28.95	0.09	138.16	388.16	13.41
30-34	1.00	5.26	26.32	0.20	118.42	250.00	9.50
35-39	1.83	9.65	21.05	0.46	81.14	131.58	6.25
40-44	1.33	7.02	11.40	0.62	39.47	50.44	4.42
45-49	0.83	4.39	4.39	1.00	10.96	10.96	2.50
50-54	0.00	0.00	0.00	0.00	0.00	0.00	0.00
55-59	0.00	0.00	0.00	0.00	0.00	0.00	0.00
60+	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Σ	19.00	100.00			2000.00		

Tab. A.11 Abridged life table for Early Bronze Age females. – (Table S. Lismann).

x	D_x	d_x	l_x	q_x	L_x	T_x	e_x
0-4	7.50	26.79	100.00	0.27	433.04	2000.00	20.00
5-9	3.00	10.71	73.21	0.15	339.29	1566.96	21.40
10-14	3.50	12.50	62.50	0.20	281.25	1227.68	19.64
15-19	2.50	8.93	50.00	0.18	227.68	946.43	18.93
20-24	1.88	6.70	41.07	0.16	188.62	718.75	17.50
25-29	1.88	6.70	34.38	0.19	155.13	530.13	15.42
30-34	1.88	6.70	27.68	0.24	121.65	375.00	13.55
35-39	1.38	4.91	20.98	0.23	92.63	253.35	12.07
40-44	1.13	4.02	16.07	0.25	70.31	160.71	10.00
45-49	1.13	4.02	12.05	0.33	50.22	90.40	7.50
50-54	1.13	4.02	8.04	0.50	30.13	40.18	5.00
55-59	1.13	4.02	4.02	1.00	10.04	10.04	2.50
60+	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Σ	28.00	100.00			2000.00		

Tab. A.12 Abridged life table for Early Bronze Age unsexed individuals. – (Table S. Lismann).

Appendix C

Study III

Evaluating the impact of Final Neolithic-Early Bronze Age transition on pathology prevalence
in populations from Southwest Germany

Stephanie Lismann, Michael Francken, Katerina Harvati, Martin Bartelheim, André Spatzier

Manuscript ready for submission³

³ The version submitted for publication in a journal may differ slightly from the version included in this thesis.

Evaluating the impact of Final Neolithic-Early Bronze Age transition on pathology prevalence in populations from Southwest Germany

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Abstract

The populations of the Corded Ware culture and Neckar group in Southwest Germany largely lack diachronic bioarchaeological research. Consequently, there is scarce knowledge about the impact of the cultural transition on the societies and biological stress. This study presents the palaeopathological research of Final Neolithic and Early Bronze Age (2900-1600 BC) skeletal remains from the regions of the rivers Tauber and Neckar in Southwest Germany. The aim is to investigate variations in the frequencies of different palaeopathological conditions among the different sites and to assess if these are connected to mortality patterns or cultural change. The results show sex related differences in dental diseases, suggesting variation in diet among males and females. Degenerative joint disease indicates sex-related division of labour through time and regionally diverging subsistence strategies in the Corded Ware population, followed by homogenisation and labour specialisation in the Neckar group. Non-specific stress indicators suggest severe early childhood stress and different sex-related weaning practices through time. Trauma prevalence was largely specific to cultural periods, highlighting the practice of

trepanations in the Corded Ware populations, and increasing strenuous labour through traumatic joint lesions in the Neckar group, whereas fracture rates remained constant. Neoplastic diseases emerged in the Early Bronze Age, suggesting changes in lifestyle, working conditions or genetics. These findings contribute to the bioarchaeology and sociocultural history of Corded Ware and Neckar group populations in Southwest Germany and stress the importance of including further samples to investigate the scale and context of cultural transition in regional settings in more detail.

Introduction

Bioarchaeological research focusing on palaeopathology has greatly increased our knowledge about the burdens past populations had to face during the Final Neolithic and Early Bronze Age in Europe (Ernée, 2015; Fibiger et al., 2013; Gualdi-Russo et al., 2024; Hukelova, 2016; Nicklisch, 2017). However, in Southwest Germany emphasis has been frequently placed on specific pathology types as part of a broader archaeological and palaeoanthropological study of Final Neolithic populations (Dresely, 2004; Trautmann, 2012). Consequently, the palaeopathological profile was not thoroughly examined despite the potential for more nuanced interpretations when multiple diseases are considered in combination. Moreover, no palaeopathological studies have yet focused on Early Bronze Age populations in this region. This research gap is particularly relevant, as analyses of skeletal remains from different cultural and temporal backgrounds may elucidate aspects of cultural dynamics, social status, gender division and other factors impacting disease prevalence. Yet, the consequences of the cultural transition in terms of physiological stress markers, patterns of disease expression, and shifts in morbidity in Southwest Germany are not well known.

Accordingly, diachronic palaeopathological analyses offer a valuable approach to elucidate how biocultural processes shaped Final Neolithic and Early Bronze Age societies. Here, we evaluate the prevalence of diseases based on palaeopathological data from human skeletal remains dating between ca. 2900-1600 BC covering the Final Neolithic cultural phenomena of the Corded Ware complex (CW) and the Early Bronze Age Neckar group (NG) in Southwest Germany. Our aim is to evaluate how the cultural shift influenced biological stress in these populations and to assess whether the palaeopathological profile of the remains coincides with previously identified mortality patterns (Lismann et al., 2024).

Materials and Methods

This study encompasses 144 human skeletons and their dentition recovered from nine archaeological sites in the state of Baden-Württemberg, Southwest Germany, dating to the Final Neolithic (ca. 2900-2100/1800 BC) and Early Bronze Age (ca. 2200-1600 BC). The sites are geographically separated, which is accompanied by a cultural and chronological division. The Final Neolithic sites (n = 5, 30 adults, 42 subadults, totalling 72 individuals) of the Corded Ware complex, are located in the North of Baden-Württemberg along the river Tauber, except for the site of Heilbronn situated in the Centre of Baden-Württemberg near the river Neckar. The Early Bronze Age sites are also situated in this region (n = 4, 30 adults, 42 subadults, totalling 72 individuals) (Figure 1). Table 1 provides summary data (i.e., culture, geographic origin, date, sample size).

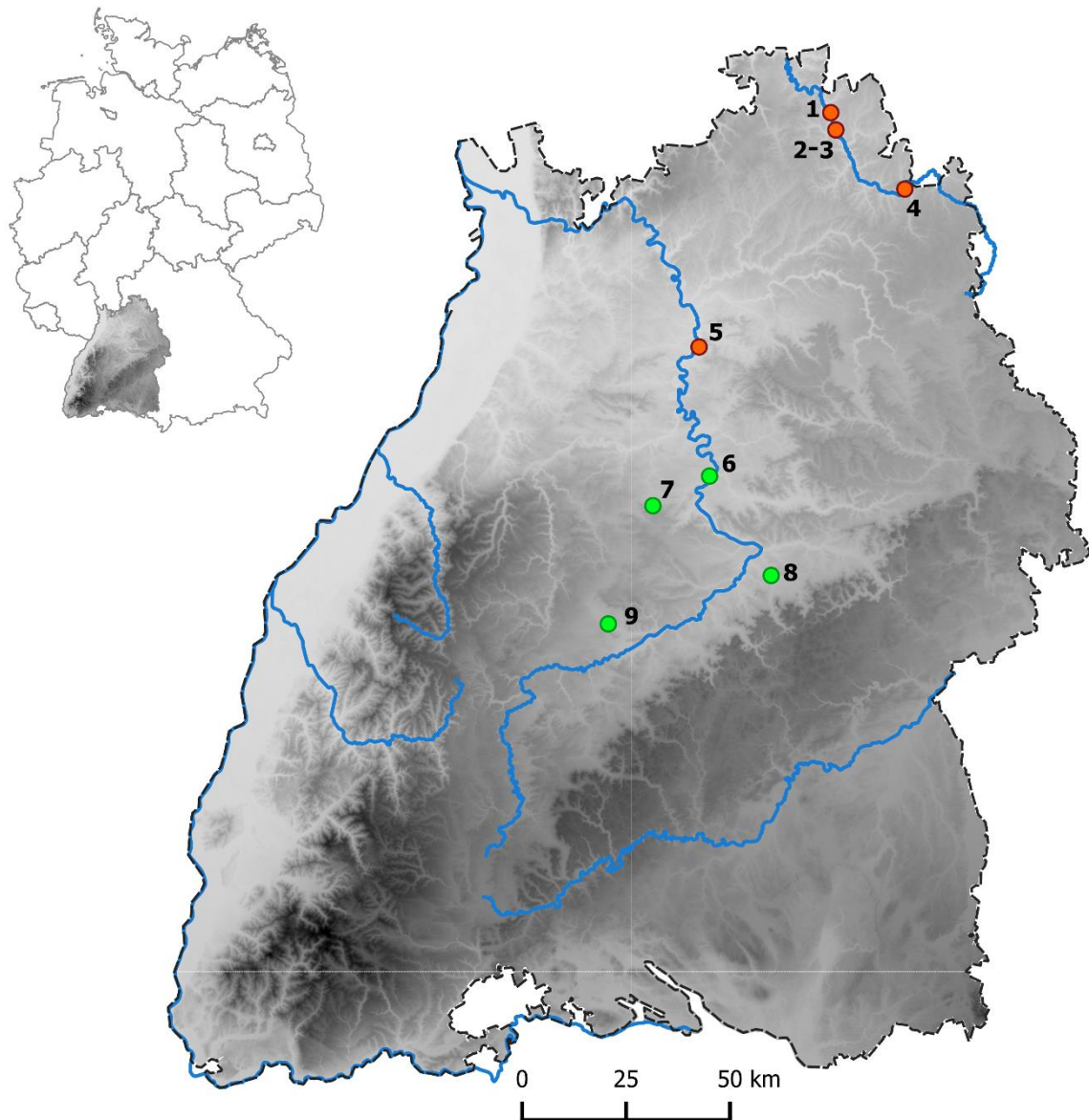


Figure 1 Map of Baden-Württemberg (Southwest Germany) showing the geographic locations of the human skeletal remains analysed in this study. Final Neolithic sites are indicated in orange, Early Bronze Age sites in green. (1) Tauberbischofsheim-Impfingen, (2-3) Tauberbischofsheim (two sites), (4) Weikersheim, (5) Heilbronn, (6) Remseck-Aldingen; (7) Gerlingen; (8) Kirchheim unter Teck; (9) Ammerbuch-Reusten. - A. Spatzier, S. Lismann

The Tauberbischofsheim-Impfingen cemetery was partially excavated in 1970-1973 (Dresely, 2004). The superposition with a Hallstatt culture necropolis and the impact of recent farming and construction works potentially destroyed parts of the Corded Ware culture occupation. Twenty-three graves were found containing 42 human skeletal remains in single, double and multi burials. Individuals are generally lying in simple rectangular to oval grave pits in crouched

position usually oriented northeast-southwest or east-west. It is noteworthy that the Tauber Valley group deviates from the typical Corded Ware gender differentiated burial practice (females lying on their left body side and males on their right) with a high number of inverted positions, especially left-sided males (Dresely, 2004). Grave goods included Corded Ware ceramics and tools of stone and bone. The individuals were dated to ca. 2622-1885 cal BC, with one radiocarbon date extending to 1624 cal BC. It must be emphasized that these are old, conventional radiocarbon dates with high standard deviation. The current study includes 36 human remains from the Impfingen Corded Ware cemetery.

In Tauberbischofsheim two sites were excavated. At “Kirchelberg/Acker Noe West” site excavations in 1968-1969 revealed five burials with nine individuals in three single, one double and one multi burial (Dresely, 2004). The Corded Ware culture site was potentially partly destroyed by younger features. Mortuary practices were similar to the Tauberbischofsheim-Impfingen site. The individuals were dated to ca. 2847-2031 cal BC. However, this date again should be treated with caution due to the same limitations as in the case of Impfingen. All nine individuals were included in the present study.

The site at “Gärtnerei Scheuermann” was excavated in 1971 comprising two graves which contained three individuals in one single and one double burial (Dresely, 2004). Mortuary practices were similar to the Tauberbischofsheim-Impfingen site. One individual was dated between 3007-2494 cal BC, once more an old, conventional date with high standard deviation. The current study includes one individual from this site.

In Weikersheim due to construction works in 1950 and 1961 at least two graves were discovered with five individuals in one double and one potential multi burial (Dresely, 2004). The skeletons were presumably buried in crouched position with ceramics as grave goods. The site was attributed to the Corded Ware culture. Radiocarbon dates are not available. The present study includes two human remains from this site.

Heilbronn was excavated in 2016 and 2018-2019 (Garcia and Neth, 2019). Twenty-four graves contained 26 individuals, of which two were recently recognised, in single and double burials. Individuals were buried in crouched position mainly along the east-west axis, facing south. However, common Corded Ware gender differentiation seems to be generally inverted as anthropologically determined males were lying on their left body side and females on their right body side, except for two left-sided females. The burials contained typical Corded Ware grave goods as decorated beakers, stone axes, and arrowheads. The radiocarbon dates range between 2863 and 2299 cal BC. For the present analysis 24 individuals were included.

The site of Remseck-Aldingen was excavated in 1987, likely to its full extent (Krause,

1988). Thirty-four graves comprised potentially 37 individuals, however, only 34 skeletal remains are preserved in single and one multi burials. In accordance with local Early Bronze Age burial customs, the dead had been interred in rectangular to oval grave pits, mostly with stone constructions that also suggest wooden coffins (Keefer and Krause, 1992; Krause, 1988; Spatzier, 2023). Bipolar gender differentiation is also exhibited, with males lying on their left body side and females on their right, in a crouched position. However, contrary to the common orientation of Neckar group burials along the northeast-southwest and east-west axis, Remseck-Aldingen exhibits mostly north-south orientations. Multiple burials contained objects and adornments made of bone, to a lesser extent also of bronze. The radiocarbon dates range between 2276 and 1743 cal BC. The current study includes 33 skeletal remains from Remseck-Aldingen.

Excavations at the site of Ammerbuch-Reusten were conducted in 2000, 2020-2021 and 2023 (Bofinger et al., 2024, 2022; Bofinger and Hald, 2000; Krauß et al., 2021), revealing separated burial areas belonging to one large cemetery. In total, 35 Early Bronze Age individuals were uncovered as single burials in simple grave pits, although poor preservation suggests an originally higher number of inhumations. Frequent deviations from the traditional Early Bronze Age burial practice are striking: there is no evidence for stone constructions within the graves and even though most individuals had been buried according to the local traditions in a crouched position, oriented along the northeast-southwest and west-east axis. Furthermore, gender differentiated body orientation is highly variable, and the almost complete absence of grave goods is unusual. The radiocarbon dates range between 1870 and 1511 cal BC. For the present analysis 34 individuals were included.

Kirchheim unter Teck site was excavated in 1937 (Lau, 1950). Three single graves contained three individuals in a crouched position, oriented northeast-southwest lying on their left side. Grave goods made of bronze date the site to the end of the Early Bronze Age. Today, only the skeletal remains of one individual are available and were included in this study. Excavations at Gerlingen took place in 1970 (Zürn, 1975), uncovering three graves and five individuals in one single and two double burials. In accordance with local funerary customs the graves contained inner stone packings in which the individuals were lying in a crouched position on their left side, oriented along the east northeast-west southwest axis. Grave goods of bronze and stone artifacts were found in two graves. Radiocarbon dates are not available. Four individuals were suitable for our analysis.

Table 1 Summary of skeletal samples used in this study.

Sample	Archaeological site	Time period	Cultural affiliation	Radiocarbon date	Sample size ^a
Tauberbischofsheim- Impfingen	Rebhuhn	Final Neolithic	Corded Ware complex	2622-1885, 1624 cal BC	36 (8/2/2/24)
Tauberbischofsheim	Gärtnerei Scheuermann	Final Neolithic	Corded Ware complex	3007-2494 cal BC	1 (1/-/-)
Tauberbischofsheim	Kirchelberg/Acker Noe West	Final Neolithic	Corded Ware complex	2847-2031 cal BC	9 (2/-/-/7)
Weikersheim	Katholische Kirche	Final Neolithic	Corded Ware complex	NA	2 (-/-/1/1)
Heilbronn	Kirschengartenstraße	Final Neolithic	Corded Ware complex	2863-2471, 2299 cal BC	24 (5/5/4/10)
Remseck-Aldingen	Halden II	Early Bronze Age	Neckar group	2276-1743 cal BC	33 (6/1/6/20)
Gerlingen	Seefeld	Early Bronze Age	Neckar group	NA	4 (2/-/-/2)
Kirchheim unter Teck	Stuttgarter Straße	Early Bronze Age	Neckar group	NA	1 (1/-/-)
Ammerbuch-Reusten	Stützbrunnen/Grüninger	Early Bronze Age	Neckar group	1870-1511 cal BC	34 (3/4/7/20)

^a *Number of individuals, in parentheses number of adult males/adult females/adults of unknown sex/subadults.*

All remains were analysed in the Osteological Collection in Tübingen by the first author, including the previously evaluated and published remains of Tauberbischofsheim and Weikersheim (Dresely, 2004). The overall bone preservation was moderate, ranging from poor to very good in terms of surface preservation and fragmentation. Dental preservation was with some exceptions very good with generally intact enamel.

Age-at-death estimation in subadults was based on dental (AlQahtani et al., 2010; Ubelaker, 1989) and skeletal development and bone dimensions (Scheuer et al., 2010; Stloukal and Hanáková, 1978). Age-at-death in adults was estimated from cranial and maxillary suture closure (Mann et al., 1991; Vallois, 1937), morphological changes of the pubic symphysis (Brooks and Suchey, 1990), auricular surface (Buckberry and Chamberlain, 2002), sternal rib ends (İşcan et al., 1984) and dental attrition (Brothwell, 1981). Sex was determined only in adults based on macroscopic analyses of the skull, mandible and pelvis (Ferembach et al., 1979; Phenice, 1969), aided by pelvic dimensions (Murail et al., 2005).

Skeletal and dental remains were examined macroscopically for a set of pathological conditions: dental diseases, degenerative joint disease, non-specific stress, trauma, and neoplasm.

Dental and oral diseases. Dental calculus are deposits of mineralised bacterial plaque, food debris and other materials accelerated by plaque accumulation, protein rich diet, alkaline oral environment and other factors (Kinaston et al., 2019; Lieverse, 1999). Dental calculus was recorded based on depositional size following Brothwell (1981).

Dental caries is a destructive infection in which oral bacteria ferment dietary carbohydrates and cause cavities in tooth structures (Kinaston et al., 2019). However, caries formation is a multifactorial process, further influenced by tooth morphology, age, sex, oral pH, and hygiene, as well as diet (Fejerskov and Nyvad, 2025). The severity of carious lesions was assessed following Grupe et al. (2015), albeit excluding the first caries stage, which is enamel discolouration, to prevent misclassifications with taphonomic staining.

Dental abrasion is the progressive reduction of the tooth crown resulting from contact between teeth and food or other objects (Kinaston et al., 2019). The degree of dental wear was recorded for each tooth based on the method by Smith (Smith and Knight, 1984). Periapical lesions are different types of cavities (abscesses, cysts, and granulomas) near tooth roots, frequently caused by carious or attritional exposure of the pulp cavity (Dias and Tayles, 1997). Due to the difficult differentiation of periapical granulomas, periodontal cysts and periapical abscesses in skeletal material, no distinction was made and only the presence of general periapical lesions was recorded.

Periodontitis is a multifactorial bacterial inflammation which results in progressive damage to the tooth-supporting structures (Bertl et al., 2020). Periodontitis was recorded based on presence or absence.

Degenerative joint disease. Degenerative joint disease is a progressive disorder of the joint, generally associated with advancing age and repeated physiological stress, however, its aetiology is complex and multifactorial (Waldron, 2019; Weiss and Jurmain, 2007).

Degenerative joint disease was examined on ten joint systems (jaw, shoulder, elbow, wrist/hand, cervical spine, thoracic spine, lumbar spine, hip, knee, ankle/foot) in adult individuals only. Degenerative changes were scored for severity following Brothwell (1981) for vertebral joints and Steckel et al. (2006) for the remaining articulations where left and right was considered. To be scored as present, lesions need to be observed in at least one articular surface with minimum 80 % preservation. Additionally, Schmorl's nodes were recorded in vertebral bodies according to their location and size.

Non-specific stress indicators. Non-specific stress indicators are referred to lesions linked to varied disease processes.

Cribrā cranii and cribrā orbitalia are pathological lesions at the external cranial vault and orbital roof, respectively, expressed as porosity and pitting (Grauer, 2019). Contemporary studies refrain from accepting nutritional anaemia as aetiology (Grauer, 2019; O'Donnell et al., 2020; Rivera and Mirazón Lahr, 2017; Walker et al., 2009) and instead suggest a link to different disease processes and even disassociated aetiologies (O'Donnell et al., 2020; Rivera and Mirazón Lahr, 2017). Cribrā cranii was scored as present or absent when minimum one parietal was observable. The disease was considered present when slight pitting or porosities were identifiable (Steckel et al., 2006), severity was not assessed. Cribrā orbitalia was identified as present when minimum a cluster of fine foramina was visible (Steckel et al., 2006), without distinguishing severity. Cribrā orbitalia was recorded as present or absent when at least one orbit was present. To differentiate cribrā orbitalia from metabolic disease like scurvy or rickets, further macroscopic lesions on different skeletal regions need to be identified as outlined in Brickley and Morgan (2023).

Linear enamel hypoplasia refers to lines or furrows in the enamel, resulting from disrupted mineralisation during tooth crown development of different aetiology (Guatelli-Steinberg, 2016; Hillson, 1996). Linear enamel hypoplasia was identified macroscopically as a palpable and visible linear defect on the enamel surface. Teeth were examined under an oblique light source and the surface/crown was felt to identify any irregularities in the enamel. All permanent teeth were examined and scored for severity (Grupe et al., 2015), and estimated age of formation of enamel defects (Reid and Dean, 2006). As anterior teeth are most frequently affected (Goodman and Armelagos, 1985), only maxillary and mandibular incisors and canines were considered for analysis.

Periosteal reaction refers to various types of new bone formation of the periosteum, due to trauma, infection, or other factors, which are often difficult to determine in archaeological remains (Weston, 2012). Periosteal reactions were identified on the lower limb long bones and scored as present when bone formations with irregular elevations of the periosteum were observed. No distinctions were made between morphological variations in the lesions or between active and inactive status. Periosteal reactions that were associated with trauma, metabolic or infectious diseases, were omitted to include only changes of unknown aetiology. Due to the fragmented nature of the sample, the condition was recorded when more than 30 % of at least one long bone was preserved for observation.

Trauma. Trauma describes any discontinuity of a skeletal element caused by violence, cultural or medical practice, or pathological conditions (Redfern and Roberts, 2019). It was observed on all skeletal elements and subdivided into three categories: fractures, osteochondritis

dissecans and trepanation.

Bone fractures and surgical trepanations of the skull were recorded according to their location, type, time of occurrence and healing stage.

Osteochondritis dissecans is a joint disease caused by trauma, characterised by the detachment of cartilage and frequently involved subchondral bone (Grauer, 2019, pp. 500–501). Lesions were recorded in adults following Vikatou et al. (2017). However, for analysis, lesions were still included without exposed subchondral bone and joint surfaces were combined to joint types (shoulder, elbow, hand, hip, knee, foot).

Neoplasm. Neoplasms denote pathological conditions that manifest as lytic, blastic, or mixed lesions in the skeletal system (Ragsdale et al., 2018).

Neoplasms were examined for presence on each skeletal element and were recorded per location and lesion type. However, only neoplastic prevalence will be considered since a detailed discussion about potential aetiologies and differential diagnoses is beyond the scope of the present palaeopathological research and will be addressed in a future study.

Dental calculus, carious lesions, linear enamel hypoplasia, and degenerative joint diseases, were originally scored and recorded ordinally, as detailed above. However, due to conservational constraints and small sample sizes, the recorded data were converted into dichotomous (presence/absence) scores prior to statistical analysis (Mardini et al., 2023; Vergidou et al., 2022). Furthermore, scores for dental wear (tooth types from the upper and lower, left and right jaw), and for vertebral degenerative joint disease (body and intervertebral joint) were combined to an average score per tooth type and vertebrae type, respectively. Additionally, to increase the sample size of adult males and females, subadults in transition to adulthood (Final Neolithic: two females; Early Bronze Age: two males, three females, one unsexed), and adult individuals with fewer diagnostic traits, who could not be assigned to sex securely (Final Neolithic: three females; Early Bronze Age: one male, one female), were nonetheless included in the respective adult sex categories. Although pathologies accumulate or are more severely expressed with increasing age, no distinction was made between specific age groups due to low sample size. The frequency of each pathology was estimated per individual, additionally, the frequency of dental calculus and caries per tooth. Statistical comparisons were conducted to examine the association for each pathology with sex and cultural period using Chi-square tests, or Fisher's exact tests where appropriate. For the ordinally recorded dental wear, Wilcoxon ranks-sum test, or Kruskal-Wallis test was used. Statistical significance was set at 95% confidence interval ($p \leq 0.05$). All statistical analysis were performed in RStudio (Posit team, 2024).

Results

Results of frequencies per individual are detailed in Table 2, Tables 4-7, and Figures 2-6. Average dental wear scores are presented in Table 3. Frequencies for calculus and caries per tooth, joint specific degenerative joint disease, and joint specific osteochondritis dissecans can be found in the appendix in Tables A1-A3 and Figure A1, as well as all statistical results in Tables A4-A10.

Dental and oral diseases. Calculus was nearly equally frequent in the Final Neolithic and Early Bronze Age, but on a different rate per individual and per tooth (Table 2 and A1, Figure 2). However, frequencies vary between sites. When age categories are considered, CW subadults are always less frequently affected than adults, which is less expressed in the NG. Male frequencies are slightly lower across the periods. When analysed per tooth, the CW sites exhibit more affected males ($\chi^2 = 6.53$; $p = 0.0106$), even though this compensates in the composite sample, while NG females are consistently more affected than males ($\chi^2 = 8.28$; $p = 0.004$).

Caries frequencies remained largely stable and showed no significant temporal trends, despite lowest values in Tauberbischofsheim-Impfingen and marked inter-site differences in adults (Table 2 and A1, Figure 2). However, an increase in the Early Bronze Age is discernible per tooth ($\chi^2 = 4.14$; $p = 0.0419$). Although males had, on average, more carious lesions per individual, NG females were most affected in terms of caries rate per tooth.

For dental wear, in both periods and among sites comparable average wear scores were prevalent in adults (Table 3). Especially CW males shared nearly identical wear scores. Females exhibited slightly lower wear scores than males (for statistically significant results see Table A6), except for I1, C, and P1 in Tauberbischofsheim-Impfingen. However, NG males had a very distinct wear pattern among sites, whereas female wear scores were more homogeneous with few exceptions.

The occurrence of periapical cavities was generally very low, and only males were affected (Table 2, Figure 2). The frequency was higher in the Final Neolithic, and equal among sites, compared to the Early Bronze Age with only one affected individual. Periodontal disease was equally frequent in both periods, although inter-site differences occurred (Table 2, Figure 2). In the Early Bronze Age many nonadults were affected. Regarding sex, in the Final Neolithic males were most affected. This trend shifts in the Early Bronze Age where females were most affected.

Table 2 Frequency of dental pathologies by age and sex per individual.

Skeletal lesion	Age/Sex	HB	TI	CW	AR	RA	NG
		% (n/N)	% (n/N)	% (n/N)	% (n/N)	% (n/N)	% (n/N)
Calculus	Males	100.0 (5/5)	85.7 (6/7)	92.9 (13/14)	100.0 (5/5)	100.0 (4/4)	100.0 (11/11)
	Females	100.0 (8/8)	100.0 (3/3)	100.0 (12/12)	100.0 (5/5)	100.0 (3/3)	100.0 (9/9)
	Total adults	100.0 (14/14)	90.9 (10/11)	96.4 (27/28)	100.0 (14/14)	81.8 (9/11)	92.9 (26/28)
	Subadults	83.3 (5/6)	44.4 (4/9)	61.1 (11/18)	92.3 (12/13)	60.0 (3/5)	84.2 (16/19)
	Total assemblage	95.0 (19/20)	70.0 (14/20)	82.6 (38/46)	96.3 (26/27)	75.0 (12/16)	89.4 (42/47)
Caries	Males	40.0 (2/5)	28.6 (2/7)	42.9 (6/14)	60.0 (3/5)	50.0 (2/4)	54.5 (6/11)
	Females	37.5 (3/8)	0.0 (0/3)	25.0 (3/12)	40.0 (2/5)	66.7 (2/3)	44.4 (4/9)
	Total adults	35.7 (5/14)	18.2 (2/11)	32.1 (9/28)	50.0 (7/14)	36.4 (4/11)	42.9 (12/28)
	Subadults	16.7 (1/6)	0.0 (0/9)	5.6 (1/18)	7.7 (1/13)	20.0 (1/5)	10.5 (2/19)
	Total assemblage	30.0 (6/20)	10.0 (2/20)	21.7 (10/46)	29.6 (8/27)	31.33 (5/16)	29.8 (14/47)
Periapical lesion	Males	20.0 (1/5)	16.7 (1/6)	23.1 (3/13)	33.3 (1/3)	0.0 (0/5)	10.0 (1/10)
	Females	0.0 (0/7)	0.0 (0/2)	0.0 (0/9)	0.0 (0/4)	0.0 (0/3)	0.0 (0/8)
	Total adults	8.3 (1/12)	11.1 (1/9)	13.0 (3/23)	14.3 (1/7)	0.0 (0/11)	4.8 (1/21)
	Subadults	0.0 (0/3)	0.0 (0/12)	0.0 (0/19)	0.0 (0/13)	0.0 (0/9)	0.0 (0/22)
	Total assemblage	6.7 (1/15)	4.8 (1/21)	7.1 (3/42)	5.0 (1/20)	0.0 (0/20)	2.3 (1/43)
Periodontal disease	Males	100.0 (5/5)	100.0 (6/6)	100.0 (13/13)	75.0 (3/4)	60.0 (3/5)	72.7 (8/11)
	Females	71.4 (5/7)	100.0 (2/2)	77.8 (7/9)	100.0 (4/4)	100.0 (3/3)	100.0 (8/8)
	Total adults	83.3 (10/12)	100.0 (9/9)	91.3 (21/23)	87.5 (7/8)	63.6 (7/11)	77.3 (17/22)
	Subadults	0.0 (0/2)	8.3 (1/12)	11.1 (2/18)	53.8 (7/13)	0.0 (0/8)	33.3 (7/21)
	Total assemblage	71.4 (10/14)	47.6 (10/21)	56.1 (23/41)	66.7 (14/21)	36.8 (7/19)	55.8 (24/43)

Abbreviations: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar group, n = number of affected individuals, N = number of observed individuals.

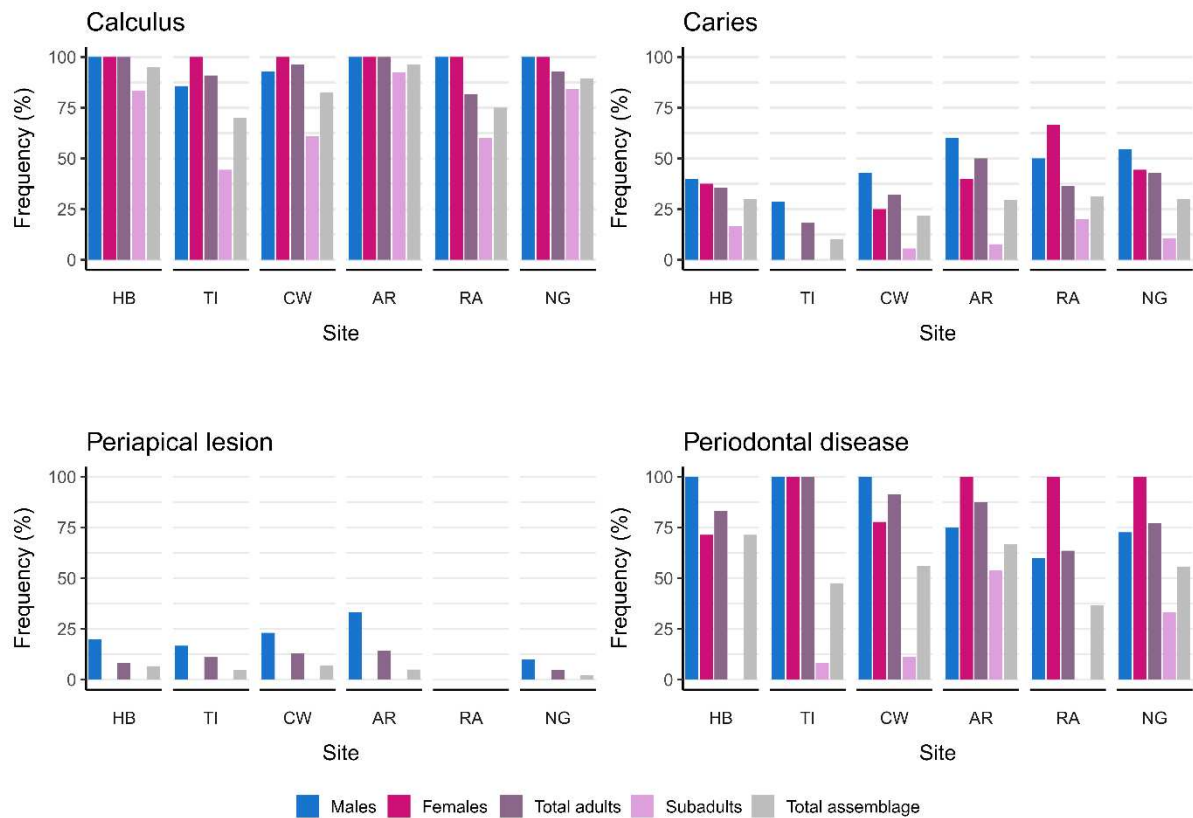


Figure 2 Frequency of dental pathologies by age and sex per individual.

Table 3 Average tooth wear scores by tooth type, age, and sex.

Tooth	Age/Sex	HB		TI		CW		AR		RA		NG	
		WS	(n teeth)	WS	(n teeth)	WS	(n teeth)	WS	(n teeth)	WS	(n teeth)	WS	(n teeth)
I1	Males	5	10	5	5	5	18	6	5	4	5	5	13
	Females	4	14	6	2	4	16	5	6	4	3	5	9
	Total adults	5	25	5	8	5	36	6	12	4	9	5	24
	Subadults	2	8	2	8	2	17	3	18	2	3	3	21
	Total assemblage	4	33	4	16	4	53	4	30	4	12	4	45
I2	Males	5	10	5	7	5	20	6	8	3	6	5	18
	Females	3	13	3	1	3	14	2	6	4	3	3	9
	Total adults	4	23	4	10	4	36	4	14	4	12	4	30
	Subadults	2	11	2	6	2	19	2	19	2	3	2	22
	Total assemblage	3	34	3	16	3	55	3	33	3	15	3	52
C	Males	5	10	5	9	5	22	5	7	3	5	4	16
	Females	3	13	5	2	4	16	4	7	4	4	4	12
	Total adults	4	24	5	13	4	41	4	15	4	10	4	30
	Subadults	2	8	2	2	2	12	1	14	2	3	2	18
	Total assemblage	3	32	4	15	4	53	3	29	3	13	3	48

P1	Males	4	10	4	9	4	23	5	6	3	7	4	17
	Females	3	13	6	3	4	16	3	7	4	4	4	12
	Total adults	4	24	4	14	4	42	4	15	3	13	4	33
	Subadults	1	6	2	3	2	11	2	16	2	3	2	19
	Total assemblage	3	30	4	17	4	53	3	31	3	16	3	52
P2	Males	4	10	4	10	4	23	4	7	2	6	4	17
	Females	3	14	5	2	4	16	4	7	4	3	4	11
	Total adults	4	24	4	14	4	41	4	16	3	13	4	34
	Subadults	1	6	3	4	2	12	2	15	2	4	2	19
	Total assemblage	3	30	4	18	3	53	3	31	3	17	3	53
M1	Males	5	10	6	13	6	27	6	6	4	7	5	16
	Females	4	13	5	2	4	17	5	7	5	3	4	12
	Total adults	5	23	6	17	5	46	5	13	5	12	5	30
	Subadults	2	10	3	14	3	29	3	22	2	6	2	28
	Total assemblage	4	33	4	31	4	75	3	35	4	18	4	58
M2	Males	4	10	5	11	4	25	4	5	3	8	3	16
	Females	3	14	3	2	3	17	4	8	6	4	4	14
	Total adults	4	24	4	15	4	44	4	14	4	16	4	35
	Subadults	1	8	3	4	2	14	2	14	3	4	2	18
	Total assemblage	3	32	4	19	3	58	3	28	4	20	3	53
M3	Males	3	8	4	8	4	19	4	6	2	8	3	17
	Females	3	14	2	1	2	16	2	4	4	5	3	11
	Total adults	3	22	4	11	3	37	3	11	3	17	3	33
	Subadults	1	4	1	1	1	7	2	3	-	0	2	3
	Total assemblage	3	26	4	12	3	44	3	14	3	17	3	36

Abbreviation: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar group, WS = wear score, n = number of affected individuals, N = number of observed individuals.

Degenerative joint disease. Appendicular degenerative joint diseases were relatively equally frequent in both periods, except for lower rates in Ammerbuch-Reusten (Table 4, Figure 3). When considering sex, distinct differences are apparent. CW sex frequencies are opposing between sites and, therefore, reached equal levels in the composite sample. In contrast, all NG females are always most affected. In terms of specific joints, due to low sample sizes further statistical analyses were not applied and only the most prominent distributions are mentioned (Table A2, Figure A1). The affected joints differ among the CW sites in males but are similar in females. In NG men degenerative joint diseases seem to prevail in the upper body whereas in females both upper and lower body were affected.

Regarding vertebral joint degeneration both periods had overall similar frequencies (Table 4, Figure 3). CW males were in all sites more often affected than females, particularly in Heilbronn. This shifts in the Early Bronze Age to a slightly higher female frequency, with highest rates in Ammerbuch-Reusten. Again, because of the limited sample sizes of spinal segments further statistical analyses were not conducted and only the most prominent distributions are mentioned. CW males had similar frequencies in cervical and lumbar joints as NG males, but higher frequencies in thoracic vertebrae. The different vertebral types in CW females were too underrepresented for any inferences. Cervical vertebrae were the most affected part of the spine in NG males, while in females it was the thoracic spine.

The frequency of Schmorl's nodes was very similar in both periods, but differently distributed among sites per sex (one female: Heilbronn, Ammerbuch-Reusten; one male: Remseck-Aldingen, Tauberbischofsheim-Impfingen).

Table 4 Frequency of degenerative joint disease by sex.

Joint	Sex	HB	TI	CW	AR	RA	NG
		% (n/N)	% (n/N)	% (n/N)	% (n/N)	% (n/N)	% (n/N)
Appendicular	Males	80.0 (4/5)	57.1 (4/7)	66.7 (10/15)	50.0 (2/4)	71.4 (5/7)	71.4 (10/14)
	Females	57.1 (4/7)	100.0 (2/2)	60.0 (6/10)	100.0 (5/5)	100.0 (3/3)	100.0 (8/8)
	Total adults	66.7 (8/12)	72.7 (8/11)	66.7 (18/27)	61.5 (8/13)	78.6 (11/14)	73.3 (22/30)
Spinal	Males	100.0 (5/5)	66.7 (4/6)	84.6 (11/13)	50.0 (2/4)	60.0 (3/5)	63.6 (7/11)
	Females	50.0 (3/6)	50.0 (1/2)	55.6 (5/9)	100.0 (5/5)	50.0 (1/2)	75.0 (6/8)
	Total adults	66.67 (8/12)	55.6 (5/9)	66.7 (16/24)	72.7 (8/11)	66.7 (6/9)	69.6 (16/23)

Abbreviation: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar group, n = number of affected individuals, N = number of observed individuals.

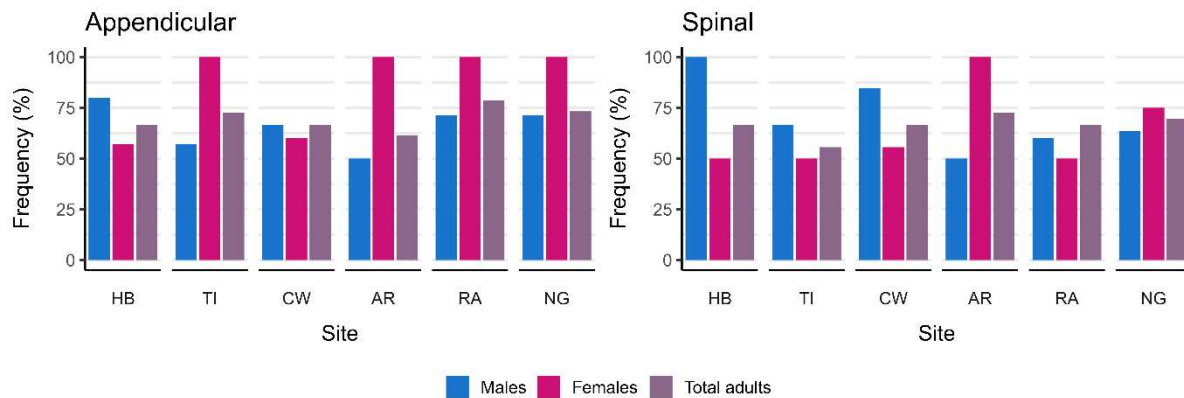


Figure 3 Frequency of degenerative joint disease by sex.

Non-specific stress indicators. Cribra cranii was slightly more frequent in the CW sample, with more adults than subadults, compared to the NG where the frequency was relatively uniform albeit more subadults than adults were affected (Table 5, Figure 4). The inter-site distribution was, however, very different. In Heilbronn, cribra cranii prevailed only in adults, with higher frequencies in females. In Tauberbischofsheim-Impfingen, the condition was only observed in males and subadults. In contrast, in Ammerbuch-Reusten only subadults were affected. In Remseck-Aldingen, cribra cranii was observed throughout the population, but its frequency was highest among females.

Nearly half of the total population was affected by cribra orbitalia in both periods (Table 5, Figure 4). However, Tauberbischofsheim-Impfingen stands out in particular with highest frequencies among all sites in age and sex, except for subadults (Fisher's test; $p = 0.0075$). Besides this, subadults were in all periods most affected, followed by females, whereas male individuals were rarely affected.

Linear enamel hypoplasia exhibited equal frequencies in both periods and among sites (Table 5, Figure 4). This also accounts for adult and subadult prevalence, except for Ammerbuch-Reusten, where more adults were affected. There is, however, a marked difference in sex. Males seemingly are more frequently affected than females in the Final Neolithic, a trend that is reversed in the Early Bronze Age.

Periosteal reactions in the lower limbs were by far more common in the Final Neolithic than in the Early Bronze Age (Table 5, Figure 4) (Fisher's test; $p = 0.002$). The frequencies were lower in nonadults than in adults in all CW sites, and vice versa in the NG. A similar prevalence is observed for the sexes, where females are more affected than males in the CW, but more

males than females in the NG (Fisher's test; $p = 0.0152$). The generally low frequency of this condition in Remseck-Aldingen is striking (Fisher's test; $p = 0.0115$).

Table 5 Frequency of non-specific stress by age and sex.

Skeletal lesion	Age/Sex	HB	TI	CW	AR	RA	NG
		%	%	%	%	%	%
		(n/N)	(n/N)	(n/N)	(n/N)	(n/N)	(n/N)
Cribra cranii	Males	20.0 (1/5)	25.0 (1/4)	33.3 (4/12)	0.0 (0/3)	28.6 (2/7)	15.4 (2/13)
	Females	28.6 (2/7)	0.0 (0/0)	37.5 (3/8)	0.0 (0/4)	50.0 (1/2)	14.3 (1/7)
	Total adults	21.4 (3/14)	25.0 (1/4)	31.8 (7/22)	0.0 (0/8)	27.3 (3/11)	13.0 (3/23)
	Subadults	0.0 (0/6)	16.7 (1/6)	14.3 (2/14)	33.3 (5/15)	7.7 (1/13)	21.4 (6/28)
	Total assemblage	15.0 (3/20)	20.0 (2/10)	25.0 (9/36)	21.7 (5/23)	16.7 (4/24)	17.7 (9/51)
Cribra orbitalia	Males	0.0 (0/4)	75.0 (3/4)	27.3 (3/11)	0.0 (0/3)	0.0 (0/4)	0.0 (0/10)
	Females	16.7 (1/6)	100.0 (1/1)	37.5 (3/8)	0.0 (0/4)	50.0 (1/2)	28.6 (2/7)
	Total adults	10.0 (1/10)	80.0 (4/5)	31.6 (6/19)	0.0 (0/7)	14.3 (1/7)	11.1 (2/18)
	Subadults	50.0 (1/2)	75.0 (6/8)	72.7 (8/11)	80.0 (8/10)	63.6 (7/11)	71.4 (15/21)
	Total assemblage	16.7 (2/12)	76.9 (10/13)	46.7 (14/30)	47.1 (8/17)	44.4 (8/18)	43.6 (17/39)
Linear enamel hypoplasia	Males	100.0 (5/5)	40.0 (2/5)	75.0 (9/12)	50.0 (2/4)	100.0 (4/4)	60.0 (6/10)
	Females	57.1 (4/7)	100.0 (1/1)	55.6 (5/9)	100.0 (4/4)	33.3 (1/3)	75.0 (6/8)
	Total adults	69.2 (9/13)	57.1 (4/7)	65.2 (15/23)	75.0 (6/8)	60.0 (6/10)	61.9 (13/21)
	Subadults	71.4 (5/7)	63.6 (7/11)	60.0 (12/20)	50.0 (7/14)	71.4 (5/7)	59.1 (13/22)
	Total assemblage	70.0 (14/20)	61.1 (11/18)	62.8 (27/43)	59.1 (13/22)	64.7 (11/17)	60.5 (26/43)
Periosteal reaction	Males	25.0 (1/4)	80.0 (4/5)	54.6 (6/11)	25.0 (1/4)	14.3 (1/7)	21.4 (3/14)
	Females	71.4 (5/7)	100.0 (1/1)	77.8 (7/9)	20.0 (1/5)	0.0 (0/3)	11.1 (1/9)
	Total adults	50.0 (6/12)	83.3 (5/6)	61.9 (13/21)	23.1 (3/13)	7.1 (1/14)	16.1 (5/31)
	Subadults	25.0 (1/4)	44.4 (4/9)	33.3 (6/18)	66.7 (10/15)	10.0 (1/10)	42.3 (11/26)
	Total assemblage	43.8 (7/16)	60.0 (9/15)	48.7 (19/39)	46.4 (13/28)	8.3 (2/24)	28.1 (16/57)

Abbreviation: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar group, n = number of affected individuals, N = number of observed individuals.

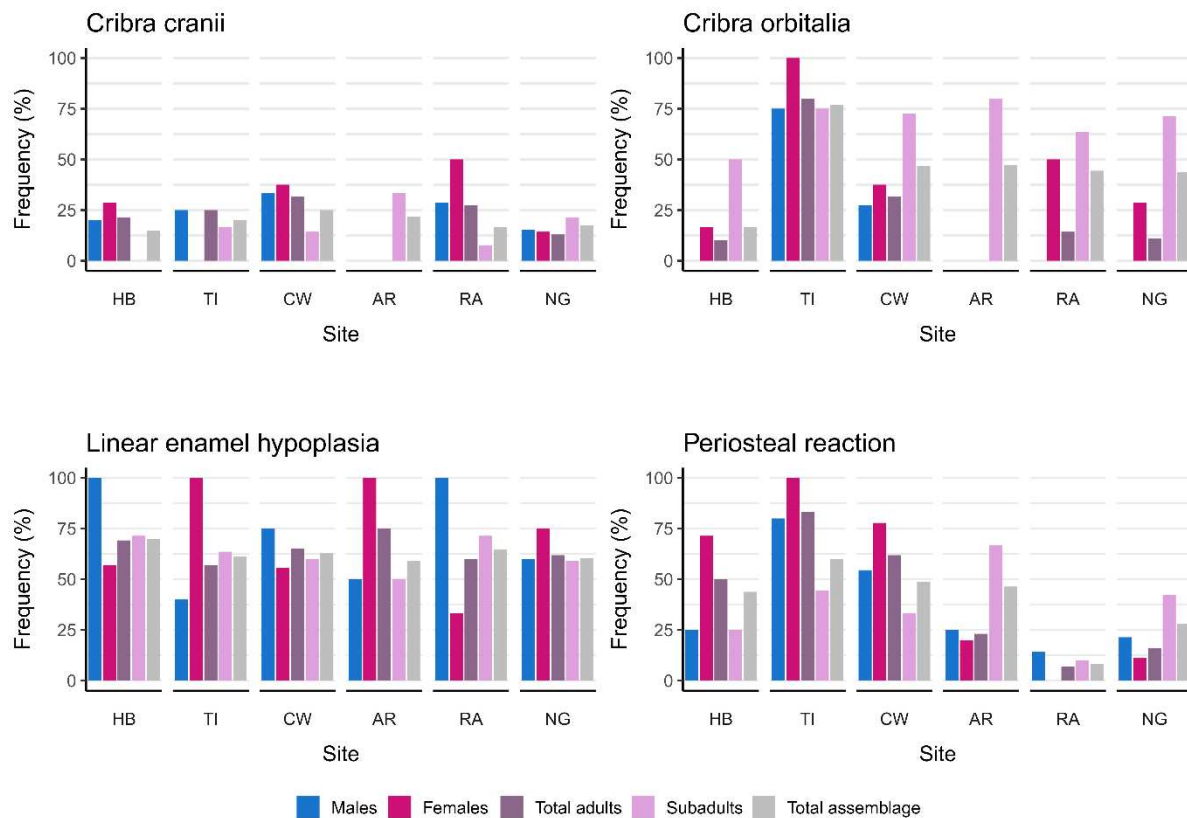


Figure 4 Frequency of non-specific stress by age and sex.

Trauma. Four CW and four NG adults displayed at least one fracture. Subadults were not affected (Table 6, Figure 5). The incidence in males was slightly higher in the Final Neolithic than in the Early Bronze Age, but in the Early Bronze Age females showed a higher percentage than males. Among the observed fractures, the ulna (n = 3) and ribs (n = 3) were most commonly affected, followed by the clavicle (n = 2), radius (n = 1), and metacarpal (n = 1). All fractures healed completely.

Trepanations were only observed in two CW males. The first individual from Tauberbischofsheim “Kirchelberg/Acker Noe West” potentially exhibited one fully and one incompletely conducted trepanation, which was examined in an earlier study (Dresely 2004, 228-229) and is not further considered here. The second individual from Heilbronn is a 40–50-

year-old male which displayed a healed trepanation in the parietal bone at the obelion. The ellipsoid foramen measures externally 40x20 mm and internally 25x16 mm (transverse x sagittal).

Osteochondritis dissecans frequencies were equally low in all CW sites, and higher in the NG sites (Table 6, Figure 5). Frequencies were relatively similar for both sexes in the pooled samples, however, they were more distinct in single sites. Foot joints were most affected in both periods, followed by the elbow in the Early Bronze Age (Table A3). Due to a low sample size, statistical comparisons were not conducted.

Table 6 Frequency of trauma by age and sex.

Skeletal lesion	Age/Sex	HB	TI	CW	AR	RA	NG
		% (n/N)	% (n/N)	% (n/N)	% (n/N)	% (n/N)	% (n/N)
Fracture	Males	20.0 (1/5)	25.0 (2/8)	18.8 (3/16)	0.0 (0/3)	14.3 (1/7)	15.4 (2/13)
	Females	0.0 (0/6)	0.0 (0/2)	11.1 (1/9)	40.0 (2/5)	0.0 (0/3)	25.0 (2/8)
	Total adults	8.3 (1/12)	18.2 (2/11)	14.8 (4/27)	18.2 (2/11)	7.1 (1/14)	14.3 (4/28)
	Subadults	0.0 (0/2)	0.0 (0/14)	0.0 (0/22)	0.0 (0/15)	0.0 (0/10)	0.0 (0/26)
	Total assemblage	7.1 (1/14)	8.0 (2/25)	8.2 (4/49)	7.7 (2/26)	4.2 (1/24)	7.4 (4/54)
Osteochondritis dissecans	Males	20.0 (1/5)	0.0 (0/6)	14.3 (2/14)	50.0 (2/4)	42.9 (3/7)	46.2 (6/13)
	Females	14.3 (1/7)	50.0 (1/2)	20.0 (2/10)	20.0 (1/5)	100.0 (2/2)	42.9 (3/7)
	Total adults	16.7 (2/12)	12.5 (1/8)	16.7 (4/24)	23.1 (3/13)	41.7 (5/12)	33.3 (9/27)

Abbreviation: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar group, n = number of affected individuals, N = number of observed individuals.

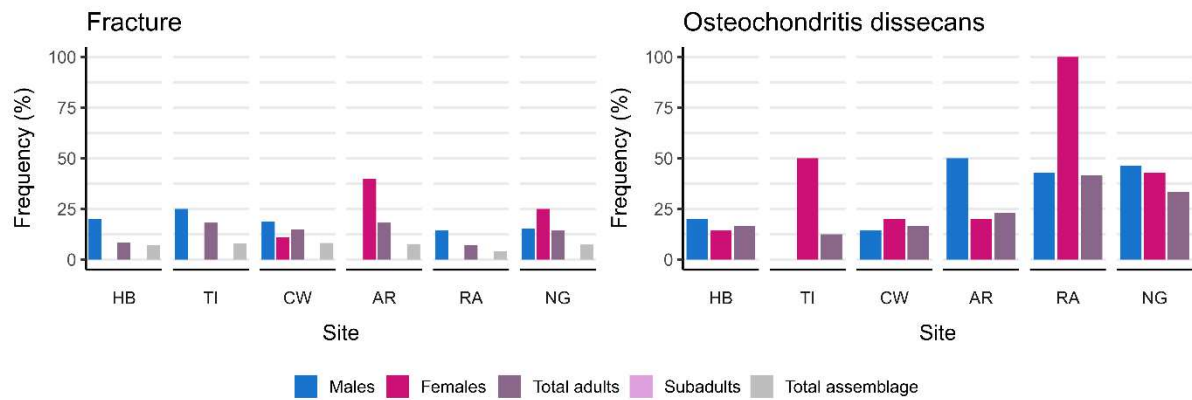


Figure 5 Frequency of trauma by age and sex.

Neoplasms. Neoplastic diseases occurred only in the Early Bronze Age (Table 7, Figure 6) (Fisher’s test; $p = 0.0455$). In total six individuals suffered from potential neoplastic diseases. Adult frequency was higher than in subadults, and males were more often affected as females.

Table 7 Frequency of neoplasms by age and sex.

Age/Sex	HB	TI	CW	AR	RA	NG
	%	%	%	%	%	%
	(n/N)	(n/N)	(n/N)	(n/N)	(n/N)	(n/N)
Males	0.0 (0/5)	0.0 (0/7)	0.0 (0/15)	50.0 (2/4)	0.0 (0/7)	21.4 (3/14)
Females	0.0 (0/7)	0.0 (0/2)	0.0 (0/10)	0.0 (0/5)	0.0 (0/3)	11.1 (1/9)
Total adults	0.0 (0/12)	0.0 (0/9)	0.0 (0/25)	16.7 (2/12)	0.0 (0/13)	13.8 (4/29)
Subadults	0.0 (0/3)	0.0 (0/12)	0.0 (0/20)	12.5 (2/16)	0.0 (0/9)	7.7 (2/26)
Total assemblage	0.0 (0/15)	0.0 (0/21)	0.0 (0/45)	14.3 (4/28)	0.0 (0/22)	10.9 (6/55)

Abbreviation: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar group, n = number of affected individuals, N = number of observed individuals.

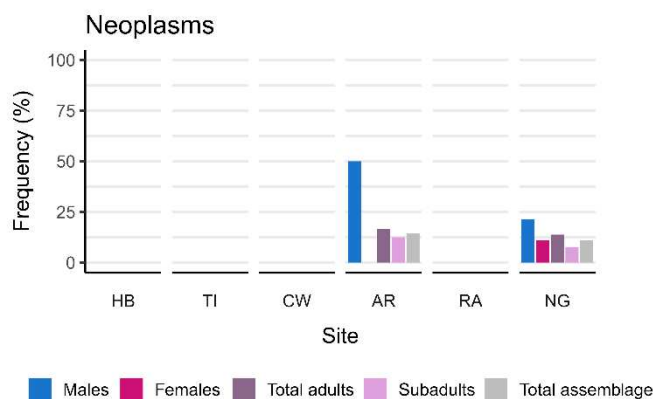


Figure 6 Frequency of neoplasms by age and sex.

Discussion

The current study focuses on the palaeopathological profile of CW and NG populations. Previous mortality trends show that females in the infant, juvenile, and adult age groups were most affected, reflecting potential sociocultural stressors (Lismann et al., 2024). Although these trends may also indicate biological stress, our results suggest that mortality and morbidity were not directly correlated. Furthermore, while some chronological trends are evident, many of the observed differences are site-specific, indicating primarily local relevance.

Dental pathologies are directly indicative of dietary habits, which can reveal access to food sources, other factors impacting dietary patterns, and cultural dynamics. Due to the frequently observed post-mortem loss of dental calculus, actual frequencies were probably higher and may have been comparable across sites. Therefore, the results need to be considered with caution. The difference in subadults could arise from more calculus inducing weaning diet in the NG than in the CW or general differences in subadult diet. However, the relatively equal number of infants in both cultural phenomena suggests that the higher number of juveniles in the NG is responsible for higher calculus frequencies.

Caries frequencies basically remained constant through time, as also observed in Central Germany (Nicklisch, 2017, p. 156), even though the CW site of Tauberbischofsheim-Impfingen deviates from this pattern with lower values. Interestingly, other CW sites in the Tauber region display caries frequencies ranging from ca. 23 % to 43 % (Dresely, 2004, pp. 230–231; Trautmann, 2012, p. 397), which is comparable to the samples examined here. While micro abrasion and isotopic analyses are currently unavailable for the sites included in this study, higher meat consumption in some populations in the Tauber River region could explain this lower prevalence, as demonstrated by Trautmann (2012, pp. 414–417). Although females are

more susceptible to caries (Lukacs and Largaespada, 2006; Walter et al., 2016), this trend is less distinctive in the sites investigated, contrary to findings for other Tauber region populations (Dresely, 2004, pp. 230–231; Trautmann, 2012, p. 397). A marked difference only persisted in the Early Bronze Age per tooth, which is also indicated in eastern Central Europe (Hukelova, 2016, p. 177). This could point to a change in female diet with more cariogenic foods and drinks, or frequent snacking during food procurement and food preparation (Lukacs and Largaespada, 2006, p. 541).

The generally similar levels of tooth abrasion scores suggest that the CW and NG populations relied on a similarly abrasive diet. Within the CW samples, nearly equal tooth abrasion in males could imply that, despite their temporal and geographical distance, some food was prepared in a different manner or was reserved particularly for men, as also suggested by Dresely (2004, p. 230). Moreover, comparatively lower scores in CW women may further hint at sex-related differences in diet. Dietary variation between sites and sex has also been demonstrated using isotopes in Central and South Germany (Münster et al., 2018; Sjögren et al., 2016). Yet, elevated scores in Tauberbischofsheim-Impfingen females in the first incisor, canine and first premolar may signify a certain degree of manipulative use of the dentition, although usually front teeth are more affected (Frayser, 2004; Sperduti et al., 2018), as observed in a male individual in the Tauber region (Dresely, 2004, pp. 230–233). This is also indicated by high incisal abrasion in NG men in the site of Ammerbuch-Reusten. Intriguingly, the men from Remseck-Aldingen had the lowest values of all samples. Greater consumption of softer foods with low fibre content or animal protein, or a mix of these, and different food preparation techniques with less abrasive components or less chewing effort may explain this pattern. Similar results were observed at Early Bronze Age sites in northeastern Spain, reflecting refined food, cooking techniques, and male dental abrasion patterns indicative of a soft diet (Gluitz et al., 2023). However, to corroborate this, dental microwear or isotope analyses are needed.

Interestingly, only male individuals were affected by periapical lesions, and in the CW more often than in the NG. Hukelova (2016, p. 178) noted comparable values (20 %) for earlier Neolithic sites in eastern Central Europe, and lower incidences in the Final Neolithic and Early Bronze Age, and males were always more affected than females. Similarly, Shbat et al. (2009, p. 202) also observed only males with periapical lesions in their Final Neolithic sample in the same study region, hinting at a better oral hygiene for females, or a versatile and strenuous use of the dentition in men. This is indicated in a male individual from Ammerbuch-Reusten, where the periapical lesion of the lower central incisors was associated with ante mortem tooth loss, which can likely be associated with increased abrasion and potential use of the teeth as tool or

third hand, as mentioned above.

Periodontal disease seems to correlate in adult individuals to some extent with calculus frequencies. In Ammerbuch-Reusten, the high prevalence of periodontal disease in subadults can presumably be attributed to higher numbers of older nonadults within the sample. Contrary to the findings in Hukelova (2016, p. 181) where males were predominantly affected in both periods, we observe a gender shift. In synthesis, the sex-related differences may reflect variations in diet or oral hygiene over time.

Although the incidence of appendicular degenerative joint disease was generally similar between the CW and NG samples, there were marked differences in joints both in chronology and sex, suggesting a chronological shift in physical activity and male-female role division. Young and middle-aged adults make up a large proportion of the samples analysed, and age-related degenerative joint disease in older individuals did not drastically affect the incidence in the current study.

CW men exhibited population-specific differences in most of the examined joints, whereas habitual activities in women were uniformly dominated by symmetrical upper and lower limb loading. This suggests that males from Heilbronn and Tauberbischofsheim-Impfingen spend their time with differing activities, hinting at particularly lateralised shoulder related activities in Tauberbischofsheim-Impfingen, and habitual use of the left elbow and hand, and lower limbs in Heilbronn. This is also reflected in spinal joints, as in Tauberbischofsheim-Impfingen the cervical spine was most affected, and in Heilbronn the thoracic spine. Therefore, Tauberbischofsheim-Impfingen men potentially participated in overhead activities with throwing or lifting motions related to carpentry, hunting, herding or hide-processing (Schmitt et al., 2003; Shaw et al., 2012; Villotte and Knüsel, 2014). Contrastingly, in Heilbronn men likely conducted a wide range of activities which involve mobility, related to one-handed tool use, agricultural fieldwork, and livestock tending (A. A. Macintosh et al., 2014, p. 384; Alison A. Macintosh et al., 2014, p. 8). In Lauda-Königshofen, another CW site in the Tauber region, men most frequently suffered from knee joint disease, followed by foot, elbow, and hand, while the frequency of spinal joint disease was comparable to that observed in the present CW men (Trautmann, 2012, p. 394). Macintosh et al. (2014) and Sládek et al. (2006a, 2006b) also found regional variation in lower limb biomechanics in Neolithic and Bronze Age samples. Macintosh et al. (2014, p. 385) ascribe this to an asynchronous introduction of plows and wheeled vehicles. Therefore, we hypothesise that the populations were regionally differently specialised, as also concluded from Sládek et al. (2006a, pp. 329–330, 2006b, p. 480) and from isotope data in South Germany, suggesting diverging subsistence strategies among populations (Sjögren et al.,

2016). In Lauda-Königshofen for example, Trautmann (2012) assumed a nomadic pastoral subsistence.

In contrast, CW females conducted similar tasks among sites involving high levels of bimanual labour. This suggests that female behaviour was dominated by intensive and repetitive manual activity, such as cereal processing with a saddle quern, presumably in a sitting or kneeling position. Bone cross-sectional analyses in other Neolithic samples support our results, even though lower limb loading was still relatively high in their Neolithic females (Macintosh et al., 2017). Therefore, since the lower limbs are partially unaffected in the present sample, subsistence tasks related to gathering, agriculture and livestock that do not require high-impact lower limb loading and high-level mobility are also conceivable. Trautmann (2012, pp. 393–394) came to similar conclusions as the females in Lauda-Königshofen display frequent feet and hip joint disease related to squatting or walking in rough terrain. Nevertheless, researchers also consider high mobility in the Tauber region (Großmann, 2021, p. 163), which could be reflected in the increased incidence of degenerative joint disease of the feet, particularly in Tauberbischofsheim-Impfingen. An expected concomitant increase in affected hip and knee joints may go unnoticed due to the low preservation of these joints. Unfortunately, as mentioned above, spinal joints were not considered for interpretation due to their underrepresentation.

A clear shift in affected joints is indicated in NG individuals, and role divisions between males and females are still evident. The incidence of affected joints was more evenly distributed among men, suggesting that their tasks became more homogeneous compared to the CW. The pattern skewed towards the upper body, with an accumulation in the cervical spine and opposing unilateral loading in the shoulder and elbow. It appears that they were occupied in more specialised manual labour relative to the CW men, like construction and woodworking, processing of metals, or leatherworking, which took on greater significance in the Bronze Age due to social and ecological development (Harding, 2002; Alison A. Macintosh et al., 2014). Nevertheless, agricultural fieldwork was still a major part of subsistence (Bartelheim, 2009). Furthermore, the observation of degenerative processes in the temporomandibular joint in combination with higher wear scores and ante mortem tooth loss of front teeth supports the hypothesis of teeth used as tools. In eastern Central Europe, however, similar correlations were more frequent in Final Neolithic populations and in Early Bronze Age females, pointing at a different distribution of labour (Hukelova, 2016, pp. 198–199).

Changes in the behavioural repertoire through time were also observed in NG females. The female activity pattern is complemented by the appearance of high incidences of degenerative joint disease in the hip and knee joints, which had been largely unaffected in the

CW samples, whereas the frequency of affected foot joints slightly decreased. This may suggest that NG women spend a large proportion of their time in mobile and lower limb loading tasks, or in relatively stationary activities, which is also mirrored in higher proportions of thoracic and lumbar joint degeneration. The latter was also noticed in eastern Central European Neolithic and Bronze Age samples, indicating settlement bound tasks like manual activities in kneeling or squatting positions (Hukelova, 2016, pp. 195, 198). Our findings are further supported by Macintosh et al. (2014, p. 387; 2017, p. 8) who hypothesised a change in female activities from predominantly agricultural processing in the Neolithic to additional pottery, textile and leather production in the Bronze Age.

The low incidence of Schmorl's nodes suggests that single individuals may have performed particularly strenuous labour or were more susceptible to develop such lesions due to intrinsic factors, like genetic predisposition. Furthermore, the equal distribution between both cultures contrasts with the increasing incidence over time in eastern Central Europe (Hukelova, 2016, pp. 201–202). This may be due to geographical differences in lifestyle as already mentioned, or due to a bias resulting from insufficient vertebral preservation. However, these inferences should only be considered as tentative, as the joint specific sample was small, particularly for spinal joints.

In terms of nonspecific stress indicators, higher prevalences of cribra orbitalia, cribra cranii and lower limb periostitis shows that physiological stress is more evident for the CW, but generally differently distributed among age.

Cribra orbitalia afflicted most of the subadults throughout both cultural periods, while cribra cranii was less frequent, and, even though not explicitly scored for this study, only mildly expressed (“orange-peel” texture (O'Donnell et al., 2022, p. 394)). A comparable distribution of cribrotic lesions was noted by Dresely (2004, p. 239) in the other Tauber region samples. The difference might be explained by the different aetiology and distinct underlying disease processes prevailing in the populations, resulting in a higher frequency of cribra orbitalia (Rivera and Mirazón Lahr, 2017, p. 88). Since both cribrotic lesions form during the growth period in subadult individuals and are assumed as childhood stressors (O'Donnell et al., 2023; Stuart-Macadam, 1985; Walker et al., 2009), the high incidences in all samples indicate that physiological stress was prevalent from an early age. Therefore, adults with cribra orbitalia and cribra cranii generally represent children who survived episodes of childhood stress and reached adulthood. Nevertheless, the number of adults with lesions is relatively low in all sites, which suggests that the populations experienced severe childhood stress and the majority of nonadults succumbed. Striking is the excess of adult female individuals with orbital lesions throughout

all samples and the near absence of males, except for Tauberbischofsheim-Impfingen. This contradicts the findings in O'Donnell et al. (2022), where no significant differences in sex-biased mortality or immune response were discovered in childhood stress. Thus, either similar stress levels in boys and girls or even less stress in boys would have been expected, as boys could have been valued more in patrilocal societies. Hence, other socioeconomic factors and nutrition could have influenced this pattern (O'Donnell et al., 2022, p. 395), or this hints at resilience in female subadults which fits well with the previously analysed lower mortality rate compared to infant males (Lismann et al., 2024, p. 321). The population of Tauberbischofsheim-Impfingen seemed to suffer from a prolonged period of stress as both adults and subadults exhibit high frequencies of cribra orbitalia. This was not observed in the remaining Tauber region populations (Dresely, 2004, p. 239; Trautmann, 2012, pp. 395–396), even though Trautmann noticed that due to insufficient preservation the original incidence might have been higher in Lauda-Königshofen. The variation could result from nutritional impairment due to the above-mentioned different subsistence strategies.

The overall similar and high distribution of linear enamel hypoplasia among CW and NG sites points to general systemic stress factors and complements the picture of increased childhood stress in these populations. All sites share an accumulation of enamel defects equivalent to an average age estimate ranging from 2.7 to 3.0 years of age, which is most likely indicative of weaning or the post-weaning period (Fernández-Crespo et al., 2022, p. 15; Katzenberg et al., 1996). While the CW sites remain constant (2.8 years), the NG sites exhibit more variation, which is in line with Early Bronze Age populations in south-western Poland (Howcroft, 2013). In contrast, Trautmann (2012, p. 396) observed in only 30 % of the CW Lauda-Königshofen population linear enamel hypoplasia accumulating between three and five years. Remseck-Aldingen displays the youngest average age of occurrence and Ammerbuch-Reusten the oldest average age of this range. This corroborates the previously assumed early weaning age and the probably related increased mortality of infants in Remseck-Aldingen and their sociocultural distinction (Lismann et al., 2024, p. 321; Rathmann et al., 2023, p. 7). Furthermore, a noticeable disproportion in enamel hypoplasia prevalence between adults and subadults in Ammerbuch-Reusten suggests that the population experienced an event or a certain period of elevated stress. Since drastic sociocultural changes causing an increase in adult and decrease in subadult frequency within a population seem unlikely, the divergence presumably resulted from environmental factors like restricted access to food resources or diseases. Moreover, enamel defects emerge distinctly earlier in NG females than in males (females: 2.7 years, males: 3.4 years), which is less pronounced in the CW (females: 2.9 years, males: 3.0

years), but also evident in Lauda-Köngishofen (females: ca. 3.5 years, males: ca. 4.0 years) (Trautmann, 2012, p. 422). Assuming that this pattern reflects stress from the weaning process, the populations seemed to practice differential weaning and child-rearing practices by sex. Therefore, an early introduction of complementary foods and early cessation of breastfeeding was potentially pursued for female children. Differences in social status (Pokutta and Howcroft, 2012, p. 248) and gender specific diet (Münster et al., 2018, pp. 22–23) may also have existed, even though this is only indicated for adults in these studies. Ultimately, isotopic analyses will be necessary for more precise assumptions.

A different pattern is seen in periosteal reactions, where CW adults were most affected. As periosteal reactions can form throughout life (Caruso and Nikita, 2024, p. 7), the results indicate increased stress in adulthood during the CW, particularly among females. However, the decline in the NG may also be suggestive of extreme stress in which individuals were dying before a periosteal response was developed (Pilloud and Schwitalla, 2020, p. 9). Such an interpretation could explain the higher mortality of NG males compared to the CW, but does not fully account for the lower mortality observed in young and middle adulthood females (Lismann et al., 2024, p. 321). Therefore, when considering that the formation of periosteal reactions can be related to productive activities or movement across the landscape (Caruso and Nikita, 2024, p. 8; Pilloud and Schwitalla, 2020, pp. 7–8), increased stress in the adult CW population could indeed be a factor. This would be consistent with the above supposed subsistence tasks for both sexes and female migration in the Final Neolithic. In contrast, the increase in periosteal reactions in Ammerbuch-Reusten subadults highlights the harsh conditions some Early Bronze Age communities had to face, which also has been demonstrated for infants in the Austrian site of Unterhautzenthal (Furtwängler et al., 2025; Rebay-Salisbury et al., 2018).

Results on fractured bones suggest a nearly equal risk of trauma among adults in the CW and NG samples, although more females were affected in the Early Bronze Age than in the previous period. The location and fracture type indicate accidental trauma potentially related to (sex-specific) daily labour, as females more often displayed forearm fractures and males more often clavicular and rib fractures. However, even though most of the injuries were oblique fractures, hinting at an accidental indirect force provoked for example by falling (Grauer and Roberts, 1996, p. 539), interpersonal violence cannot be excluded with certainty (Redfern and Roberts, 2019, p. 242). All injuries presumably did not result in serious physical impairment since the fractures healed in the proper anatomical position, which indicates medical knowledge, treatment and care of injured community members. Previous studies in the CW Tauber region

report similarly low fracture prevalences, predominantly affecting the forearm (Dresely, 2004, pp. 235–236; Trautmann, 2012, pp. 394–395). Yet, these also document cranial trauma, which has not been observed in the present assemblage. Notably, adult trauma prevalence in the present periods (Corded Ware: 14.8%; Neckar group: 14.3%) is also comparable to the Final Neolithic rate in eastern Central Europe (18.6%), yet approximately half that of the Early Bronze Age frequency (32.9%) reported for the same region (Hukelova, 2016, pp. 142, 206, 217). Contrary to Hukelova’s observations in eastern Central Europe (2016, pp. 213–222), fractures in children and intentional violence have not been detected in our study. Her analysis included only well-preserved skeletons, whereas the incomplete preservation of the present samples may have led to undetected fractures and an underestimation of trauma prevalence. It would, therefore, be premature to assume that populations in Southwest Germany had fewer accidents or were less violent than in other regions.

The trepanation of an adult male individual from Heilbronn represents a special case of trauma. The skull was opened by potentially using the scraping technique with a flat lithic object, indicated by an abrasion ring around the orifice (Giuffra and Fornaciari, 2017, p. 758; Gualdi-Russo et al., 2024, p. 132). However, the inclination of the margins along the sagittal axis are relatively steep, which is unusual for scraping, and a mixed technique of scraping and grooving/cutting is also conceivable (Giuffra and Fornaciari, 2017, p. 760; Gualdi-Russo et al., 2024, p. 132). Remodelled surfaces suggest healing after the trepanation, but interestingly, cut or scraping marks at the abrasion ring are visible. Due to preservation, it cannot be said with certainty if this happened intentionally perimortem or postmortem, or due to taphonomy. As no inflammatory signs are present, the treatment of an infection seems unlikely. Besides other therapeutic motives, ritual and experimental purposes are usually suggested (Giuffra and Fornaciari, 2017, pp. 761–764). But since no direct indications are identifiable, the reason for the trepanation remains speculative. Nevertheless, the risky but successful procedure close to the superior sagittal sinus indicates that the person in charge was skilled and had medical knowledge. Interestingly, two male individuals from Lauda-Königshofen and one from Dittigheim display nearly identical trepanations in size and shape (“tongue-shaped”) (Dresely, 2004, p. 229; Trautmann, 2012, pp. 398–399), indicating similar applied trepanation techniques. Hence, frequent findings of trepanations in the Tauber region suggest an area of specialisation in this field (Wahl, 2012; Weber and Wahl, 2006).

Lesions diagnosed as osteochondritis dissecans were more frequent in the NG than in the CW. Moreover, the variety of affected joints increased over time and sex differences in affected joints are observable, except for the foot joint which is similarly affected in all sites.

However, it should be noted that the small sample size may have biased the distribution pattern. Osteochondritis dissecans lesions are frequently found in contemporary athletes (Aicale et al., 2018; Baker et al., 2010) but also archaeological samples (Vikatou et al., 2017; Zúñiga Thayer et al., 2021), which leads to the conclusion that the prehistoric individuals were engaged in high mechanical loadings. The fact that both cultural periods exhibit osteochondritis dissecans in the foot indicates that pedal stress and strain was a common cause. Furthermore, the increase in variety of lesions from the Final Neolithic to the Early Bronze Age may be related to mechanical demands associated with new Bronze Age economic strategies and specialisations (e.g., smithing, farming equipment). This reinforces the present findings of joint diseases and potentially related activity patterns suggesting role division in labour and task specialisation related to diversification of tasks.

Reasons for the absence of neoplastic diseases in the Final Neolithic are diverse and difficult to determine. Generally, neoplastic conditions exceeding the last four millennia are exceptionally rare (David and Zimmerman, 2010; Hunt et al., 2018, pp. 19–20; Lieverse et al., 2014, p. 2). The rate of preservation declines over time which can lead to misidentifications as postmortem damage or skeletal remains become incomplete and former cancer conditions are irretrievably lost. Assuming that the natural environment (e.g., ultraviolet rays, radiation, certain viruses) was similar in both periods, this factor can be excluded as a driving force. However, human induced causes could have increased the carcinogenic risk through time. Given the dynamic population history and the numerous migration and admixture events during that time (Allentoft et al., 2015; Haak et al., 2015; Heyd, 2023; Papac et al., 2021; Sjögren et al., 2016), genetic predisposition related to race, ethnicity, and ancestry appeared to be a more pertinent contributor (Churpek et al., 2015; Saad et al., 2022; Siegel et al., 2020). Additionally, changes in culture and lifestyle may have influenced potential carcinogenic factors from the Early Bronze Age onwards (e.g., manufactured food, smoke exposure during metal working and pottery production). Therefore, cancer could be the result of an accumulation of risk factors (Hunt et al., 2018, p. 12) which may explain the predominance in the Early Bronze Age population detected in our samples.

Finally, despite the fundamental role of palaeopathological analyses in bioarchaeological studies, it must be acknowledged that such analyses are susceptible to significant biases and limitations. Since pathology prevalences represent the proportion of individuals or skeletal elements with lesions, such frequencies are directly affected by skeletal preservation. This means that once present lesions might be lost in an incomplete skeleton. The use of thresholds

for skeletal completeness would enhance the data, but similarly reduces the sample size. To balance both issues, and because of different preservation patterns in skeletal elements dependent on the bone structure, we decided to include all skeletal elements with sufficient preservation to detect pathologies in combination with completeness thresholds for individual skeletal elements instead of general thresholds for the whole skeleton. We are also conscious that by including individuals from various age groups, age specific changes will be obscured. Yet, more refined age categories would result in too small sample sizes or not represented classes, preventing meaningful conclusions. Hence, we decided to only differentiate between adults and subadults for the purposes of our study. In addition, individuals have different susceptibilities to diseases which complicates inter- and intra-sample comparisons (Wood et al., 1992). Particularly, the frequency of a disease could have different meanings (Temple and Goodman, 2014). Moreover, the absence of stressors cannot be equated with an individual's physical well-being, since not all diseases develop skeletal lesions or an individual died before lesions occurred (DeWitte and Stojanowski, 2015; Wood et al., 1992). In an attempt to remedy these biases, we included multiple stress indicators and considered the demography and context of the skeletal samples (Temple and Goodman, 2014; Vergidou et al., 2022). Nevertheless, we caution that further analyses regarding the ecology and culture of the past populations are needed for more refined inferences about the Final Neolithic and Early Bronze Age in Southwest Germany.

Conclusion

This study examined palaeopathological conditions in skeletal remains from the Final Neolithic and Early Bronze Age in Southwest Germany, considering age and sex to evaluate the impact of sociocultural change. The results reveal that pathology frequencies were influenced by a complex interplay of chronological, regional, and sex-related factors: Firstly, dental diseases reflect dietary variation and teeth used as tools, with patterns particularly associated with sex: caries frequencies increased in females from the CW to the NG, and different tooth abrasion in CW males and females indicates sex-specific diet. In contrast, distinct abrasion patterns in CW females and NG males from Ammerbuch-Reusten suggest the use of teeth as a third hand. Secondly, degenerative joint disease indicates a chronological shift in physical activity and sex-specific labour roles: CW men pursued regionally distinct subsistence strategies, while NG men showed evidence of more homogenised tasks among sites, though unilateral loading was common in both cultural periods. Females from both cultures appear to have performed similar

tasks, with some diversification observed in the NG. Thirdly, non-specific stress indicators suggest severe early childhood stress throughout time, with site and sex-specific variation in weaning practices. Fourthly, trauma patterns differ: trepanations were more frequent in the CW, while traumatic joint lesions increased in the NG, whereas fracture rates remained constant. Lastly, the emergence of neoplastic diseases in the Early Bronze Age, in contrast to the absence in the Final Neolithic, may signal socioeconomic and occupational changes related to work conditions or genetics.

Interestingly, no direct correlation was found between the mortality patterns (Lismann et al., 2024) and the palaeopathological profiles of the studied populations, indicating resilience of many of its members. Instead, these findings may suggest that cultural transition drove changes in lifestyle, which left palaeopathological traces especially in relation to sex. Future research should include further skeletal samples, particularly from the Bell Beaker culture, to cover further cultures during that time and gain more details about the lifestyle of different populations. Despite certain limitations, our findings contribute valuable insights into the relation between cultural transition and biological stress in prehistoric Southwest Germany and underscores the need for further interdisciplinary investigation in this region.

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Appendix C: Supplementary Information

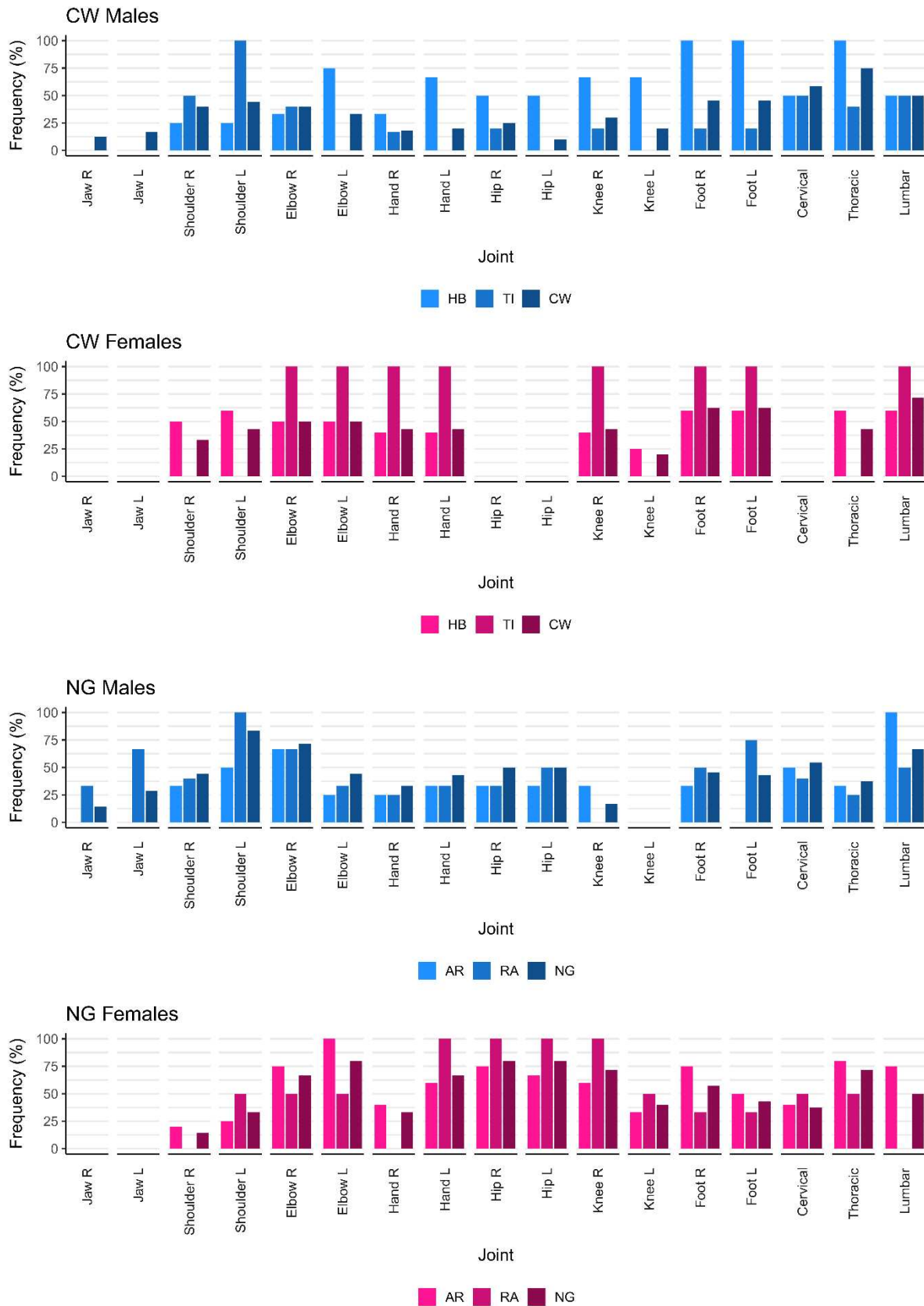


Figure A1 Frequency of degenerative joint disease by joint type and sex.

Table A1 Frequency of dental pathologies by age and sex per tooth.

Skeletal lesion	Age/Sex	HB	TI	CW	AR	RA	NG
		% (n/N)	% (n/N)	% (n/N)	% (n/N)	% (n/N)	% (n/N)
Calculus	Males	96.6 (140/145)	50.0 (58/116)	77.4 (240/310)	86.8 (66/76)	63.9 (53/83)	66.8 (137/205)
	Females	85.3 (168/197)	37.5 (9/24)	80.2 (182/227)	95.0 (76/80)	79.1 (34/43)	81.6 (111/136)
	Total adults	90.1 (311/345)	49.4 (82/166)	77.7 (440/566)	91.5 (151/165)	65.1 (99/152)	71.5 (269/376)
	Subadults	46.5 (46/99)	19.4 (14/72)	40.4 (80/198)	75.1 (151/201)	36.8 (14/38)	69.2 (166/240)
	Total assemblage	80.4 (357/444)	40.3 (96/238)	68.1 (520/764)	82.5 (302/366)	59.5 (113/190)	70.6 (435/616)
Caries	Males	3.4 (5/145)	3.4 (4/116)	3.5 (11/310)	6.6 (5/76)	3.6 (3/83)	5.4 (11/205)
	Females	4.6 (9/197)	0.0 (0/24)	4.0 (9/227)	8.8 (7/80)	14.0 (6/43)	9.6 (13/136)
	Total adults	4.1 (14/345)	2.4 (4/166)	3.5 (20/566)	8.5 (14/165)	5.9 (9/152)	6.9 (26/376)
	Subadults	1.0 (1/99)	0.0 (0/72)	0.5 (1/198)	1.0 (2/201)	5.3 (2/38)	1.7 (4/240)
	Total assemblage	3.4 (15/444)	1.7 (4/238)	2.7 (21/764)	4.4 (16/366)	5.8 (11/190)	4.9 (30/616)

Abbreviations: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar Group, n = number of affected teeth, N = number of observed teeth.

Table A2 Frequency of degenerative joint disease by joint type and sex.

Joint	Sex	HB	TI	CW	AR	RA	NG
		% (n/N)	% (n/N)	% (n/N)	% (n/N)	% (n/N)	% (n/N)
Jaw R	Males	0.0 (0/4)	0.0 (0/2)	12.5 (1/8)	0.0 (0/3)	33.3 (1/3)	14.3 (1/7)
	Females	0.0 (0/4)	0.0 (0/1)	0.0 (0/5)	0.0 (0/3)	0.0 (0/1)	0.0 (0/4)
	Total adults	0.0 (0/8)	0.0 (0/3)	7.7 (1/13)	0.0 (0/7)	25.0 (1/4)	8.3 (1/12)
Jaw L	Males	0.0 (0/4)	0.0 (0/1)	16.7 (1/6)	0.0 (0/2)	66.7 (2/3)	28.6 (2/7)
	Females	0.0 (0/2)	0.0 (0/1)	0.0 (0/4)	0.0 (0/0)	0.0 (0/0)	0.0 (0/0)
	Total adults	0.0 (0/6)	0.0 (0/2)	10.0 (1/10)	0.0 (0/2)	66.7 (2/3)	28.6 (2/7)
Shoulder R	Males	25.0 (1/4)	50.0 (2/4)	40.0 (4/10)	33.3 (1/3)	40.0 (2/5)	44.4 (4/9)
	Females	50.0 (2/4)	0.0 (0/1)	33.3 (2/6)	20.0 (1/5)	0.0 (0/2)	14.3 (1/7)
	Total adults	37.5 (3/8)	40.0 (2/5)	37.5 (6/16)	22.2 (2/9)	25.0 (2/8)	27.8 (5/18)
Shoulder L	Males	25.0 (1/4)	100.0 (3/3)	44.4 (4/9)	50.0 (1/2)	100.0 (3/3)	83.3 (5/6)
	Females	60.0 (3/5)	0.0 (0/1)	42.9 (3/7)	25.0 (1/4)	50.0 (1/2)	33.3 (2/6)
	Total adults	44.4 (4/9)	80.0 (4/5)	47.1 (8/17)	28.6 (2/7)	66.7 (4/6)	50.0 (7/14)
Elbow R	Males	33.3 (1/3)	40.0 (2/5)	40.0 (4/10)	66.7 (2/3)	66.7 (2/3)	71.4 (5/7)

	Females	50.0 (2/4)	100.0 (1/1)	50.0 (3/6)	75.0 (3/4)	50.0 (1/2)	66.7 (4/6)
	Total adults	42.9 (3/7)	50.0 (3/6)	43.8 (7/16)	71.4 (5/7)	60.0 (3/5)	69.2 (9/13)
Elbow L	Males	75.0 (3/4)	0.0 (0/4)	33.3 (3/9)	25.0 (1/4)	33.3 (1/3)	44.4 (4/9)
	Females	50.0 (2/4)	100.0 (1/1)	50.0 (3/6)	100.0 (3/3)	50.0 (1/2)	80.0 (4/5)
	Total adults	62.5 (5/8)	20.0 (1/5)	40.0 (6/15)	62.5 (5/8)	50.0 (3/6)	62.5 (10/16)
Hand R	Males	33.3 (1/3)	16.7 (1/6)	18.2 (2/11)	25.0 (1/4)	25.0 (1/4)	33.3 (3/9)
	Females	40.0 (2/5)	100.0 (1/1)	42.9 (3/7)	40.0 (2/5)	0.0 (0/1)	33.3 (2/6)
	Total adults	37.5 (3/8)	28.6 (2/7)	27.8 (5/18)	33.3 (3/9)	33.3 (2/6)	37.5 (6/16)
Hand L	Males	66.7 (2/3)	0.0 (0/5)	20.0 (2/10)	33.3 (1/3)	33.3 (1/3)	42.9 (3/7)
	Females	40.0 (2/5)	100.0 (1/1)	42.9 (3/7)	60.0 (3/5)	100.0 (1/1)	66.7 (4/6)
	Total adults	50.0 (4/8)	28.6 (2/7)	33.3 (6/18)	50.0 (4/8)	50.0 (3/6)	53.3 (8/15)
Hip R	Males	50.0 (2/4)	20.0 (1/5)	25.0 (3/12)	33.3 (1/3)	33.3 (1/3)	50.0 (4/8)
	Females	0.0 (0/4)	0.0 (0/0)	0.0 (0/5)	75.0 (3/4)	100.0 (1/1)	80.0 (4/5)
	Total adults	25.0 (2/8)	20.0 (1/5)	17.6 (3/17)	62.5 (5/8)	60.0 (3/5)	66.7 (10/15)
Hip L	Males	50.0 (1/2)	0.0 (0/5)	10.0 (1/10)	33.3 (1/3)	50.0 (2/4)	50.0 (4/8)
	Females	0.0 (0/4)	0.0 (0/1)	0.0 (0/6)	66.7 (2/3)	100.0 (2/2)	80.0 (4/5)
	Total adults	16.7 (1/6)	0.0 (0/6)	6.3 (1/16)	44.4 (4/9)	57.1 (4/7)	52.9 (9/17)
Knee R	Males	66.7 (2/3)	20.0 (1/5)	30.0 (3/10)	33.3 (1/3)	0.0 (0/2)	16.7 (1/6)
	Females	40.0 (2/5)	100.0 (1/1)	42.9 (3/7)	60.0 (3/5)	100.0 (2/2)	71.4 (5/7)
	Total adults	50.0 (4/8)	33.3 (2/6)	35.3 (6/17)	40.0 (4/10)	60.0 (3/5)	43.8 (7/16)
Knee L	Males	66.7 (2/3)	0.0 (0/4)	20.0 (2/10)	0.0 (0/3)	0.0 (0/2)	0.0 (0/6)
	Females	25.0 (1/4)	0.0 (0/0)	20.0 (1/5)	33.3 (1/3)	50.0 (1/2)	40.0 (2/5)
	Total adults	42.9 (3/7)	0.0 (0/4)	20.0 (3/15)	22.2 (2/9)	25.0 (1/4)	21.4 (3/14)
Foot R	Males	100.0 (4/4)	20.0 (1/5)	45.5 (5/11)	33.3 (1/3)	50.0 (3/6)	45.5 (5/11)
	Females	60.0 (3/5)	100.0 (2/2)	62.5 (5/8)	75.0 (3/4)	33.3 (1/3)	57.1 (4/7)
	Total adults	77.8 (7/9)	50.0 (4/8)	55.0 (11/20)	44.4 (4/9)	41.7 (5/12)	43.5 (10/23)
Foot L	Males	100.0 (4/4)	20.0 (1/5)	45.5 (5/11)	0.0 (0/2)	75.0 (3/4)	42.9 (3/7)
	Females	60.0 (3/5)	100.0 (2/2)	62.5 (5/8)	50.0 (2/4)	33.3 (1/3)	42.9 (3/7)
	Total adults	77.8 (7/9)	42.9 (3/7)	52.6 (10/19)	25.0 (2/8)	55.6 (5/9)	38.9 (7/18)
Cervical	Males	50.0 (2/4)	50.0 (3/6)	58.3 (7/12)	50.0 (2/4)	40.0 (2/5)	54.5 (6/11)

	Females	0.0 (0/4)	0.0 (0/2)	0.0 (0/7)	40.0 (2/5)	50.0 (1/2)	37.5 (3/8)
	Total adults	25.0 (2/8)	33.3 (3/9)	35.0 (7/20)	40.0 (4/10)	44.4 (4/9)	45.5 (10/22)
Thoracic	Males	100.0 (5/5)	40.0 (2/5)	75.0 (9/12)	33.3 (1/3)	25.0 (1/4)	37.5 (3/8)
	Females	60.0 (3/5)	0.0 (0/1)	42.9 (3/7)	80.0 (4/5)	50.0 (1/2)	71.4 (5/7)
	Total adults	72.7 (8/11)	33.3 (2/6)	60.0 (12/20)	60.0 (6/10)	33.3 (2/6)	52.9 (9/17)
Lumbar	Males	50.0 (2/4)	50.0 (2/4)	50.0 (5/10)	100.0 (1/1)	50.0 (2/4)	66.7 (4/6)
	Females	60.0 (3/5)	100.0 (1/1)	71.4 (5/7)	75.0 (3/4)	0.0 (0/2)	50.0 (3/6)
	Total adults	55.6 (5/9)	60.0 (3/5)	58.8 (10/17)	83.3 (5/6)	42.9 (3/7)	64.3 (9/14)

Abbreviations: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar Group, n = number of affected individuals, N = number of observed Individuals, R = right, L = left.

Table A3 Frequency of osteochondritis dissecans by joint type and sex.

Joint	Sex	HB	TI	CW	AR	RA	NG
		% (n/N)	% (n/N)	% (n/N)	% (n/N)	% (n/N)	% (n/N)
Shoulder	Males	0.0 (0/5)	0.0 (0/5)	0.0 (0/12)	33.3 (1/3)	0.0 (0/5)	11.1 (1/9)
	Females	0.0 (0/7)	50.0 (1/2)	10.0 (1/10)	0.0 (0/5)	0.0 (0/2)	0.0 (0/7)
	Total adults	0.0 (0/12)	14.3 (1/7)	4.5 (1/22)	11.1 (1/9)	0.0 (0/8)	5.6 (1/18)
Elbow	Males	20.0 (1/5)	0.0 (0/5)	8.3 (1/12)	0.0 (0/3)	50.0 (2/4)	33.3 (3/9)
	Females	0.0 (0/6)	0.0 (0/2)	0.0 (0/9)	0.0 (0/4)	100.0 (2/2)	33.3 (2/6)
	Total adults	9.1 (1/11)	0.0 (0/7)	4.8 (1/21)	0.0 (0/8)	57.1 (4/7)	29.4 (5/17)
Hand	Males	0.0 (0/4)	0.0 (0/5)	0.0 (0/12)	0.0 (0/3)	0.0 (0/4)	0.0 (0/8)
	Females	0.0 (0/5)	0.0 (0/2)	0.0 (0/8)	0.0 (0/5)	50.0 (1/2)	14.3 (1/7)
	Total adults	0.0 (0/9)	0.0 (0/7)	0.0 (0/20)	0.0 (0/9)	12.5 (1/8)	5.6 (1/18)
Hip	Males	0.0 (0/4)	0.0 (0/6)	0.0 (0/13)	25.0 (1/4)	0.0 (0/4)	10.0 (1/10)
	Females	0.0 (0/6)	0.0 (0/2)	0.0 (0/9)	0.0 (0/5)	0.0 (0/2)	0.0 (0/7)
	Total adults	0.0 (0/10)	0.0 (0/8)	0.0 (0/22)	9.1 (1/11)	0.0 (0/8)	4.8 (1/21)
Knee	Males	0.0 (0/4)	0.0 (0/6)	0.0 (0/13)	0.0 (0/3)	0.0 (0/4)	0.0 (0/9)
	Females	0.0 (0/4)	0.0 (0/2)	0.0 (0/7)	0.0 (0/5)	50.0 (1/2)	14.3 (1/7)
	Total adults	0.0 (0/8)	0.0 (0/8)	0.0 (0/20)	0.0 (0/11)	16.7 (1/6)	5.3 (1/19)
Foot	Males	0.0 (0/4)	0.0 (0/6)	8.3 (1/12)	0.0 (0/3)	14.3 (1/7)	18.2 (2/11)
	Females	20.0 (1/5)	50.0 (1/2)	25.0 (2/8)	20.0 (1/5)	100.0 (2/2)	42.9 (3/7)

	Total adults	11.1 (1/9)	12.5 (1/8)	15.0 (3/20)	10.0 (1/10)	25.0 (3/12)	21.7 (5/23)
other	Males	0.0 (0/5)	0.0 (0/5)	0.0 (0/13)	0.0 (0/3)	0.0 (0/4)	0.0 (0/8)
	Females	0.0 (0/5)	0.0 (0/2)	0.0 (0/8)	0.0 (0/5)	0.0 (0/2)	0.0 (0/7)
	Total adults	0.0 (0/10)	0.0 (0/7)	0.0 (0/21)	0.0 (0/9)	0.0 (0/7)	0.0 (0/17)

Abbreviations: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar Group, n = number of affected individuals, N = number of observed Individuals.

Table A4 Group comparisons for dental disease per individual.

Groups compared	Skeletal lesion			
	Calculus	Caries	Periapical lesion	Periodontal disease
CW vs. NG	Fisher's test; p = 1	$\chi^2 = 0.56$; p = 0.4542	Fisher's test; p = 0.6133	Fisher's test; p = 0.6486
CW males vs. NG males	Fisher's test; p = 1	$\chi^2 = 0.031$; p = 0.8592	Fisher's test; p = 0.6036	Fisher's test; p = 0.0815
CW females vs. NG females	NA	Fisher's test; p = 0.3972	NA	Fisher's test; p = 0.4706
CW males vs. CW females	Fisher's test; p = 1	Fisher's test; p = 0.4291	Fisher's test; p = 0.2403	Fisher's test; p = 0.1558
NG males vs. NG females	NA	Fisher's test; p = 1	NA	Fisher's test; p = 0.2281
HB vs. TI vs. AR vs. RA	Fisher's test; p = 0.6852	Fisher's test; p = 0.3923	Fisher's test; p = 0.8861	Fisher's test; p = 0.7451

Abbreviations: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar Group.

Table A5 Group comparisons for dental disease per tooth.

Groups compared	Skeletal lesion	
	Calculus	Caries
CW vs. NG	$\chi^2 = 3.64$; p = 0.0564	$\chi^2 = 4.14$; p = 0.0419
CW males vs. NG males	$\chi^2 = 6.53$; p = 0.0106	$\chi^2 = 0.602$; p = 0.438
CW females vs. NG females	$\chi^2 = 0.04$; p = 0.842	$\chi^2 = 3.74$; p = 0.053
CW males vs. CW females	$\chi^2 = 0.439$; p = 0.507	$\chi^2 = 0$; p = 0.0564
NG males vs. NG females	$\chi^2 = 8.28$; p = 0.004	$\chi^2 = 1.60$; p = 0.983
HB vs. TI vs. AR vs. RA	$\chi^2 = 128$; p = 0	Fisher's test; p = 0.155

Abbreviations: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar Group.

Table A6 Dental wear comparisons per tooth type.

Groups compared	Tooth							
	I1	I2	C	P1	P2	M1	M2	M3
CW vs. NG	W = 384; p = 0.624	W = 390; p = 0.593	W = 460; p = 0.634	W = 458; p = 0.361	W = 433; p = 0.312	W = 453; p = 0.135	W = 524; p = 0.304	W = 424; p = 0.465
CW males vs. NG males	W = 102; p = 0.796	W = 150; p = 0.738	W = 135; p = 0.535	W = 141; p = 0.345	W = 127; p = 0.169	W = 126; p = 0.0792	W = 97.5; p = 0.0095	W = 100; p = 0.0749

CW females vs. NG females	W = 90.5; p = 0.286	W = 52.5; p = 0.515	W = 105; p = 0.683	W = 93.5; p = 0.924	W = 93; p = 0.817	W = 100; p = 0.962	W = 150; p = 0.211	W = 102; p = 0.426
CW males vs. CW females	W = 81; p = 0.0186	W = 60; p = 0.0038	W = 85.5; p = 0.006	W = 144; p = 0.245	W = 140; p = 0.203	W = 106; p = 0.0021	W = 86; p = 0.0008	W = 68; p = 0.0032
NG males vs. NG females	W = 47; p = 0.63	W = 34; p = 0.0307	W = 67.5; p = 0.399	W = 84; p = 0.782	W = 88; p = 0.788	W = 66; p = 0.350	W = 120; p = 0.523	W = 87; p = 0.979
HB vs. TI vs. AR vs. RA	H = 8.70; p = 0.0336	H = 2.77; p = 0.428	H = 3.36; p = 0.340	H = 2.59; p = 0.460	H = 4.25; p = 0.236	H = 7.08; p = 0.0693	H = 2.95; p = 0.399	H = 3.30; p = 0.347

Abbreviations: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar Group.

Table A7 Group comparisons for degenerative joint disease.

Groups compared	Skeletal lesion	
	Appendicular degenerative joint disease	Spinal degenerative joint disease
CW vs. NG	Fisher's test; p = 0.2071	$\chi^2 = 0$; p = 1
CW males vs. NG males	Fisher's test; p = 1	Fisher's test; p = 0.3572
CW females vs. NG females	Fisher's test; p = 0.0915	Fisher's test; p = 0.6199
CW males vs. CW females	Fisher's test; p = 1	Fisher's test; p = 0.1778
NG males vs. NG females	Fisher's test; p = 0.2536	Fisher's test; p = 1
HB vs. TI vs. AR vs. RA	Fisher's test; p = 0.8681	Fisher's test; p = 0.8291

Abbreviations: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar Group.

Table A8 Group comparisons for non-specific stress.

Groups compared	Skeletal lesion			
	Cribræ cranii	Cribræ orbitalia	Linear enamel hypoplasia	Periosteal reaction
CW vs. NG	Fisher's test; p = 0.2733	Fisher's test; p = 0.2357	$\chi^2 = 0$; p = 1	Fisher's test; p = 0.002
CW males vs. NG males	Fisher's test; p = 0.3783	Fisher's test; p = 0.2143	Fisher's test; p = 0.6517	Fisher's test; p = 0.1153
CW females vs. NG females	Fisher's test; p = 0.5692	Fisher's test; p = 1	Fisher's test; p = 0.6199	Fisher's test; p = 0.0152
CW males vs. CW females	Fisher's test; p = 1	Fisher's test; p = 1	Fisher's test; p = 0.3972	Fisher's test; p = 0.3742
NG males vs. NG females	Fisher's test; p = 1	Fisher's test; p = 0.1544	Fisher's test; p = 0.638	Fisher's test; p = 1
HB vs. TI vs. AR vs. RA	Fisher's test; p = 0.4098	Fisher's test; p = 0.0075	Fisher's test; p = 0.7536	Fisher's test; p = 0.0115

Abbreviations: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar Group.

Table A9 Group comparisons for trauma.

Groups compared	Skeletal lesion	
	Fracture	Osteochondritis dissecans
CW vs. NG	Fisher's test; p = 1	Fisher's test; p = 0.0528
CW males vs. NG males	Fisher's test; p = 1	Fisher's test; p = 0.1032

CW females vs. NG females	Fisher's test; p = 0.5765	Fisher's test; p = 0.5928
CW males vs. CW females	Fisher's test; p = 1	Fisher's test; p = 1
NG males vs. NG females	Fisher's test; p = 0.6177	Fisher's test; p = 1
HB vs. TI vs. AR vs. RA	Fisher's test; p = 0.7666	Fisher's test; p = 0.2324

Abbreviations: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar Group.

Table A10 Group comparisons for neoplasms.

Groups compared	Skeletal lesion Neoplasm
CW vs. NG	Fisher's test; p = 0.0455
CW males vs. NG males	Fisher's test; p = 0.0996
CW females vs. NG females	Fisher's test; p = 0.4737
CW males vs. CW females	NA
NG males vs. NG females	Fisher's test; p = 1
HB vs. TI vs. AR vs. RA	Fisher's test; p = 0.091

Abbreviations: HB = Heilbronn, TI = Tauberbischofsheim-Impfingen, CW = Corded Ware culture, AR = Ammerbuch-Reusten, RA = Remseck-Aldingen, NG = Neckar Group.

