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RESEARCH ARTICLE

Histological and stable isotope analysis of archeological bones from St. Rombout's cemetery (Mechelen, Belgium): Intrasite, intraindividual, and intrabone variability

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Abstract

This study compares histological preservation in archeological bones from different burial types to unravel the histotaphonomy-to-funerary practices relationship. An intraskeletal approach is also adopted to explore intraindividual (inner ear part of the petrous bone vs. upper/lower limb long bones) and intrabone (proximal vs. distal diaphysis) variability in bone collagen preservation, $\delta^{13}C$, and $\delta^{15}N$. The aim is to (a) target bones that likely retain higher amounts of collagen, (b) better understand the inner ear bone collagen isotopic signature and remodeling, and (c) assess intrabone isotopic and histological homogeneity. For the histological analysis, the data have been collected from 61 specimens (20 individuals) from the medieval/postmedieval cemetery of St. Rombout, Belgium. Thin sections have been studied using optical and scanning electron microscopy. For the collagen and isotopic data, 101 samples have been collected from 21 individuals. Distinct histological patterns are observed only in bones from single coffin burials; however, bone histology can display intraindividual and intrabone variability, which are important to account for interpretations. Collagen wt.%, $\delta^{13}C$, and $\delta^{15}N$ show significant intraindividual differences but insignificant intrabone variability. This study also confirms the extraordinary nature of the petrous bone, as the inner ear bone collagen $\delta^{13}C$ and $\delta^{15}N$ values reflect the dietary input of the first approximately 2–3 years of life.

KEYWORDS
bone, collagen, histotaphonomy, intrabone, intraindividual, petrous bone, stable isotopes

1 | INTRODUCTION

This study explores the intrasite variability in bone microstructure (optical and scanning electron microscopy), and intraindividual and intrabone variability in collagen wt.%, $\delta^{13}C$, and $\delta^{15}N$ of archeological bone from the medieval/postmedieval cemetery of St. Rombout (Mechelen, Belgium). A particular focus is placed on two aspects:

1. Bone histology and its link to burial types (single coffin, single wrapped, multiple);
2. Intraindividual (inner ear part of the petrous bone vs. long bones) and intrabone variability (proximal vs. distal long bone diaphysis) in bone collagen preservation, $\delta^{13}C$, and $\delta^{15}N$ values.

1.1 | Bone histology and its link to burial types (single coffin, single wrapped, multiple)

Bone histology is a method that has been widely applied in the past decades for the identification and characterization of the diagenetic changes in the microstructure of archeological and fossil bone (Bell, 1990; Bell et al., 1996; Fernández-Jalvo et al., 2010; Hackett, 1981; Hedges et al., 1995; Hollund et al., 2012; Nielsen-Marsh & Hedges, 2000; Pesquero et al., 2018; Turner-Walker & Jans, 2008). Although these diagenetic modifications (e.g., microscopic focal destruction, cracking, generalized destruction, and staining) have been attributed to various physical, chemical, and biological processes (see Kendall et al., 2018), the postmortem microbial attack of the organic–inorganic composite has attracted most of the attention (Bell et al., 1996; Bell & Elkerton, 2008; Booth, 2020; Booth et al., 2015; Fernández-Jalvo et al., 2010; Kontopoulos et al., 2016; Kontopoulos, Penkman, Liritzis, & Collins, 2019; Turner-Walker, 2019; White & Booth, 2014).

Modifications in bone microstructure can be also strongly influenced by other factors such as funerary practices (Bell, 2012; Kontopoulos et al., 2016; Turner-Walker, 2008). It was not until recently that researchers attempted to link bone histology to funerary treatment (Booth, 2016; Booth & Madgwick, 2016; Brönnimann et al., 2018; Goren et al., 2020; Hollund et al., 2018; Kontopoulos et al., 2016; Kontopoulos, Penkman, Liritzis, & Collins, 2019; Machová et al., 2020; Papakonstantinou et al., 2020; Smith et al., 2016), as early taphonomic history and its effects on bone histology are often not distinguishable from post-burial diagenesis due to lack of relevant information.

Some researchers (e.g., Booth, 2016; Booth & Madgwick, 2016; Smith et al., 2016) claim that modifications in bone histology caused by anthropogenic processes can be distinguished from those induced by the burial environment based on a de facto acceptance of the internal origin of bacteria (Booth, 2016, 2020; Booth & Madgwick, 2016; White & Booth, 2014). Supporters of this hypothesis argue that enteric bacteria are involved in bone degradation, which travel from the gut around the body through vascular canals (Booth, 2020; e.g., White & Booth, 2014). Consequently, if an individual had not lived long enough for osteolytic bacterial species to have developed as part of their gut microbiome, or there was defleshing/removal of internal organs, there would be no evidence of bacterial attack in bone microstructure (Booth, 2020; Jans et al., 2004). An interesting but controversial example of such interpretation represent the 'mummified' Chalcolithic and Bronze Age human skeletons from Britain where the limited bacterial activity observed in these bones was interpreted as evidence of elimination of the gut microbiota during the removal of the internal organs of the bodies as part of a mummification process (Booth et al., 2015; Pearson et al., 2005). Nevertheless, there is conflicting evidence about the bacterial attack in bone (internal vs. external origin) (Kendall et al., 2018; Turner-Walker, 2019).

A lack of evidence of an enteric origin of bacteria has been reported by several studies (e.g., Fernández-Jalvo et al., 2010; Kontopoulos et al., 2016; Müller et al., 2011). Collagenolytic bacteria capable of degrading bone collagen can be commonly found within most soils (Vraný et al., 1988). New evidence supports the presence of several known collagenase-producing bacterial species in defleshed pig bones deposited in different marine and terrestrial environments, and relative increase in their abundances in bones showing microbial attack (Eriksen et al., 2020). Bone bacterial communities are found to be strongly related to the microbial community of the depositional environment and the microbial diversity increases with time after exposure (Eriksen et al., 2020). The postmortem bone microbiome also varies intraindividually depending on the body region (Emmons et al., 2020).

Therefore, the analysis of specimens from a Christian cemetery in medieval/postmedieval Belgium with a well-characterized funerary practice can offer valuable evidence in an effort to unravel the histotaphonomy-to-funerary practices relationship, the presence of microorganisms responsible for bioerosion, and how this can be affected by intraindividual and intrabone variability.

1.2 | Intraindividual (inner ear part of the petrous bone vs. long bones) and intrabone variability in bone collagen preservation, $\delta^{13}C$, and $\delta^{15}N$ values

This study adopts an intraskeletal approach to explore intraindividual variability (inner ear part of the petrous bone versus upper and lower limb long bones) in collagen preservation, and collagen $\delta^{13}C$ and $\delta^{15}N$, with an aim to improve sampling strategies for paleodietary studies (i.e., targeting skeletal elements likely to preserve higher amounts of collagen; better understanding of the inner ear diet time-span signature/remodeling).

Skeletal tissues are expected to degrade at different rates postmortem depending on the cortical bone thickness of each element, their exact microstructural characteristics, and the burial microenvironment among other variables. With reference to the ancient biomolecules, such heterogeneous intraindividual preservation is probably responsible for the preservation patterns of endogenous DNA. Pruvost et al. (2008) have reported higher DNA amplification

success rates in skeletal elements surrounded by more muscle mass (long bones, ribs, pelvis, scapula). However, the major breakthrough was the recent discovery of the consistently higher endogenous DNA yields in the inner ear compared with other hard tissues in the human skeleton (Gamba et al., 2014; Hansen et al., 2017; Parker et al., 2020).

Gamba et al. (2014) were the first to highlight the exceptional preservation of endogenous DNA in the inner ear of the petrous pyramid, while Hansen et al. (2017) found that the inner ear is more likely to preserve more endogenous DNA than tooth cementum. During the past few years, the inner ear of the petrous bone has become the most sought-after skeletal element in paleogenetic studies, which prompted Parker et al. (2020) to search for substitute skeletal elements with similar performance to the inner ear. In their study, they compared the endogenous DNA content in the inner ear to that of eight bones and teeth. It was confirmed that the inner ear displays the highest endogenous DNA yields, followed by the talus and tooth cementum (Parker et al., 2020). Unfortunately, no similar evaluation of collagen preservation has been carried out in order to assess whether or not the inner ear also retains collagen in higher amounts compared with other skeletal elements, and this study aims to cover this gap. In addition, the patterns of preservation of different types of biomolecules are impacted by similar factors and therefore can be interrelated (Kendall et al., 2018); this study therefore also has relevance for understanding aDNA preservation.

Regarding stable isotope intraindividual homogeneity, past studies have primarily assessed differences in bone trace element concentrations (Maurer et al., 2011, 2014), bone and tooth carbonate $\delta^{13}C$ and $\delta^{18}O$ (Maurer et al., 2014), tooth dentine and dental calculus versus bone collagen $\delta^{13}C$ and $\delta^{15}N$ (Balasse et al., 1999; Eerkens et al., 2014), and hair/nail keratin versus bone collagen $\delta^{13}C$ and $\delta^{15}N$ (O'Connell et al., 2001; White et al., 2009). Bone collagen $\delta^{13}C$ and $\delta^{15}N$ values reflect the average dietary input of different periods of a person's life. This is an important issue for paleodietary studies, as the exact bone turnover rates are difficult to estimate due to age, sex, within-bone variations, and so forth (Hedges et al., 2007; Matsubayashi & Tayasu, 2019). The human femur, for instance, is assumed to have a turnover rate of 1.5–4%/year in adults compared with 10–30%/year in 10–15 year old nonadults (Hedges et al., 2007; Manolagas, 2000). The inner ear part of the petrous bone, on the other hand, unlike long bones, is assumed to reach adult size in utero (Eby & Nadol, 1986; Nemzek et al., 1996; Richard et al., 2010). Although it is believed that the subcomponents of the inner ear attain their adult size by 5–6 prenatal months (e.g., Jeffery & Spoor, 2004), an increase in the overall size of the petrous bone throughout fetal life and infancy has also been supported in other studies (Fazekas & Kósa, 1978; Nagaoka & Kawakubo, 2015).

In an effort to find alternatives to dentine sources for early life dietary signals, Jørkov et al. (2009) investigated possible intraindividual differences in collagen $\delta^{13}C$ and $\delta^{15}N$ in teeth (first molar dentine), inner ear of the petrous bone, femora, and ribs in adults and nonadults from a medieval cemetery (AD 1200–1573) in Holbæk, Denmark. They argue that collagen $\delta^{13}C$ and $\delta^{15}N$ values of the inner ear should act as an archive of diet consumed during infancy and likely early childhood (Jørkov et al., 2009). This assumption was based on the small intraindividual differences in $\delta^{13}C$ (adult inner ear-to-femora/ribs: −0.4‰; nonadult inner ear-to-femora/ribs: −0.1‰), increased variation in the $\delta^{15}N$ of nonadult individuals (inner ear-to-femora: 0.7‰; inner ear-to-ribs: 0.9‰), and the small difference in the $\delta^{15}N$ values of adult individuals (inner ear-to-femora/ribs: 0.2–0.3‰) assessed (Jørkov et al., 2009). Consequently, the examination of the inner ear versus long bone isotopic differences at an intraindividual level will offer important new data for the better understanding of the characteristics of the inner ear of the petrous bone (isotopic enrichment/depletion, bone turnover) and intraindividual isotopic homogeneity.

With reference to collagen $\delta^{13}C$ and $\delta^{15}N$ intrabone variability, the study by Waters-Rist et al. (2011) is currently the only one that has compared the long bone metaphyseal to the diaphyseal collagen $\delta^{13}C$ and $\delta^{15}N$ in nonadult individuals, in that case to determine the feeding patterns of Neolithic populations in Cis-Baikal. Waters-Rist et al. (2011) concluded that nonadults show significant differences in isotopic signals (breastfeeding/weaning signals) between the metaphyseal (diet soon before death) and the diaphyseal bone (diet earlier in life until death) in infants (<3 years old). Therefore, this study attempts to enhance our understanding of within-bone (intradiaphysis) isotopic characteristics and collagen preservation in adult and nonadult long bone diaphysis.

2 | MATERIALS AND METHODS

2.1 | General

St. Rombout's cemetery (Mechelen, Belgium) was excavated in 2009–2011 by the Archaeology Service of Mechelen. The inhumations used in this study are dated from the 12th to the 18th century A.D. and include single burials in coffins, single and multiple plain burials without coffins, and a few single burials with indications of wrapping (see Supporting Information for information about the site; Van de Vijver, 2018; Van de Vijver et al., 2018). A total of 101 samples were collected (Table S1). In most individuals, five samples were collected from each individual ($n = 21$ humans), one from petrous bone and four from two long bones (either both upper or both lower limb bones). Material from the petrous bones used for the histological and collagen analyses was extracted from both b and c areas (inner ear) as reported in Pinhasi et al. (2015).

Statistical analysis was carried out using IBM SPSS v.24, and the significance level was set at $p = 0.05$. The nonparametric Mann–Whitney U and Kruskal–Wallis H tests were employed for non-normally distributed data.

2.2 | Histology

Forty-three transverse (long bones) and 18 longitudinal (petrous bones) 200-μm thin sections were prepared using an Exact 300 CL

diamond band saw (Table S1). The petrous bones were cut on the imaginary line drawn from the subarcuate fossa to the eminence between the jugular fossa and the cochlear canaliculus (Figure 1). This anatomical site intersects the inner ear into a medial part, which contains the cochlea, and a lateral part, which contains the semicircular canals and other orifices for nerve supply and vascularization.

The undecalcified thin sections were mounted onto glass microscope slides using Entellan New (Merck chemicals) for microscopy mounting medium and covered by a glass coverslip. Samples were examined under plane-polarized (PPL) and cross-polarized (XPL) transmitted light using a Leica DM750 optical microscope (total magnification: 40× to 400×). A Leica ICC50 HD camera was used to capture digital images with a capture resolution 2048 × 1536 pixels.

Six of the thin sections (MEC6, MEC9, MEC26, MEC55, MEC71, MEC90) were examined using scanning electron microscopy (SEM). This necessitated the removal of the coverslips in xylene and polishing the exposed sections with 7000 grit abrasive paper to remove excess mounting medium. They were then platinum-palladium coated under vacuum in an Eiko IB-2 ion coater to give an electrically conductive surface for subsequent SEM analysis. This was carried out at the National Museum of Natural Science, Taiwan, using a HitachiSU1510 in backscattered electron mode (BSE). The microscope was operated at 15 kV and 76 mA, with a working distance of approximately 16 mm.

The general histological index (GHI) introduced by Hollund et al. (2012) was used as a semiquantitative means to assess histological preservation. A GHI value of 5 represents excellent microstructural preservation similar to modern bone (>95% intact microstructure), whereas a GHI value of 0 indicates poor microstructural preservation (<5% intact microstructure) with almost no original histological features observed.

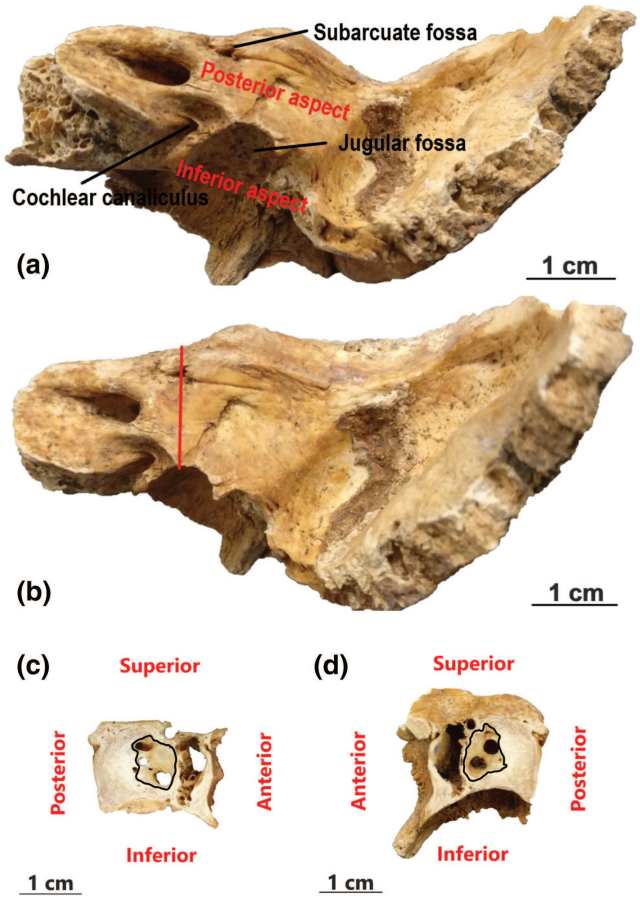

FIGURE 1 Longitudinal sectioning of a right human petrous bone—(a) Section cut from the subarcuate fossa to the eminence between the jugular fossa and the cochlear canaliculus, in a posterior–anterior direction as seen in b. (c) The medial piece that contains the cochlea. (d) The lateral piece that contains canals and other orifices for the vascular and nervous supply of the inner and middle ear. The areas of the inner ear (bony labyrinth) marked with black in (c) and (d) have been used for collagen extraction and stable isotope analysis [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Collagen and stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$)

Collagen was extracted from the cortical bone of 21 petrous bones and 80 long bones (21 individuals) (Table S1) using a modified Longin (1971) protocol as described in Kontopoulos, Penkman, Liritzis, and Collins (2019) (see Supporting Information for details). In brief, all samples were cut with a Dremel drill using a cutting wheel, the external bone surfaces were cleaned using a scalpel, and bone chunks of approximately 300–500 mg (samples from the inner ear part of the petrous bones collected from the tissue surrounding the cochlea and the semicircular canals; see Figure 1c,d) were demineralized in 8-ml 0.6-M HCl at 4°C. Following demineralization, the supernatant was removed and samples were rinsed with distilled water ×3. Gelatinization was carried out for 48 h in 8 ml pH 3 HCl at 80°C. The supernatant was filtered using Ezee™ filters and was freeze dried for 2 days. Extracted collagen was analyzed ×2 in a Sercon 20-22 mass spectrometer.

3 | RESULTS AND DISCUSSION

3.1 | Bone histology: Histotaphonomy-to-burial type

The histological preservation of archeological bones from single burials in coffins, single burials with indications of wrapping, and multiple burials show a variable picture. Distinct histological patterns can only be identified in the bones from coffin burials (Table S1). About 60% ($n = 19$) of those specimens display a black/dark brown coloration across the periosteal/subperiosteal and the endosteal/subendosteal tissues, accompanied by well-preserved areas of mesosteal tissue between the two stained zones ('sandwich pattern'; Figure 2; Figure S1–S3). When only long bones are assessed (i.e., excluding petrous bones), approximately 70% of the specimens exhibit the same pattern, which is explained by the more variable picture of the petrous bones (Figure S4). The stained tissues show a

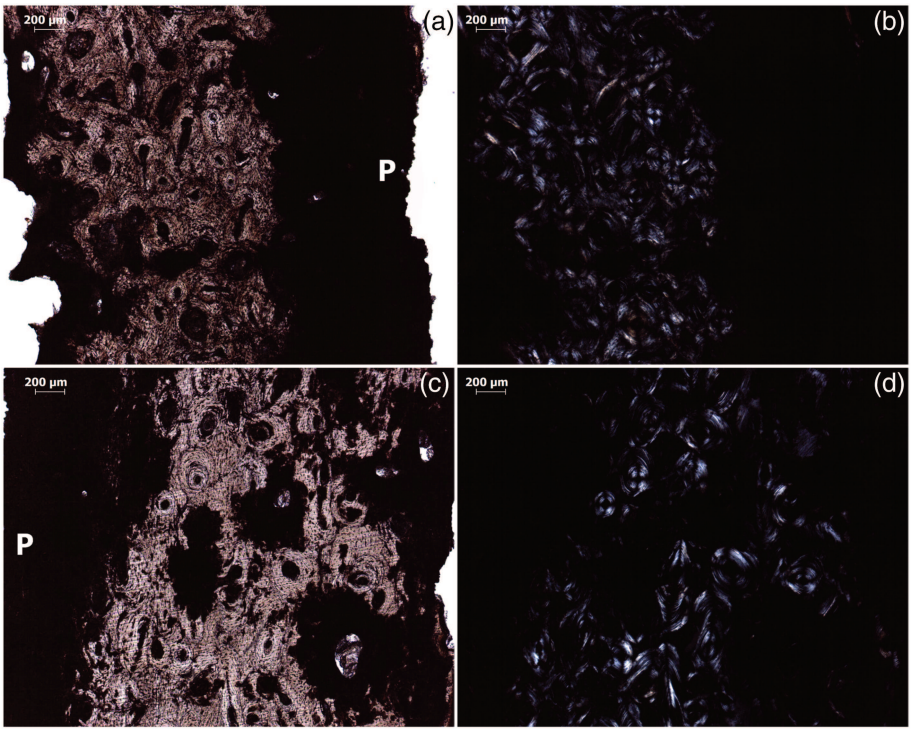

FIGURE 2 Histological modifications in long bones from coffin burials. Transverse sections. MEC51 (femur-distal diaphysis) under (a) PPL 40× and (b) XPL 40×. MEC71 (humerus-distal diaphysis) under (c) PPL 40× and (d) XPL 40×. Both specimens display the characteristic pattern observed in bones from burials in coffins. Loss of collagen birefringence is observed in degraded areas (b,d). P = periosteal tissue [Colour figure can be viewed at wileyonlinelibrary.com]

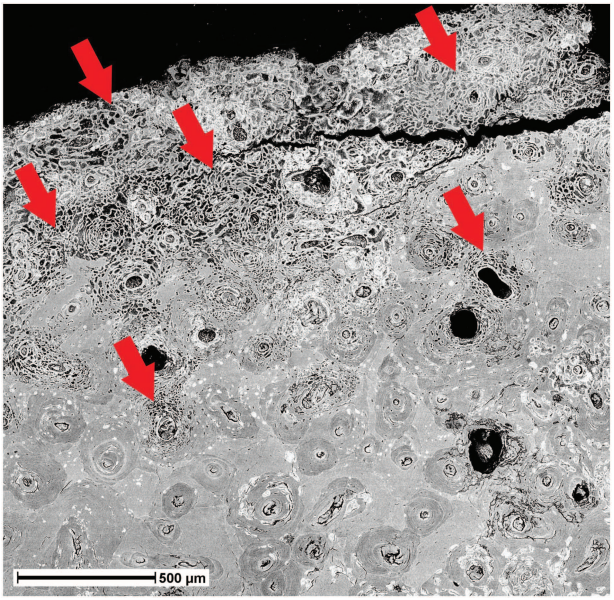

FIGURE 3 Histological modifications in long bones from coffin burials. Transverse section. MEC71 (humerus-distal diaphysis). Extensive bacterial tunneling in the dark stained areas (red arrows) that cannot be observed under light microscope. See Figure 2c for plane polarized image. Periosteal tissue is at the top of the image [Colour figure can be viewed at wileyonlinelibrary.com]

complete loss of collagen birefringence under cross-polarized light, whereas the well-preserved mesosteal tissue retains its collagen birefringence (Figure 2b,d). Extensive bacterial attack can also be identified in the stained areas (Figure 3; Figures S5 and S6).

From the remaining specimens, five that belong to the same individual display excellent histological preservation with some sections exhibiting orange/light brown staining (Figure S7). Any differences observed in the coffin burials should be related to the hydrological regime, depth, temperature, season of death, chronology, coffin wood, and so forth. Although wood can be preserved under favorable conditions for a long time, abiotic (e.g., hydrolysis, dehydration, and oxidation) and biological processes (microbial attack) gradually lead to its decay (Blanchette et al., 1991; Blanchette & Simpson, 1992; Crestini et al., 2009; Eriksson et al., 1990; Fink, 2017; Reinprecht, 2016).

A higher amount of tannins has been linked to increased durability of wood to degradation (Reinprecht, 2016; Scalbert, 1992). Tannin types (size, structure, solubility, color) and their concentration vary both between species and in wood from the same species growing in different locations (Janceva et al., 2016; Puech et al., 1999; Scalbert, 1992). Similarly, different parts of a wood (e.g., inner or outer heartwood and sapwood) have been found to contain different tannins in variable concentrations due to age-related variability (Brennan et al., 2020; Puech et al., 1999; Scalbert, 1992). Tannins have previously been linked to similar dark coloration of the exterior surfaces of bones from recent cemetery contexts (Schultz et al., 2003). Thus, the specific characteristics of the wood used to make a coffin and a variable exposure of bones to 'coffin wear' (the degradation of the skeletal remains when they come into direct contact with the coffin wood) could have a significant effect on bone degradation (Pokines & Symes, 2013; Reinprecht, 2016; Scalbert, 1992; Schultz et al., 2003).

Single burials with indications of wrapping (Figure 4) and multiple burials (Figure 5) show no specific histological pattern. Figure 4a shows the most common pattern for the wrapped burials, which is characterized by loss of collagen birefringence (Figure 4b) and

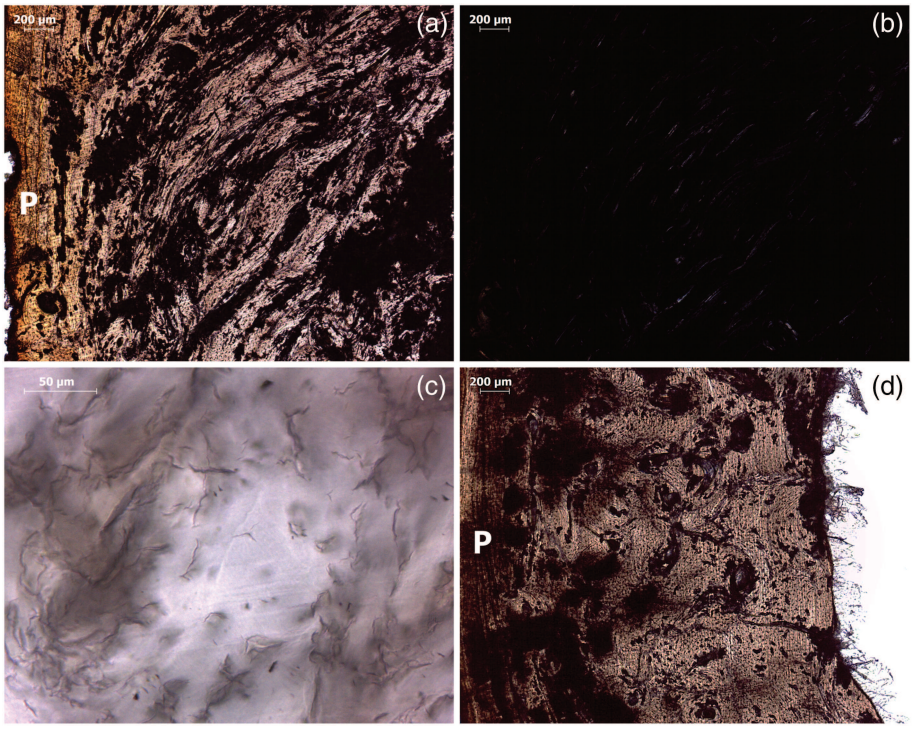

FIGURE 4 Histological modifications in long bones from wrapped single burials. Transverse sections. MEC7 (humerus-distal diaphysis): (a) PPL 40×; (b) XPL 40× showing a complete loss of collagen birefringence; and (c) PPL 400×: extensive microcracking in degraded areas. (d) MEC9 (radius-distal diaphysis) 40× PPL: dark staining in subperiosteal bone. Note the intraindividual variability. P = periosteal tissue [Colour figure can be viewed at wileyonlinelibrary.com]

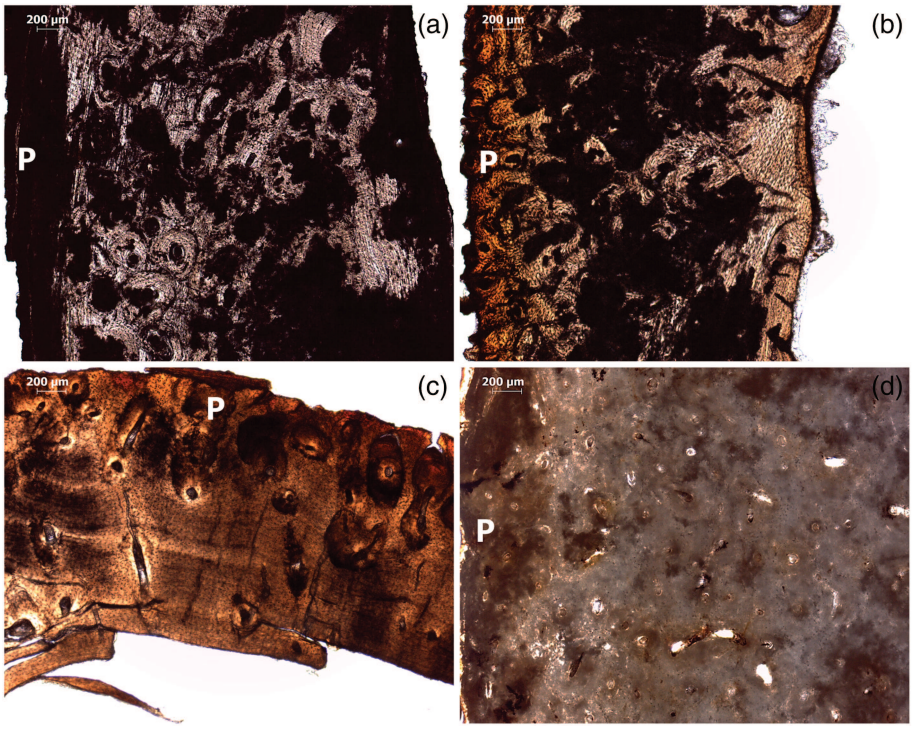

FIGURE 5 Histological modifications in long bones from multiple burials. Transverse sections. (a) MEC41 (humerus-distal diaphysis) PPL 40×: histological alterations analogous to coffined single burials. (b) MEC65 (humerus-proximal diaphysis) PPL 40×: histological modifications display a pattern opposite to coffin burials. (c) MEC43 (radius-distal diaphysis) PPL 40×: orange/brown staining throughout the section. (d) MEC75 (femur-proximal diaphysis) PPL 40×: generalized destruction throughout the section. P = periosteal tissue [Colour figure can be viewed at wileyonlinelibrary.com]

cracking in dark stained areas (Figure 4c). Samples from both groups may also exhibit dark stained subperiosteal tissue (Figure 4d), whereas patterns identical to coffin burials such as this seen in Figure 5a are not uncommon. Some samples may also display good histological preservation with orange/brown staining throughout (Figure 5c), or a total loss of histological integrity as seen in Figure 5d. It is noteworthy that the SEM images show variability in bacterial tunneling and cracking in the dark stained areas of these samples (Figures S8–S11).

Textiles used for wrapping/clothing the dead and fabric composition and decoration can significantly vary depending on the socioeconomic status of the dead, availability of sources (e.g., wool, silk, cotton, and leather), or technology. Wrapping cadavers has been

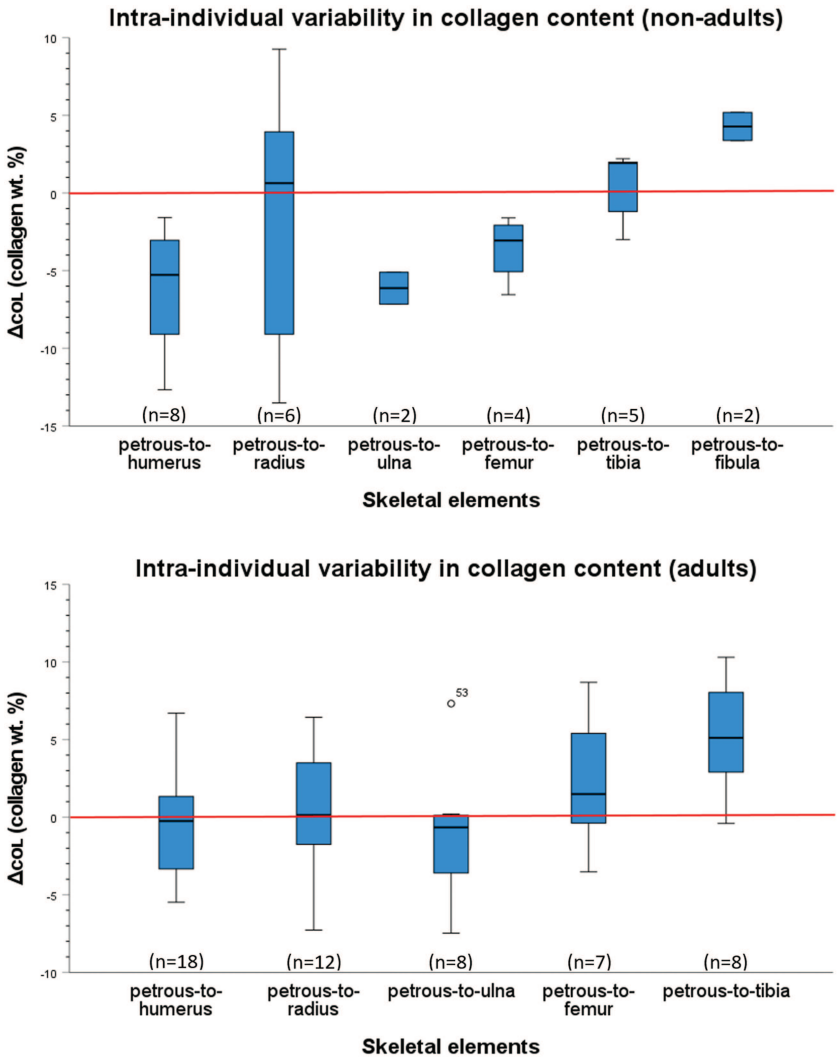

FIGURE 6 Intraindividual variability in collagen preservation. Box plots showing the difference (Δ_{COL} values) in collagen yields between the inner ear (petrous) and the other bones in nonadult (top) and adult (bottom) individuals. A larger positive collagen spacing (higher Δ_{COL} value) indicates a higher collagen content in the petrous bones compared with the other skeletal elements, and vice versa [Colour figure can be viewed at wileyonlinelibrary.com]

found to prolong soft tissue decay (Forbes et al., 2005; Lee Goff, 1992; Voss et al., 2011), whereas the degradation of different fabrics can considerably vary depending on fabric composition (Janaway, 2002, 2008; Ueland et al., 2017, 2019). It should thus be expected that the characteristics of the textiles used in a burial context might have an effect on bone histology.

Bone modifications in multiple burials can be further influenced by additional factors such as the position of the body (center or edges of burial, superimposed bodies or side-by-side, etc.) (Haglund, 2002). At Mechelen, these multiple burials were also found in many different layers (Van de Vijver et al., 2018), and burial depth is an important parameter; even at the same site, shallow versus deep burials experience differences in hydrology, oxygen availability, temperature fluctuations, microbial attack, and so forth (Hedges et al., 1995; Karkanas et al., 2000; Trueman et al., 2004). Finally, the lack of a specific pattern in these specimens may reflect differences in the treatment of the dead at St. Rombout's cemetery (wrapped or clothed placed within a coffin or not, etc.).

Sometimes intraindividual and intrabone variability can also be observed at St. Rombout (Figure S12). This highlights the importance of not making inferences about the funerary treatment an individual has received based on evidence from a single sample. For example, well-preserved specimens that exhibit dark stained subperiosteal tissue can be seen in both coffin (Figure S12d) and wrapped burials (Figure 4c) at St. Rombout. This pattern appears similar to those seen in bones from prehistoric Britain assumed to be intentionally mummified (Booth et al., 2015; Pearson et al., 2005), but it is also similar to bone thin sections of a modern pig buried in a mass burial for 7 years in Riseholme, UK (Kontopoulos et al., 2016).

Unfortunately, the lack of relevant detailed information from experimental taphonomic projects is a significant limitation on the effort to confidently link the effects of burial practices to bone histology. No experimental project has heretofore thoroughly and systematically investigated the effects of burial practices on bone preservation and the characteristics of the burial microenvironment. Consequently, future experimental analyses may help a deeper understanding of the sequence of the alterations observed in bone.

3.2 | Bone collagen wt.%, $\delta^{13}C$, and $\delta^{15}N$: Intraindividual (inner ear part of the petrous bone vs. long bones) and intrabone variability

The preservation of collagen (wt.%) shows high variability with values ranging from −13.51% to 10.31% and displays a very strong linear ($R^2 = 0.98$) correlation to GHI (Table S1; Figure S13). Some intraindividual differences can be observed in the Δ_{COL} petrous-to-other bones collagen (wt.%) spacing ($F(4,52) = 8.386$, $p = 0.000$). Overall, it seems that the inner ear part of the petrous bone outperforms femur, tibia, fibula, and ulna, which display much lower collagen yields, but it underperforms relative to humerus and radius (Figure S14). This is observed within the cohort assessed as a whole, and it is actually influenced by age-related variability (adult vs. nonadult: $t(78) = -1.956$, $p = 0.054$). In particular, in the majority of cases, the inner ear part of the petrous bone in the nonadult individuals exhibits lower collagen yields (Figure 6), whereas in adults, it seems to perform better than lower limb bones, with similar abundances seen relative to upper limb long bones (Figure 6).

The picture observed in nonadult individuals at St. Rombout's cemetery is unanticipated, as the inner ear bone would be expected to retain more collagen than long bones due to the increased porosity observed in the latter in vivo (Schnitzler & Mesquita, 2013). Cortical bone porosity is considered a major determinant of bone collagen preservation, as increased macroporosity and microporosity determine bone interaction with groundwater (Nielsen-Marsh & Hedges, 1999, 2000; Smith et al., 2002; Turner-Walker et al., 2002).

Nonadult long bones have been found to contain large primary osteons with large Haversian canal areas that give way to a higher number of secondary osteons but with a much smaller canal area in the young adult stage (Schnitzler & Mesquita, 2013). On the other hand, the inner ear part of the petrous bone contains a low number of osteons with small Haversian canals but a much higher number of osteocyte lacunae (Kontopoulos, 2018; Kontopoulos, Penkman, McAllister, et al., 2019). Collagen loss should be thus expected to be lower in the inner ear bone compared with the long bones in nonadults, despite its likely increased porosity in the 0.1- to 10-μm range (representing the lacuno-canalicular network). Therefore, there seems

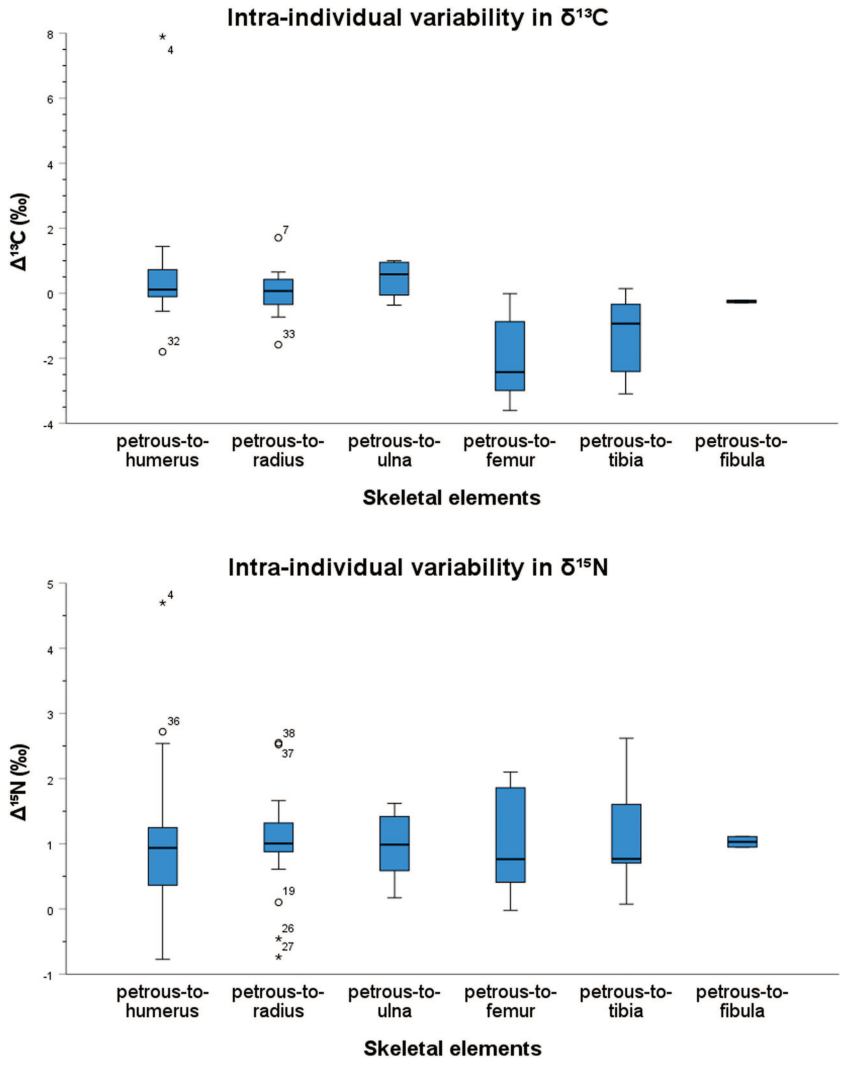

FIGURE 7 Box plots showing the spacing ($\Delta^{13}C$) in collagen $\delta^{13}C$ (top) and ($\Delta^{15}N$) in collagen $\delta^{15}N$ (bottom) values between the inner ear (petrous) and the long bones intraindividually. Number of samples as in Figure 6 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Isotope spacings

	All		Adults		Nonadults	
Skeletal elements	**$\Delta^{13}C$ (‰)**	**$\Delta^{15}N$ (‰)**	**$\Delta^{13}C$ (‰)**	**$\Delta^{15}N$ (‰)**	**$\Delta^{13}C$ (‰)**	**$\Delta^{15}N$ (‰)**
Petrous-to-humerus	0.14 ± 0.67	0.80 ± 0.87	−0.44 ± 0.64	0.45 ± 0.66	0.63 ± 0.50	1.71 ± 0.67
	NI = 14; NS = 26		NI = 10; NS = 18		NI = 4; NS = 8	
Petrous-to-radius	0.05 ± 0.70	1.02 ± 0.84	−0.23 ± 0.57	0.64 ± 0.66	0.62 ± 0.60	1.78 ± 0.63
	NI = 9; NS = 18		NI = 5; NS = 10		NI = 4; NS = 8	
Petrous-to-ulna	0.45 ± 0.53	1.00 ± 0.49	−0.33 ± 0.54	0.87 ± 0.46	0.90 ± 0.08	1.52 ± 0.14
	NI = 5; NS = 10		NI = 4; NS = 8		NI = 1; NS = 2	
Petrous-to-femur	−1.94 ± 1.26	1.00 ± 0.78	−1.35 ± 1.17	1.01 ± 0.70	−2.97 ± 0.53	0.97 ± 1.03
	NI = 6; NS = 11		NI = 4; NS = 7		NI = 2; NS = 4	
Petrous-to-tibia	−1.33 ± 1.15	1.11 ± 0.71	−0.96 ± 1.14	1.14 ± 0.72	−1.92 ± 0.99	1.06 ± 0.77
	NI = 7; NS = 13		NI = 4; NS = 8		NI = 3; NS = 5	
Petrous-to-fibula	−0.25 ± 0.05	1.03 ± 0.12	N/A	N/A	−0.25 ± 0.05	1.03 ± 0.12
	NI = 1; NS = 2				NI = 1; NS = 2	
Average	−0.38 ± 1.18	0.96 ± 0.76	−0.34 ± 0.94	0.73 ± 0.68	−0.47 ± 1.59	1.42 ± 0.73

Note: Average inner ear (petrous) bone to long bones $\Delta^{13}C$ (‰) and $\Delta^{15}N$ (‰) offsets in the adults, nonadults, and whole sample set (excluding MEC6 outlier). NI: number of individuals; NS: number of samples. 1σ standard deviation.

to be an inconsistency between an increased in vivo porosity assumed for the long bones in nonadult individuals, and their better performance relative to the inner ear bone in collagen preservation. On the contrary, the picture for the adult individuals is more clear, as our data indicate that the inner ear bone yields similar or higher amounts of collagen (wt.%) relative to long bones.

The inner ear bone collagen $\delta^{13}C$ and $\delta^{15}N$ signals consistently differ from those of the upper and lower limb long bones (Figure 7; Table 1), while all samples fall within the accepted range for C:N, %C, and %N (Table S1). The $\delta^{13}C$ values appear depleted in the inner ear of the petrous pyramid relative to all other long bones by −0.38 ± 1.18‰ on average (excluding MEC6 outlier due to low C/N, %C and %N), with $\Delta^{13}C$ offsets ranging from −3.6‰ to 1.71‰ (Table 1; Table S1). The $\Delta^{13}C$ spacings ($\Delta^{13}C = \delta^{13}C_{petrous\_bone} - \delta^{13}C_{long\_bone}$) do not display the same pattern intraindividually ($\chi^2(4) = 35.754$, $p = 0.000$) as the offsets of the petrous-to-lower limb long bones appear negative, while the petrous-to-upper limb long bones $\Delta^{13}C$ values are slightly positive (Table 1). This seems to be primarily affected by the nonadult individuals as the inner ear bone in adults is consistently depleted on average in $\delta^{13}C$ relative to both upper and lower limb long bones with offsets ranging from −3.03‰ to 1.0‰ (Table 1; Figure S15). However, this age-related variability in $\Delta^{13}C$ observed in the individuals from St. Rombout's cemetery is not statistically significantly different ($U = 613.000$, $z = -0.793$, $p = 0.428$).

On the contrary, the $\Delta^{15}N$ offsets ($\Delta^{15}N = \delta^{15}N_{petrous\_bone} - \delta^{15}N_{long\_bone}$) appear homogeneous intraindividually ($\chi^2(4) = 1.347$, $p = 0.853$) with the inner ear bone demonstrating an average enrichment of 0.96 ± 0.76‰ (−0.77‰ to 2.70‰ range, excluding MEC6 outlier) relative to long bones (Figure 7). The $\Delta^{15}N$ enrichment is significantly higher in nonadult individuals than in adults ($U = 310.000$, $z = -3.954$, $p = 0.000$) with offsets ranging from −0.77‰ to 2.62‰ in the former group and from −0.02‰ to 2.70‰ in the latter, excluding MEC6 outlier (Figure S16).

Our results confirm that the inner ear bone of the petrous pyramid is an extraordinary skeletal element with remodeling proceeding in a different manner compared with long bones (Bast, 1932; Doden & Halves, 1984; Ekdale, 2010; Kontopoulos, 2018; Kontopoulos, Penkman, McAllister, et al., 2019; Toyoda et al., 2015). Jørkov et al. (2009) have observed a similar picture for the petrous-to-femora and petrous-to-ribs offsets, while the petrous bone $\delta^{13}C$ and $\delta^{15}N$ values were also found to be close to the permanent first molar dentine isotopic composition (cemento-enamel junction area) (Jørkov et al., 2009). Because this part of the first molar dentine is assumed to reflect the dietary input from about 3 to 5 years old (Henderson et al., 2014), Jørkov et al. (2009) have suggested that the petrous bone collagen encapsulates in utero, infancy, and perhaps early childhood isotopic signals.

3.3 | Inner ear (petrous) bone offsets and the extent of remodeling

What can the differences in isotope values between skeletal elements reveal about the rate of turnover in the inner ear part of the petrous bone? We will consider three alternative scenarios (Figure 8).

3.3.1 | Scenario 1: No remodeling after birth

It is generally believed that the inner ear bone is fully developed in utero not only in humans (no remodeling after birth) but also in several animal species (Jeffery & Spoor, 2004; Richard et al., 2010, 2017). In this *scenario 1*, the inner ear bone collagen $\delta^{13}C$ and $\delta^{15}N$ values

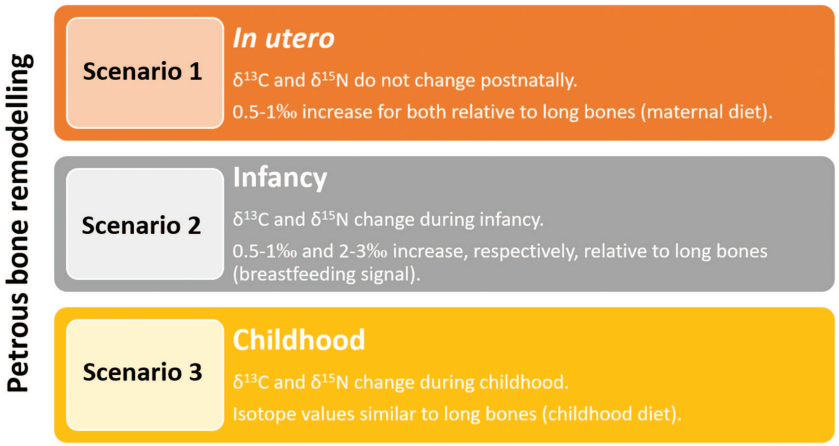

FIGURE 8 The three different scenarios for the inner ear (petrous) bone remodeling [Colour figure can be viewed at wileyonlinelibrary.com]

should thus remain unchanged postnatally. This means that its isotopic signals would be similar or slightly increased (approximately 0.5–1‰ for both $\delta^{13}C$ and $\delta^{15}N$) compared with those of the mother, as the fetus relies primarily on the mother's placenta for nutrients (de Luca et al., 2012; Fuller et al., 2004, 2006; Herrscher et al., 2017; Jenkins et al., 2001; Lübcker et al., 2020).

The bone collagen isotopic record in long bones reflects a multiyear average of the isotope composition of the food protein eaten over the last several years of life (Hedges & Reynard, 2007; Katzenberg, 2008). If no bone remodeling takes place in the inner ear postnatally, variability would be expected to be seen in our individuals' $\Delta^{13}C$ and $\Delta^{15}N$ offsets (petrous-to-long bones difference). This small initial in utero enrichment in $\delta^{13}C$ and $\delta^{15}N$ may often be masked due to small differences in the dietary habits of the child (long bones signal) relative to the mother (inner ear bone signal) (Dufour et al., 1999; Heaton, 1999; Hedges & Reynard, 2007; Lee-Thorp, 2008; Richards & Hedges, 1999). However, it has to be noted that the sampling position may influence bone collagen isotopic values when there is within-bone isotopic heterogeneity (Matsubayashi & Tayasu, 2019).

3.3.2 | Scenario 2: Remodeling during infancy

Some researchers support a further development/remodeling of the inner ear during infancy (Costeur et al., 2017; Doden & Halves, 1984; Ekdale, 2010). For an exclusively breastfed infant, its bone collagen nitrogen isotopic composition are directly related to that of mother's milk and increased by approximately 2–3‰ relative to the maternal nitrogen values (Beaumont et al., 2018; Fuller et al., 2003, 2006; Schurr, 1998). The elevated $\delta^{15}N$ values in infants eventually drop to or near the maternal levels when weaning is completed (Reynard & Tuross, 2015; Schurr, 1998). In this *scenario 2*, the inner ear bone $\delta^{15}N$ values should remain elevated relative to long bones due to the capture of the breastfeeding signal and the subsequent cessation of remodeling at around the age of 2 years.

An indication of trophic level change due to breastfeeding is also an increase of approximately 0.5–1‰ in the bone collagen carbon isotopic record (Beaumont et al., 2018; Fuller et al., 2003, 2006). The shift in $\delta^{13}C$ values toward the adult levels is completed at a faster rate compared with $\delta^{15}N$ values (Fuller et al., 2006) as the carbon pool is also influenced by glucose and lipids (de Luca et al., 2012). Therefore, unlike $\delta^{15}N$ values, it should not necessarily retain the offset relative to the $\delta^{13}C$ values in long bones.

3.3.3 | Scenario 3: Remodeling during childhood

Finally, Bast (1932) has argued that there is undoubtedly some growth change in parts of the petrous bone during early childhood as the shape and size of the adult petrous bone is not the same with that of fetuses or neonates. Based on the comparison to the permanent first molar dentine isotopic composition, Jørkov et al. (2009) have also argued that the inner ear continues remodeling in childhood. In this *scenario 3*, the inner ear bone isotopic composition should appear similar or identical to that of the long bones, as the continuous remodeling throughout childhood would have eliminated any differences attributed to breastfeeding.

The $\delta^{15}N$ values at St. Rombout's cemetery indicate that scenario 2 is most probable. Our data also display a noteworthy feature. When the $\delta^{15}N$ value in the inner ear is >12‰, all nine adult and nonadult individuals exhibit an enrichment of 1.33 ± 0.57‰ relative to long bones (range: 0.63‰ to 2.72‰). This likely indicates that when bone $\delta^{15}N$ values in the inner ear reach high levels due to an incorporated breastfeeding signal (trophic level increase), a diet with marine fish as a staple food would be required for the child to maintain an approximately 2–3‰ increase in the $\delta^{15}N$ values of long bones when weaning takes place (Hedges & Reynard, 2007). As a result, the $\Delta^{15}N$ offset can remain positive throughout an individual's life. We therefore presume that the inner ear bone actually records the nitrogen isotope signals during the first approximately 2–3 years of an individual's life. This would also explain a possible drop in the inner ear $\delta^{15}N$ values related to an incorporation of the isotopic signal of food during weaning, which results in the average approximately 1.0–1.5‰ offset at St. Rombout's cemetery.

However, variable breastfeeding and weaning practices could also have an effect on the $\Delta^{15}N$ offsets (e.g., different time at weaning or less breastfeeding) as fluctuations attributed to such events have been observed in the $\delta^{15}N$ values of permanent molar teeth (Henderson

et al., 2014). Variable nitrogen metabolism and environmental circumstances can also be an issue of some inconsistency (Hedges & Reynard, 2007; Polischuk et al., 2001; Tsutaya & Yoneda, 2015), with fluctuations in mother's $\delta^{15}N$ values related to her health status during gestation being recognized as another factor affecting fetal bone $\delta^{15}N$ (Burt & Garvie-Lok, 2013; Fuller et al., 2004).

Our data are not consistent with either scenario 1 or scenario 3. With reference to scenario 1, the $\Delta^{15}N$ offsets should be often negative (more variability due to the small or none in utero enrichment). However, negative $\Delta^{15}N$ offsets represent only the 7% of the variation in St. Rombout's cemetery. Regarding scenario 3, an average increase of (a) 1.0 ± 0.10‰ ($\Delta^{15}N$ offset range: 0.93‰ to 1.11‰; Table S1) can be seen in the inner ear bone $\delta^{15}N$ value relative to long bones in the 1–5 year old individual (MEC84–87); (b) 1.47 ± 0.11‰ offset ($\Delta^{15}N$ offset range: 1.39‰ to 1.62‰; Table S1) in a 12–17 years old individual (MEC 79–83); (c) 2.13 ± 0.34‰ offset ($\Delta^{15}N$ offset range: 1.88‰ to 2.62‰; Table S1) in an 18–25 years old individual (MEC74–88); and (d) enriched inner ear bone $\delta^{15}N$ by 1.38 ± 0.20‰ ($\Delta^{15}N$ offset range: 1.17‰ to 1.57‰; Table S1) in an old adult female >50 years.

Consequently, if remodeling would continue during childhood (scenario 3), the $\Delta^{15}N$ offsets should be close to zero in the teenager, young adult, and old adult individuals due to the complete loss of any breastfeeding signals. The only alternative explanation would be a shift in diet in all individuals in the years following the cessation of inner ear bone remodeling, which seems a rather unlikely scenario with current evidence. It is noteworthy that a similar pattern is observed in the 6–11 year old individual, four out of five individuals of 12–17 years old, and all but one adult individual (Table S1).

Concerning the $\Delta^{13}C$ spacings, the patterns seen here are rather unusual. While the positive $\Delta^{13}C$ offsets in nonadult upper limb long bones would be in line with a record of breastfeeding signals in the inner ear, it is difficult to understand what causes the depletion in the inner ear $\delta^{13}C$ values relative to long bones in adults, and lower limb long bones in nonadults. One possible explanation for this phenomenon could be the different remodeling rates between the non-load-bearing upper limb long bones and the load-bearing lower limb long bones (Manolagas, 2000; Mitton et al., 2019). The nonadult negative offsets could also be due to the variable contribution of milk lipids in the carbon pool. In that case, an identical pattern has been observed in the plasma of polar bear cubs when milk was their only diet (Polischuk et al., 2001). The cubs were found isotopically depleted in $\delta^{13}C$ by 0.8‰ and enriched in $\delta^{15}N$ by 1.0‰ over that of their mothers (Polischuk et al., 2001). This negative enrichment between the mother and the infant in $\delta^{13}C$ could be related to breast milk composition (enriched in lipids) as milk lipids have depleted $\delta^{13}C$ relative to milk proteins (Ballard & Morrow, 2013; Jenness, 1979; Polischuk et al., 2001).

The variability observed in the $\Delta^{13}C$ offsets at St. Rombout's cemetery could also be partly explained by the variations observed in the $\delta^{13}C$ values of the human maternal milk, which can range from approximately −27.5‰ to approximately −25‰ in the first half year, whereas variations up to 1‰ can be seen even within the same day (Herrscher et al., 2017). It is also possible that the maternal fat stores that build up during gestation become available to the fetus during the third trimester resulting in raised blood lipid levels, which can alter the mother's $\delta^{13}C$ (Beaumont et al., 2015) and result in the depleted inner ear bone $\delta^{13}C$ values during its formation. Finally, severe physical stress and/or growth disturbances, which have been observed in individuals from this assemblage (Van de Vijver, 2018) could have caused some of the variability observed in nonadults. Nevertheless, no explanation can be provided with confidence for the intraindividual differences in upper and lower limb long bone isotopic signatures.

No statistically significant intrabone differences (i.e., proximal-to-distal diaphysis offset) can be detected in the long bones from St. Rombout's cemetery for either collagen wt.% (Figure S17), $\delta^{13}C$ (Figure S18), or $\delta^{15}N$ (Figure S19), with the only exception being one nonadult individual (MEC5–9; Table S1). Waters-Rist and Katzenberg (2009) have previously reported similar insignificant intrabone differences in $\delta^{15}N$ of the diaphysis, epiphysis, and metaphysis in nonadult long bones, as well as between faster versus slower growing metaphyses. Therefore, although each person can experience individual episodes of abrupt growth and periods of no growth related to genetic and environmental factors (Beaumont et al., 2018), sampling different anatomical sites across a long bone's diaphysis has no significant effect on the retrieved isotopic signal in St. Rombout's cemetery.

4 | SUMMARY

- This is the first study to report an association between specific funerary practices and characteristic histological modifications identified in bones. Distinct histological patterns are observed in bones from single coffin burials with dark coloration and extensive bacterial attack across the periosteal/subperiosteal and the endosteal/subendosteal tissues, and well-preserved mesosteal tissue ('sandwich pattern').
- Single burials with indications of wrapping and multiple burials show more variable histological patterns.
- Intraindividual and intrabone variability in bone histology underscore the importance of avoiding assumptions about funerary treatment based on a single sample.
- The inner ear bone collagen $\delta^{13}C$ and $\delta^{15}N$ reflect the dietary input of the first approximately 2–3 years of life (i.e., in utero development and infancy remodeling). Nitrogen isotope signals maintain an average increase of approximately 1‰ relative to long bones. The picture for $\delta^{13}C$ is more complex.
- The inner ear bone shows similar or better collagen preservation relative to long bones in adult individuals.
- Long bone proximal and distal diaphyses display insignificant differences in $\delta^{13}C$ and $\delta^{15}N$ but can yield different amounts of collagen.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the suppporting information of this article. Any additional data are available from the corresponding author upon reasonable request.

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