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RESEARCH ARTICLE

Diseases and Traumas of Pleistocene Megafauna: A Perspective From Poland

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ABSTRACT

Analysis of pathologies can shed light on the health, trauma, and disease states of animals in the past. This study aims to explore the health status of megafauna during the Pleistocene and Holocene in Poland and to elucidate the diseases afflicting them, in order to gain a broader picture of the physical condition of these animals. For this purpose, species that show pathological lesions were macroscopically studied, and CT images were used for reconstruction. These results are supplemented with previously published data. Our results show cases of traumatic lesions, inflammatory diseases, arthropathies, diseases associated with the environment, dental anomalies and oral pathology, congenital anomalies and inherited disorders, and others. Lesions were found on the skeletal elements of woolly rhinoceroses, woolly mammoths, aurochs, bovids, giant deer, elks, and bears. The diversity of pathological cases and taxa demonstrated here is the first contribution to empirical pathological research in Polish paleozoology dealing with Quaternary records. Besides this, the research presented in this paper contributes to building a bridge between paleozoology and zooarcheology in support of what we call the "one pathology" concept.

1 | Introduction

The study of quaternary faunal remains contributes to our knowledge of the taxonomic structure of the assemblages and, on the basis of these, to the question of faunal exchange over time (Koufos, Kostopoulos, and Vlachou 2005). The osteometric approach leads to the determination of animal morphotypes (i.e., Stefaniak et al. 2014). By taking taphonomic aspects into account, we can establish hominid subsistence strategies (Huguet et al. 2013; Rendu et al. 2019; Yravedra-Sainz de los Terreros et al. 2016), their use of the environment (Wolfhagen et al. 2020), and some depositional aspects (Hrynowiecka et al. 2022; Pawłowska 2010). Extended studies using DNA signatures also make it possible to detect genetic changes in a population (Hofreiter and Stewart 2009; Mattucci et al. 2016). Dating methods, particularly radiocarbon dating, allow us to study the temporal and spatial dispersion of animals, particularly at the Pleistocene–Holocene boundary; this has been associated with faunal reductions and extinctions (Ceregatti et al. 2023; Ugan and Byers 2007, 2008).

Paleopathological evidence can help determine the past condition of particular animal individuals and to some extent the population (Brothwell 2008; Bartosiewicz 2021; Holmes, Thomas, and Hamerow 2021; Upex and Dobney 2012). However, not every study includes the study of pathological lesions, not every lesion can be easily attributed to a disease, and not all diseases leave an imprint on skeletal parts that are represented

TABLE 1 | The pathological specimens from Pleistocene and Holocene contexts in Poland used in this study.

Site	Site chronology	Taxon	Element	Inventory number	Pathological lesions and classification	References
Chlewice	Holocene	*Alces alces*	Antler	—	Trauma	This study
Koło	Holocene	*Alces alces*	Antler	UAM/IG/KP/21.F1	Healed trauma/ Developmental disorder	This study
Zaniemyśl	Late Pleistocene	*Mammuthus primigenius*	Ulna	—; KP/4.F1	Periostitis	This study
Mosina	Late Pleistocene	*Mammuthus primigenius*	Upper M3	KP/112.F1	Dental hypoplasia	This study
Pyskowice	Pleistocene	*Mammuthus primigenius*	Thoracic vertebra	UAM/IG/KP/39.F2	Inflammation/ Congenital anomaly	This study
Ławy and unknown locality	Late Pleistocene	*Mammuthus primigenius*	Two lower M3; upper M3	MZ VIII/Vm 861, MZ VIII/Vm 862 and MZ VIII/Vm 76	Developmental disorders	Hrynowiecka et al. (2018) & This study
Barycz	Late Pleistocene	*Megaloceros giganteus*	Antler	UAM/IG/KP/12.F1	Antler malformation	Pawłowska, Stefaniak, and Nowakowski (2014)
Szczęśliwickie Lake	Late Pleistocene	*Coelodonta antiquitatis*	Axis	MUZ.PIG 1451.II.1–2	Blood vessels or to post-mortem modifications	This study
Szczęśliwickie Lake	Late Pleistocene	*Bos/Bison*	Ulna	MUZ.PIG 1451.II.15	Entheseal reaction	This study
Kadzielnia	Late Pleistocene	*Ursus sp.*	Metacarpal II	MUZ.PIG 39.II.28	Entheseal reaction	This study
Kadzielnia	Late Pleistocene	*Ursus spelaeus*	Maxilla and teeth	MUZ.PIG 39.II.12	Caries	This study
Góra Winnica near Kamień Mściowski	Late Pleistocene	*Mammuthus primigenius*	Lower M2	MUZ.PIG 40.II.9	Caries	This study
Wiercica cave	Late Pleistocene	*Bos/Bison*	Metatarsus	MUZ.PIG 335.II.14	Periostitis	This study
Wiercica cave	Late Pleistocene	*Alces alces*	Metatarsus	MUZ.PIG 335.II.18	Entheseal reaction; buttresses; trauma	This study
Sitkówka	Middle to Late Pleistocene (MIS 11 and MIS 5d–2)	*Ursus spelaeus/ Ursus deningeri*	Femur	MUZ.PIG 157.II.6	Entheseal reaction; inflammatory arthritis	This study
Sitkówka	Middle to Late Pleistocene (MIS 11 and MIS 5d–2)	*Ursus spelaeus/ Ursus deningeri*	Humerus	MUZ.PIG 157.II.40	Entheseal reaction; inflammatory arthritis	This study

in records (Pawłowska 2018). By focusing on opportunities rather than on limitations, this paper aims to trace diseases and injuries of Polish megafauna—that is, of the largest terrestrial species in the Quaternary community or ecosystem. Tracing is possible due to recent faunistic studies at several sites in Poland, which have revealed the presence of mammalian remains, from the Middle Pleistocene to the early Holocene, which display pathological or adaptive changes in bone tissue (Pawłowska 2022, 2023; Pawłowska et al. 2022; Puzachenko, Markova, and Pawłowska 2022). Their origins in a range of taxa, such as woolly rhinos (*Coelodonta antiquitatis*), woolly mammoths (*Mammuthus primigenius*), bovids (*Bos*/*Bison*), giant deer (*Megaloceros giganteus*), elks (*Alces alces*), and bears (*Ursus spelaeus/Ursus deningeri*), make this the first contribution to empirical pathological research in Polish paleozoology dealing with Quaternary records. Beside this, the research here contributes to building a bridge between paleozoology and zooarchaeology in support of what we call the "one pathology" concept.

2 | Material and Methods

The subjects of the study were fossil and subfossil mammalian remains from sites in Poland that displayed macroscopic pathological changes. The specimens are indirectly dated through the context to the Pleistocene and Holocene.

The specimens are part of museum and institutional collections, such as that of the Polish Geological Institute–National Research Institute (PGI-NRI henceforth) in Warsaw, the Museum of Myślibórz Lake District, the Institute of Geology at Adam Mickiewicz University in Poznań (UAM/IG/KP), the Faculty of History at Adam Mickiewicz University in Poznań, the Archaeological Museum in Giecz, and the Polish Academy of Sciences Museum of the Earth in Warsaw. These collections were examined as part of the basic research component of various project, including a PGI-NRI project, by one of us (KP). In these examinations, specimens with pathological lesions were classified and selected for detailed examination, which was carried out in collaboration with the Division of Animal Anatomy (DP and ACH) of the Faculty of Veterinary Medicine, Wrocław University of Environmental and Life Sciences. All pathological changes were documented and examined in line with the rules of differential diagnosis used in veterinary medicine (Madej and Rotkiewicz 1998; Madej, Rotkiewicz, and Nozdryn-Płotnicki 2007). Moreover, the use of computed tomography (CT) allowed the construction of full 3D images of the specimens, making it possible to present the internal structure of

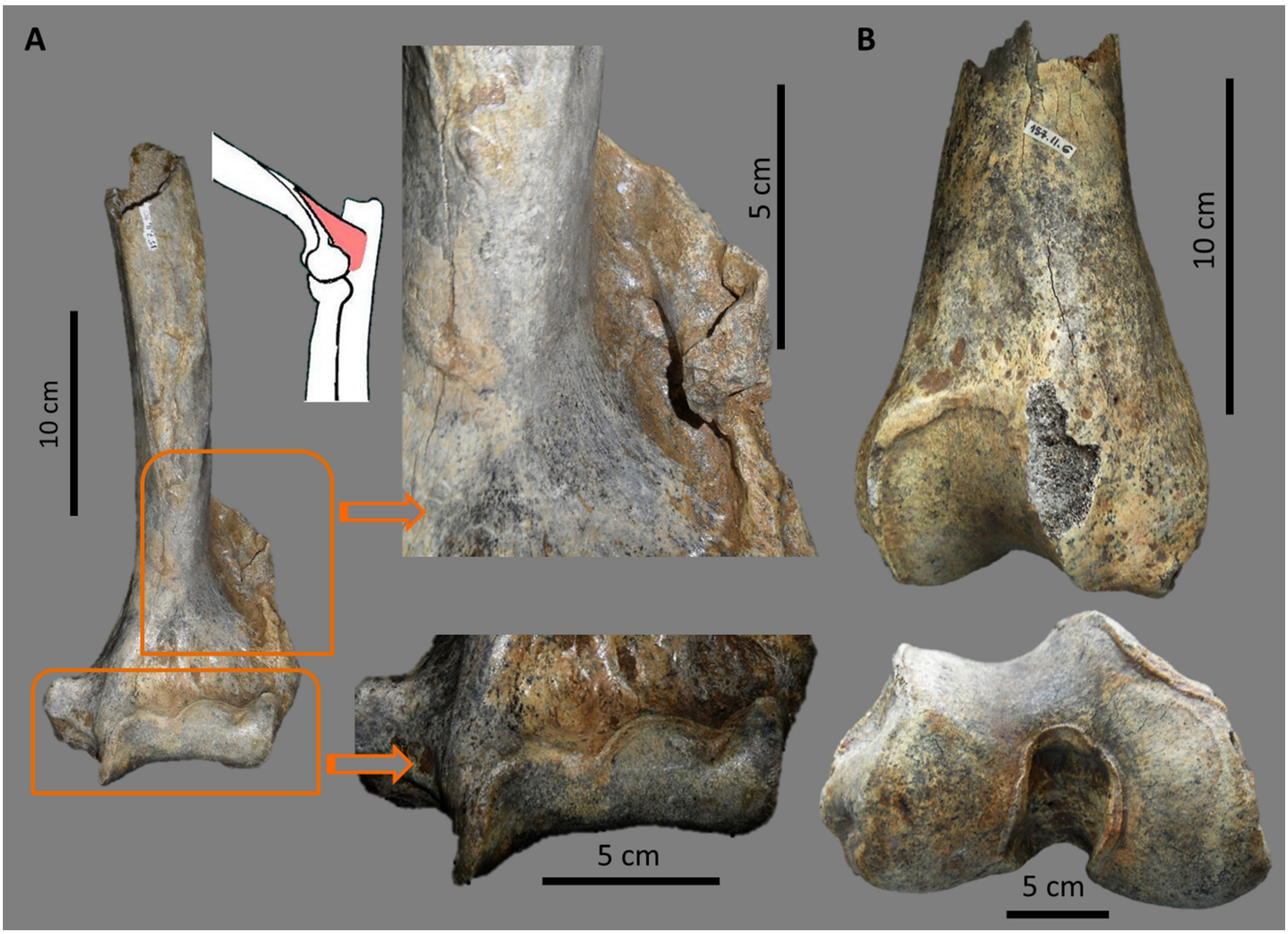

FIGURE 1 | The Sitkówka site: (A) bear humerus with exostoses and (B) bear femur with lipping (photo by K. Pawłowska). [Colour figure can be viewed at wileyonlinelibrary.com]

skeletal remains and to evaluate the visible bone tissue changes. CT analysis was carried out at the Department and Clinic of Surgery, Faculty of Veterinary Medicine, Wrocław University of Environmental and Life Sciences (DKN, WB). A 64-slice 128-layer Siemens go. TOP CT scanner was used for radiological examination. The specimens were scanned along the longitudinal axis of the bones in the cranial and caudal directions, with the exposure parameters set to 120 kV and 60 mAs. Cross-sectional imaging was carried out using a bony window and bone filter with a layer thickness equaling 0.8 mm. The CT images were postprocessed using the Siemens Syngo.via software. We used the image multiplanar reconstruction function in sagittal, dorsal and transverse sections, and the three-dimensional image function.

3 | Results

Pathological changes were found on 16 specimens from 11 sites. The sites are presented here chronologically from the oldest to the youngest.

3.1 | Sitkówka

A bear (*U. spelaeus/U. deningeri*) humerus (MUZ.PIG 157.II.40) displays an entheseal spur on the lateral supracondylar ridge (*crista supracondylaris lateralis*)—that is, at the insertion of the anconeus muscle, one of the extensors of the elbow joint that functionally cooperates with the lateral cubital collateral ligament (*ligamentum collaterale laterale*); there is also marginal lipping on the articular surface (Table 1 and Figure 1A).

Marginal lipping of the articular surface of the distal epiphysis was observed in a bear (*U. spelaeus/U. deningeri*) femur (MUZ.PIG 157.II.6) from Sitkówka site (Table 1 and Figure 1B).

3.2 | Wiercica Cave

Two metatarsal bones with pathological changes come from Wiercica cave. An elk (*A. alces*) metatarsal bone (MUZ.PIG 335.II.18) displays an entheseal reaction on the lateral side of

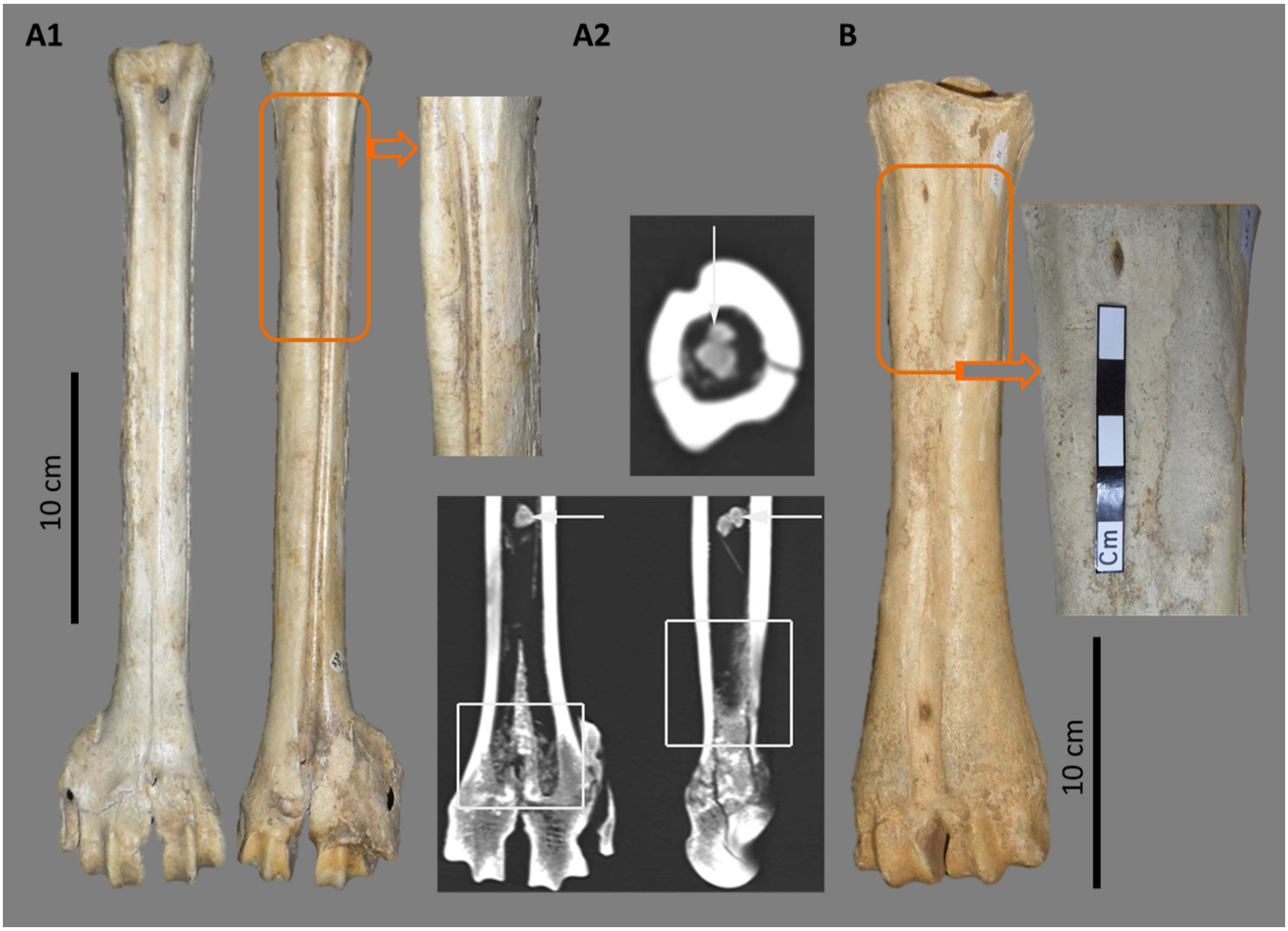

FIGURE 2 | Wiercica Cave. Photo (A1) and CT scan (A2) of elk metatarsal with an entheseal reaction on the distal end and buttresses on the shaft. A coronal (lower left), transverse (lower right), and sagittal (upper) CT images (bone window) of metatarsal bone are shown; (B) large Bovidae metatarsal with periostitis (photo by K. Pawłowska). [Colour figure can be viewed at wileyonlinelibrary.com]

the distal epiphysis of the bone (Table 1 and Figure 2A1, A2). In addition, the dorsal and plantar surfaces of the metaphysis have developed buttresses (Figures 2A1,2). One third of the way along the metatarsal bone, in the middle part of the medullary cavity, a very hyperdense, well-demarcated area with irregular edges is visible under CT scan. The lesion does not damage the cortical layer (Figure 2A2). Moreover, the distal extremity shows moderate hyperdense areas (Figure 2A2).

The metatarsal bone of a large bovid (MUZ.PIG 335.II.14) has a smooth lesion on the dorsal and plantar surfaces of the bone's metaphysis, with well-defined margins (Table 1 and Figure 2B1, B2). This plaquelike sheet over the cortex is a function of the production of new periosteal bone, quite solid in structure, and not a taphonomic exfoliation of the cortical part of the bone, which is usually observed as a result of weathering.

3.3 | Góra Winnica, Near Kamień Mściowski

A woolly mammoth (*M. primigenius*) lower M2 (MUZ.PIG 40.II.9) with quite significant cavities was found at the Góra Winnica site near Kamień Mściowski (Table 1 and Figure 3). The cavities are 1.5 cm deep and are associated with a few lamellae (Figure 3). The degree of wear on the occlusal surface of the tooth indicates that the mammoth was an adult at its death.

3.4 | Kadzielnia

The collection of Pleistocene fauna from the Kadzielnia site (Woroncowa-Marcinowska et al. 2017) included a bear (*U. spelaeus*) maxilla fragment with P4-M2, with the M2 displaying a cavity (MUZ.PIG 39.II.12; Table 1 and Figure 4A1, 4A2). An area of hypodensity was seen around the apex of the tooth root under CT scan (Figure 4A2).

The formation of new bone tissue is visible on the dorsal part of the shaft of the second metacarpal of a bear (*Ursus* sp.) (MUZ.PIG 39.II.28; Table 1 and Figure 4B), the second specimen from this site, in the insertion of radial carpal extensor muscle (*m. extensor carpi radialis*).

3.5 | Szczęśliwickie Lake

The ulna bone of a bison or aurochs from the Szczęśliwickie Lake site (MUZ.PIG 1451.II.15) is characterized by an entheseal reaction on the medial surface (Table 1 and Figure 5A). The area near the ulnar trochlear notch is the insertion point of the collateral (humerus–ulna) and transverse ligaments (radius–ulna).

The cervical vertebra (axis) of the woolly rhinoceros (*C. antiquitatis*) (MUZ.PIG 1451.II.1-2) from this site has curly furrows on the vertebral arch that are roughly symmetrical with respect to each other (Table 1; Figure 5B1). A texture of some sort is visible within these marks (Figure 5B1, B3). A hyperdense, well-demarcated area with irregular edges is visible in the cavities of the trabecular bone (Figure 5B2).

3.6 | Barycz

A giant deer (*M. giganteus*) skull from the Barycz site (UAM/IG/KP/12.F1; 39800 ± 1000 BP) shows antler deformation. The right antler features a downward bend in its main beam of 110°C. A bony outgrowth, which is concave, is visible just above the brow tine, in the posterior part of the bend.

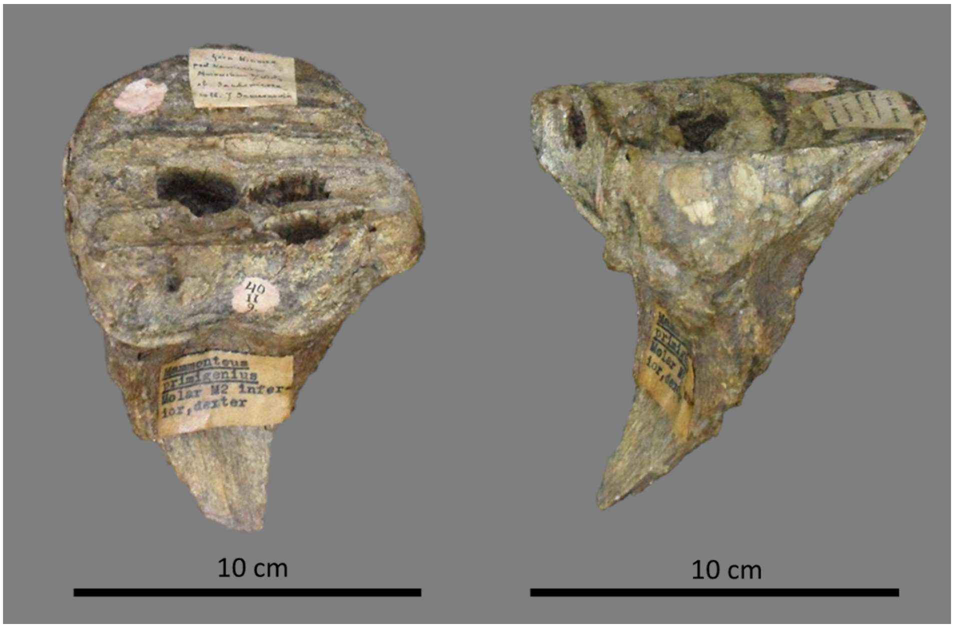

FIGURE 3 | Góra Winnica site, near Kamień Mściowski. Mammoth tooth, lower M2, with caries (photo by K. Pawłowska). [Colour figure can be viewed at wileyonlinelibrary.com]

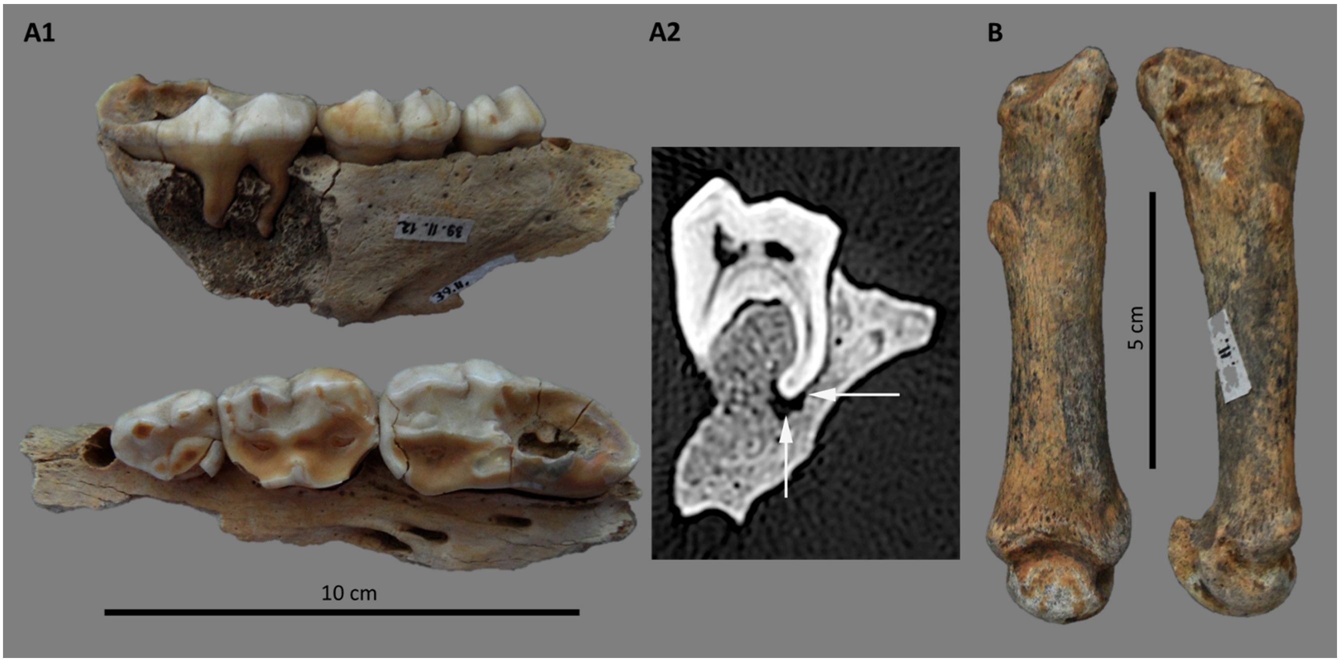

FIGURE 4 | Kadzielnia. Photo (A1) and CT scan (A2) of bear maxilla with caries of M2; (B) bear metacarpal II with an entheseal reaction (photo by K. Pawłowska). [Colour figure can be viewed at wileyonlinelibrary.com]

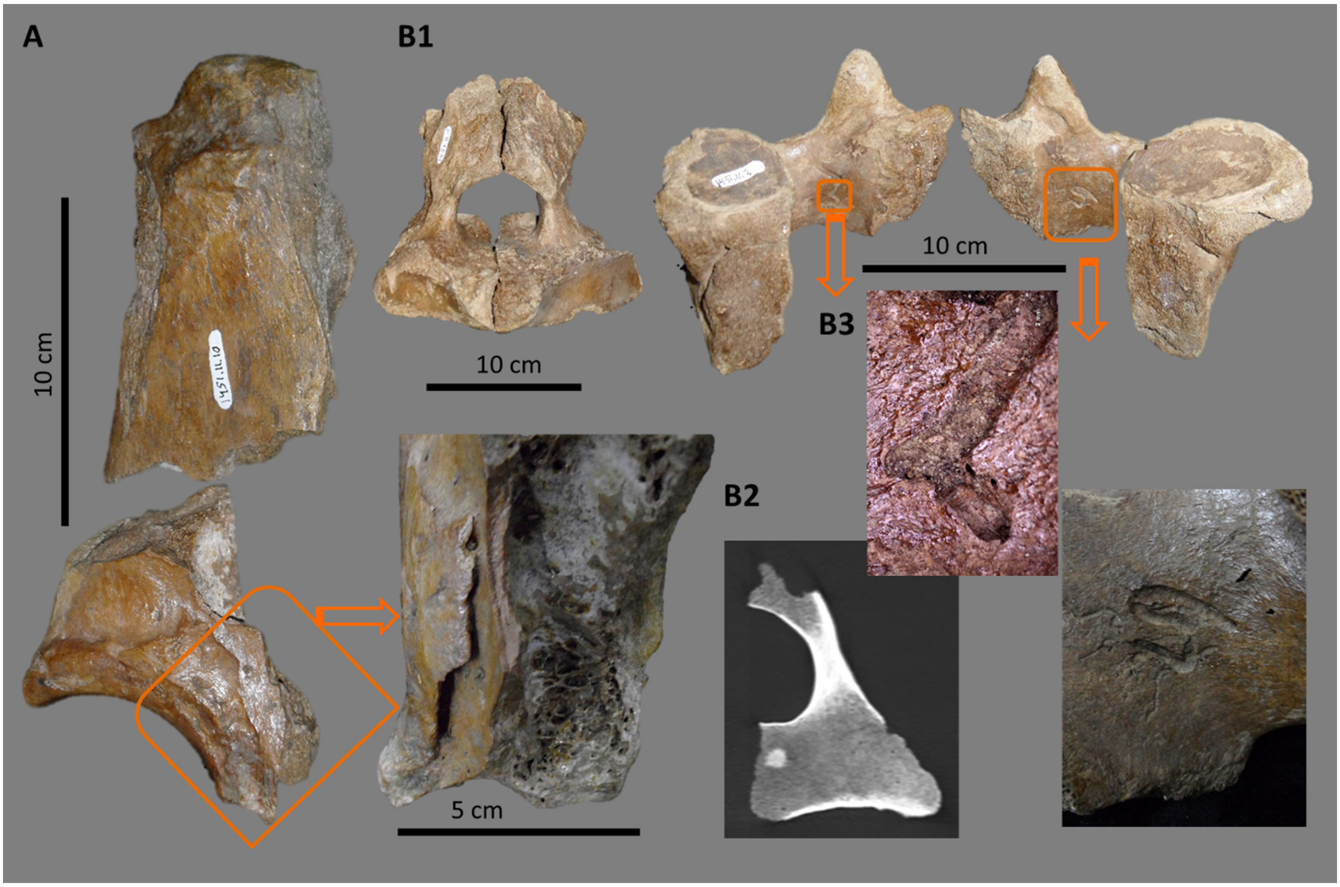

FIGURE 5 | Szczęśliwickie Lake site. (A) Large Bovidae ulna with exostosis; photo (B1) and CT scan (B2) of woolly rhino vertebra with furrows, partially filled with sediment (B3) (photo by K. Pawłowska). [Colour figure can be viewed at wileyonlinelibrary.com]

The antler was analyzed in terms of gross morphology, radiography, CT, and histopathology (Figure 6A–C). Radiography and CT scan of the antler cross-section at its bend reveal two foci of different tissue density within a cancellous core; the more ventral focus has greater density (Arrow 1), whereas the more dorsal focus suggests normal antler structure (Arrow 2). Increased tissue density was also seen in the antler margin (Arrow 3). Histology of the focus with a normal radiological shadow (asterisk) revealed the expected features of an orderly arrangement of osteons of similar diameter and well-developed Haversian systems (Figure 6B). The focus with the higher radiodensity (cross) and tissue from the bony outgrowth revealed disorganized primary bone with no osteons visible, disorganized lamellar bone, and numerous blood vessels (Figure 6B). The conclusion was that the antler deformity appears to be of traumatic origin, with a healing component in the form of a callus formation (Pawłowska, Stefaniak, and Nowakowski 2014).

3.7 | Ławy

A right lower molar (M3; MZ VIII/Vm 861), a left lower molar (M3; MZ VIII/Vm 862), and an upper molar (MZ VIII/Vm 76) of a woolly mammoth (*M. primigenius*) came from the Ławy site and unknown locality, respectively (Table 1 and Figure 7A,B). These mammoth teeth have unusual plate morphology in the form of bent lamellae.

3.8 | Pyskowice

From the Pyskowice site comes a mammoth (*M. primigenius*) thoracic vertebra (UAM/IG/KP/39.F2). This element, preserved as a spinous process, has concavity on the caudal side (Table 1 and Figure 7C) and presents signs of periostitis. Periostitis is also evident on the dorsal side on the articular surface.

3.9 | Mosina

The Mosina site yielded a mammoth (*M. primigenius*) upper M3 (KP/112.F1) (Table 1) that displays three furrows on the lingual surface, parallel to each other and to the occlusal surface of the tooth (Figure 8A). The edges of the furrows are uneven.

3.10 | Zaniemyśl

A mammoth (*M. primigenius*) ulna from the Zaniemyśl site (no inventory number; KP/4.F1) has periostitis on the medial surface (Table 1 and Figure 8B).

3.11 | Koło

The Koło site yielded an elk (*A. alces*) antler (UAM/IG/KP/21.F1; 9890 ± 50 BP) that has undergone a slight change

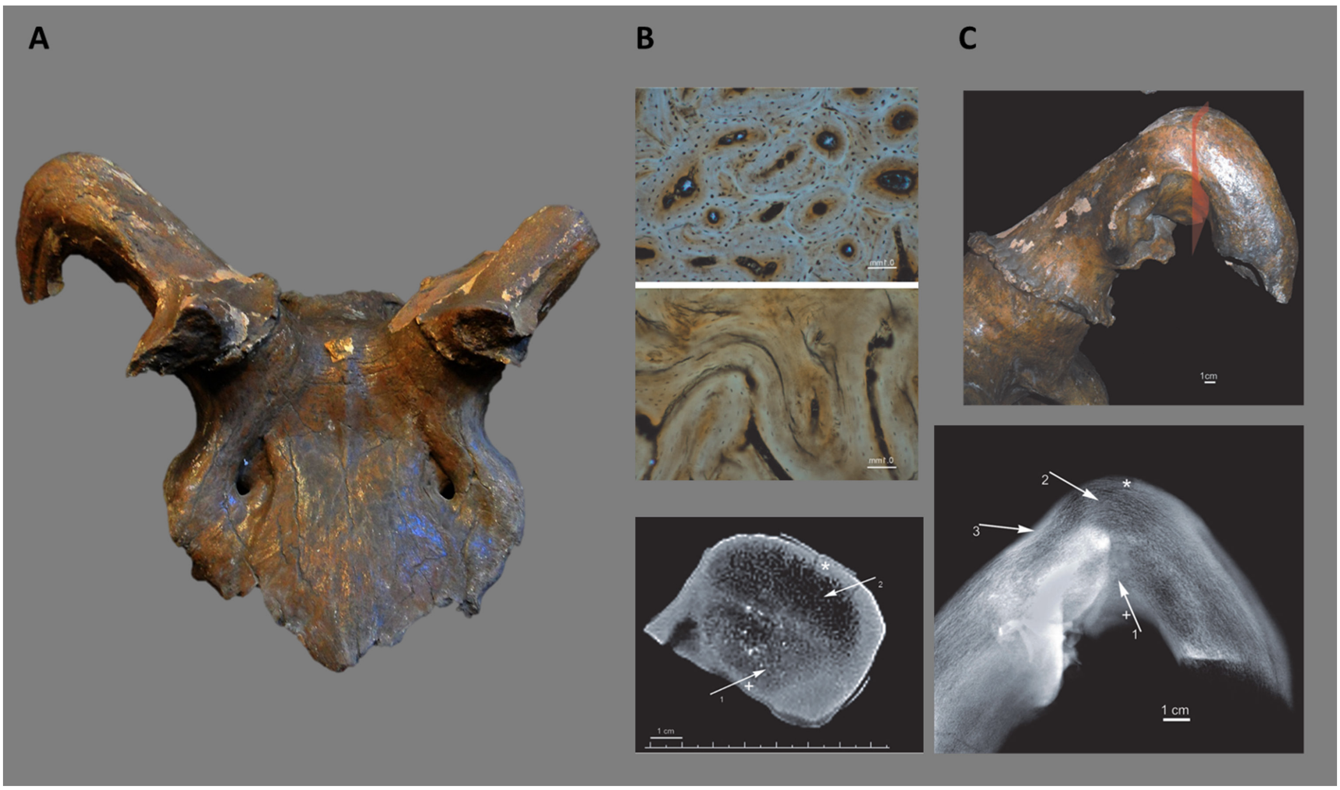

FIGURE 6 | Barycz site. Photo (A), histology (B), and radiology and computer tomography (C) of a giant deer skull with a bent right antler (Pawłowska, Stefaniak, and Nowakowski 2014). The asterisk indicates a focus with a normal radiological shadow, cross focus with the higher radiodensity and the arrows indicate two foci with different tissue densities. [Colour figure can be viewed at wileyonlinelibrary.com]

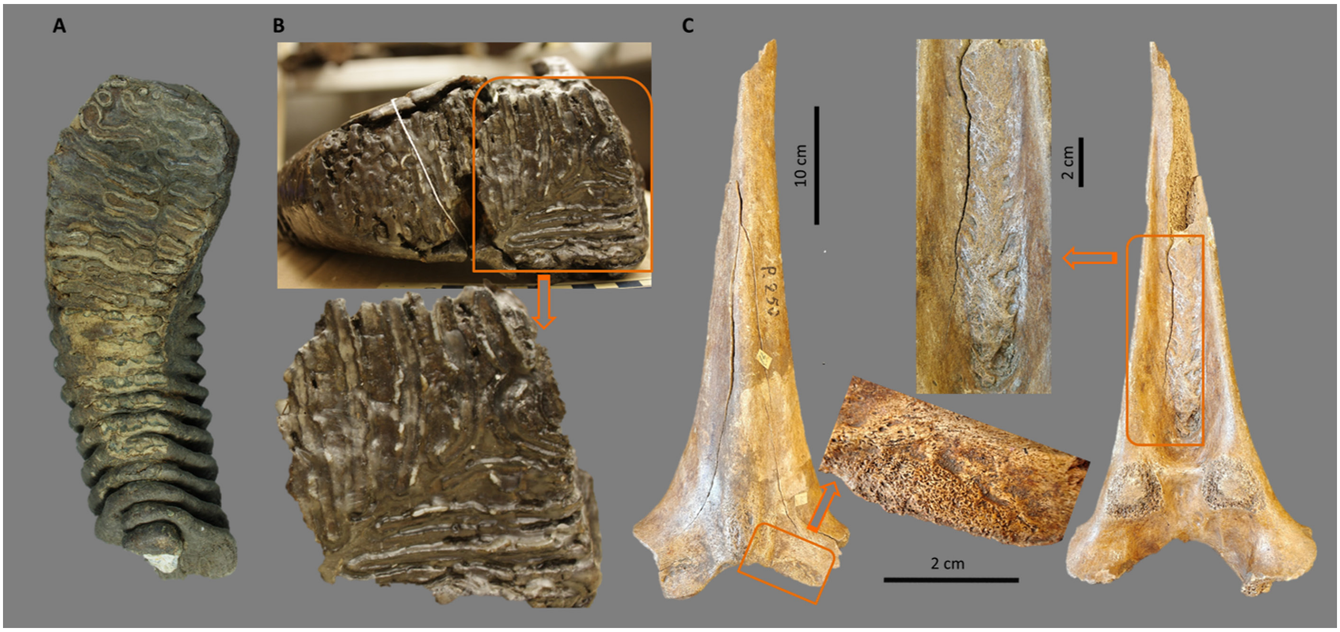

FIGURE 7 | (A and B) Mammoth teeth showing malformation, Ławy site, and unknown locality; (C) a mammoth thoracic vertebra with periostitis, Pyskowice site (photo by K. Pawłowska). [Colour figure can be viewed at wileyonlinelibrary.com]

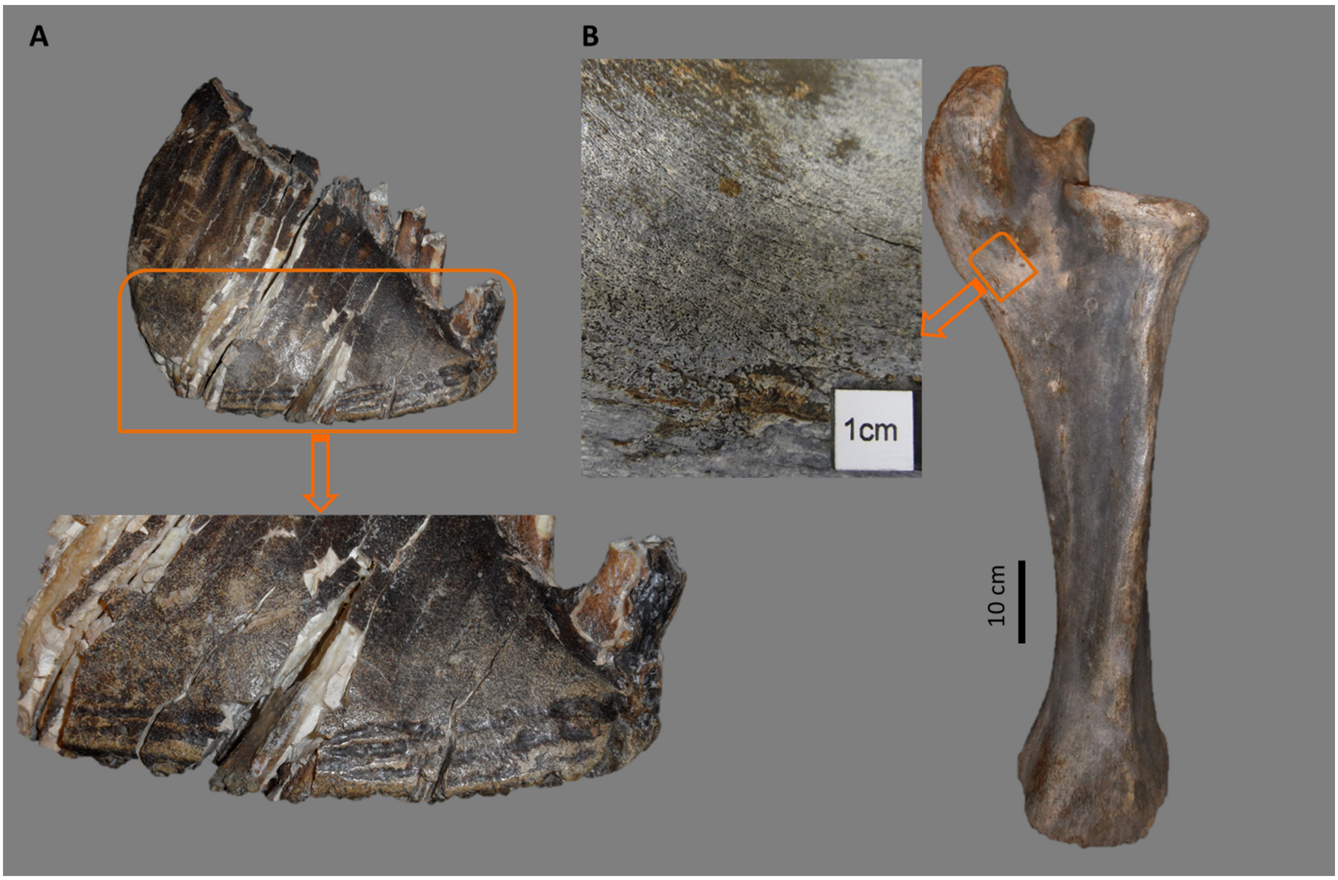

FIGURE 8 | (A) Mammoth tooth showing furrows, Mosina site; (B) mammoth ulna with periostitis, Zaniemyśl site (photo by K. Pawłowska). [Colour figure can be viewed at wileyonlinelibrary.com]

in its structure in the form of surface remodeling (Table 1 and Figure 9A). The lesion is superficial with visible disruption of the antler tissue.

3.12 | Chlewice

An elk (*A. alces*) antler from Chlewice (no inventory number) has two holes, each located on one side of the antler, and two more holes between the two tines (Table 1 and Figure 9B). The holes are more likely parts of the cavitary system. One hole is accompanied by a shallow furrow (asterisk in Figure 9). The holes are surrounded by signs of regeneration of the antler structure. The antler has at least five branches (Figure 9B).

4 | Discussion

Paleopathological studies of large mammal skeletal remains from Pleistocene contexts are much less frequent in zooarcheology than similar investigations of Holocene remains (Bartosiewicz and Gal 2013; Bartosiewicz and Mansouri 2022; Houldcroft and Underdown 2023; Pawłowska 2020a, 2020b). The examples of megafauna pathological changes shown here are meant to redress this imbalance. Pathological changes have been found on various skeletal elements of Pleistocene mammals, such as the woolly rhinoceros, woolly mammoth, giant deer, bovids, elk, and bear. According to the classification of Bartosiewicz and Gal (2013), they represent cases of different types of pathology, such as traumatic lesions, inflammatory diseases, arthropathies, diseases associated with the environment, dental anomalies and oral pathology, and congenital anomaly and inherited disorders.

4.1 | Traumatic Lesions

Traumatic lesions visible on skeletal elements are usually associated with mechanical injury

(The data will also be publicly available in the repository. D'lima et al. 2001; Madej, Rotkiewicz, and Nozdryn-Płotnicki 2007). This was the case for a malformed giant deer antler (IG-Br 12.F1) from the Barycz site. A mechanical impact caused a disruption of tissue continuity encompassing half of the antler's thickness. As a result, the antler was first displaced upward, and then, the fractured part shifted downward under gravity and became fixed in this position with the formation of a fracture callus. The fracture of the antler still in velvet did not lead to the loss of the distal fragment, because it was apparently held by the skin and periosteum (Pawłowska, Stefaniak, and Nowakowski 2014). Malformated antlers are also known from white-tailed deer, where they have also been interpreted as the result of injuries to the antlerogenic periosteum region rather than of congenital origin (Karns and Ditchkoff 2013).

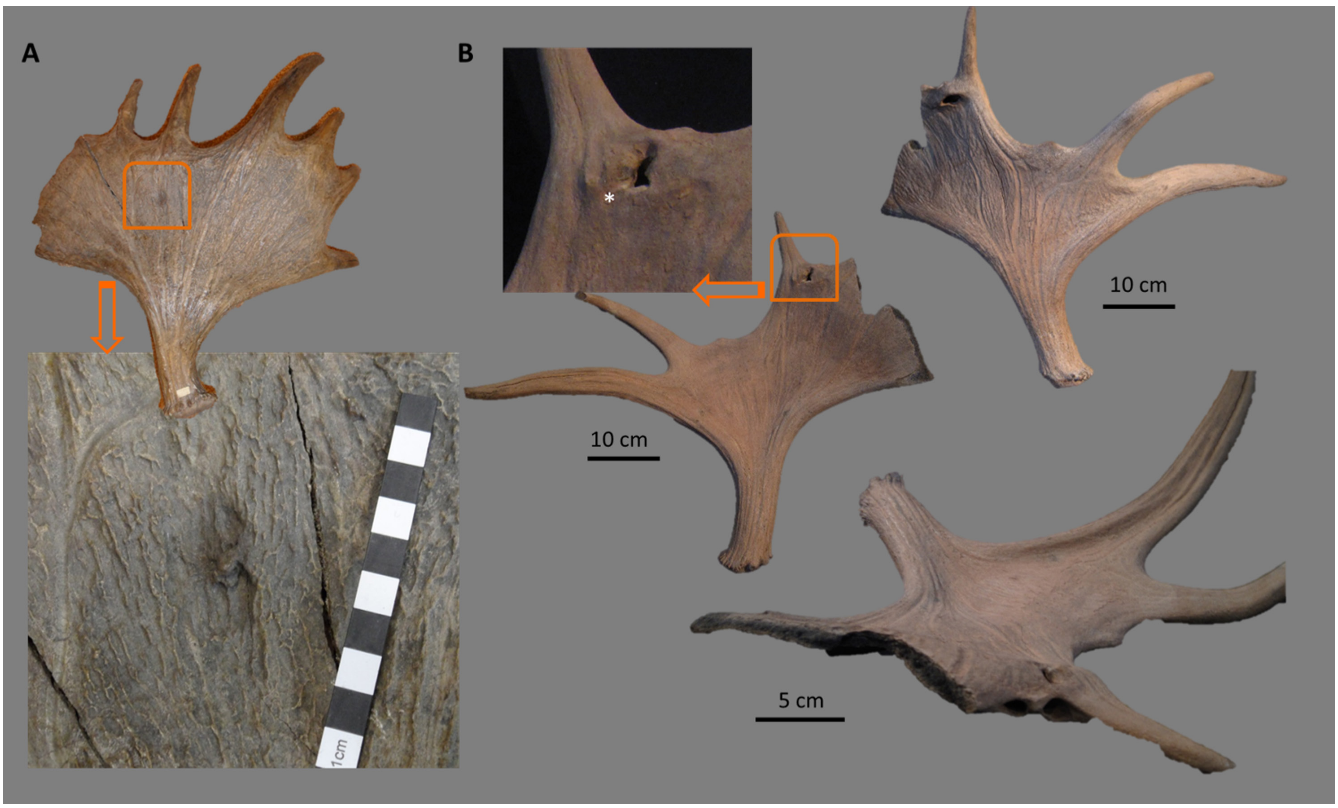

FIGURE 9 | (A) Elk antler with malformation, Koło site; (B) elk antler with holes, Chlewice site. The asterisk indicates bone resorption caused by pressure exercised by pus or blood that was held underneath the periosteum and velvet (photo by K. Pawłowska). [Colour figure can be viewed at wileyonlinelibrary.com]

An entheseal reaction—the proliferation of bone tissue as a result of a periosteal reaction—was found on an elk metatarsal from Wiercica cave (MUZ.PIG 335.II.18). The origin of these can be multifarious. Such alterations can be produced by lesions of traumatic origin, such as fracture scars, or with neoplastic or tumorous changes, like osteosarcoma (Madej, Rotkiewicz, and Nozdryn-Płotnicki 2007). Such a lesion can also arise from chronic inflammatory process resulting from damage to the tubercles and ligamentous fovea for the lateral collateral ligament of the metatarsophalangeal joint, which are located in this area (Najbrt et al. 1980; Nickel, Schummer, and Seiferle 2005). The CT scan indicated that this is the result of a chronic process, with the periosteal reaction driving a mixed lytic and sclerotic bone transformation. We associate this with the fracture, which is consistent with the nature of entheseal reactions—the Sharpey's fiber alterations that underlie sudden or unconditioned repetitive stresses of mechanical or inflammatory origin (Rothschild 2024).

It is likely that lesions of the distal epiphysis have caused hypertrophy in the metashaft section. However, similar changes, called buttresses, on the metatarsal bone shaft are well known in other species, in both paleozoological and archeozoological materials (Vann and Grimm 2010; Thomas and Grimm 2011). In sheep, for example, three observations have been made regarding the formation of buttresses on the dorsal surface of the metatarsals: The first is that the condition is more frequent in older (and larger) individuals; the second is that the condition is more frequent in males, which exhibit more pronounced (longer, wider, and deeper) buttresses. The third remark is that buttresses become more pronounced with age. It is an open question whether they should be classified as pathologies: They are often considered a normal condition. Many such bone alterations are better classified as anatomical variations than pathologies. In the middle part of the medullary cavity, our study also revealed a hyperdense, well-demarcated area with irregular edges, which can be associated with sequestration within the bone marrow due to chronic repetitive trauma (Steward et al. 2022). The suggestions of Thomas and Grimm (2011) thus seem to be reasonable, and the behavioral mobility of animals and overloading of the limbs should be taken into consideration.

The formation of new bone tissue on the surface of the bear second metacarpal from the Kadzielnia site (MUZ.PIG 39.II.28) is associated with the entheseal reaction in the insertion of radial carpal extensor muscle (*m. extensor carpi radialis*), most likely the result of prolonged mechanical irritation of the tissue, as has been described in other studies (Dietz and Huskamp 2009; Madej, Rotkiewicz, and Nozdryn-Płotnicki 2007) and thus has a traumatic origin. This process is well understood in horses, where the development of bony excrescences can be the result of hitting an obstacle while jumping (Bertoni et al. 2012). Damage to the tendons of the digital flexor muscles, as well as the associated entheseal reaction, causes pain and lameness in animals.

Benign growths of bone extending outwards from the surface of the bone, as found on the ulna of a bison or aurochs from Szczęśliwickie Lake (MUZ.PIG 1451.II.15), may be triggered by a number of factors, with an entheseal reaction being the most plausible, but does not seem to have a more serious cause than inflammation due to the size of its growth. Entheseal reactions are associated with stress experienced by the attaching muscles, acute injury, tendon tears, weakness of attachments, inflammatory arthritis, vitamin deficiency, and aging (Bilezikian et al. 1996; Rothschild 2019 with further references). In the present case, this reaction involves the collateral and transverse ligaments that cross at this location.

4.2 | Inflammatory Diseases

Periostitis present on different skeletal elements may have a polyetiological cause, as bone formation in the periosteum may be a response to any stimulus and concomitant with many pathological conditions (Bartosiewicz and Gal 2013; Madej and Rotkiewicz 1998; Madej, Rotkiewicz, and Nozdryn-Płotnicki 2007). Hence, periosteal new bone formation is frequently recorded on historical animal remains (Bartosiewicz and Gal 2013; Cramer 2018). This makes it difficult to demonstrate its origin (Vandemergel, Blocklet, and Decaux 2004; Roberts 2019) in the case of individual skeletal elements, such as the one found on a mammoth ulna from the Zaniemyśl site (KP/4.F1) and on a metatarsal bone of a bovid from the Wiercica Cave (MUZ.PIG 335.II.14), both of which are inflammatory in nature. In the bovid metatarsal, smooth lesions with well-defined margins indicate a nonaggressive form, and the process of bone formation was chronic (Rana, Wu, and Eisenberg 2009). The lesion is superficial and did not develop lytic bone changes or sclerotic formations, which could have been caused by an abscess.

A concavity on the caudal side of the processus spinosus of a mammoth thoracic vertebra (from the Pyskowice site, UAM/IG/KP/39.F2) shows sign of periostitis (also on the cranial side) and is associated with inflammatory conditions between the vertebrae.

The hyperdense area within the cervical vertebra (axis) of the woolly rhinoceros (*C. antiquitatis*) (MUZ.PIG 1451.II.1-2) from Szczęśliwickie Lake site is the result of a postinflammatory condition. The inflammation leads to a discrete increase in bone production by osteoblasts.

4.2.1 | Inflammatory Arthritis

The entheseal spur and marginal lipping found on the distal end of the bear humerus from Sitkówka site (MUZ.PIG 157.II.40) may be a manifestation of the early stages of arthropathy, which is well known in records in the past (Jurmain and Kilgore 1995). Arthropathies are the most frequent joint pathologies in bone materials; they are caused by a range of factors, including inflammation and degeneration, and its diagnostic criteria have a long tradition (Stevanović et al. 2015). Osteoarthritis (OA), as example of degenerative arthropathies, can be recognized by (1) the formation of marginal osteophytes or new bone on the joint surface, (2) the reaction of the subchondral bone, (3) the presence of irregular joint surfaces, and, in severe cases, (4) alterations in the contour of the joint (Ventades et al. 2018 with further references therein). However, the marginal lipping on the specimens from Sitkówka is not typical of OA, as it reflects internally, unlike osteophytes that reflect externally to the joint margin surface. Although lipping can correlate with OA, its nature is the subject of controversy; it is perhaps related to calcium pyrophosphate deposition (CPPD). CPPD disease, known as pyrophosphate arthropathy or sometimes "pseudogout," is a consequence of the immune response to the pathological presence of calcium pyrophosphate (CPP) crystals inside joints, which causes acute or chronic inflammatory arthritis (Pascart et al. 2024). Common risk factors, such as aging and previous joint trauma, are shared by CPPD and osteoarthritis, which makes it difficult to clarify the direction of causality between the two conditions (Pascart et al. 2024). This condition has been described in humans (Pascart et al. 2024) and in dogs (Heimann, Carpenter, and Halverson 1990; Henschen et al. 2020). In both cases, CPPD was diagnosed at advanced age and the recurrent disease attacks, lameness, and chronic degenerative arthropathy strongly affected the individual's life comfort. Lesions at the elbow joints, at the attachment of the anconeus muscle, could also have been at least partly the result of overloading of the thoracic limb, given that degenerative arthropathies can affect joints both bilaterally and unevenly in the thoracic or pelvic limbs. Entheseal reactions are also a feature of the second specimen from the Sitkówka site, where the proliferation of bone tissue was evident at the distal end of a bear femur (MUZ.PIG 157.II.6).

4.3 | Diseases Associated With the Environment

The transverse lines on the mammoth tooth (KP/112.F1) from the Mosina site are defects in enamel development. These disturbances, known as dental enamel hypoplasia (DEH), represent a condition that is also characterized by pits and grooves on the surface of tooth crowns (El-Najjar, Desanti, and Ozebek 1978). A variety of factors, such as premature birth, malnutrition, bacterial and viral infections, and trauma, can cause hypoplasia in newly developing teeth (Towle and Irish 2020). As a result, enamel hypoplasia caused by hereditary or environmental factors—such as a deficiency state or a systemic condition—have the same symptoms. This makes it difficult to pinpoint a singular cause for the changes in enamel structure (Goodman 1989), including the impact of paleoenvironments, which may have led to such changes.

The lesion on the elk specimen from the Koło site (UAM/IG/KP/21.F1) is associated with a local developmental disorder. Because the development of antlers is affected by many factors, including the type and quality of food, mineral deficiency, hormonal balance, and trauma (Landete-Castillejos et al. 2019), all or some of these things could have played a role. The change is not sufficiently large or extensive; the factor had a long impact on antler development. It most likely represents a trauma that healed when the antler had been covered over with velvet (antler skin). Velvet provides a blood supply and so allows the growth and development of the antler. When the velvet is shed, the antler tissue undergoes ischemic necrosis (Li and Suttie 2012).

4.4 | Dental Anomalies and Oral Pathology

The presence of a cavity in the mammoth tooth from Góra Winnica near Kamień Mściowski (MUZ.PIG 40.II.9) can be linked to dental caries, which tends to appear at the junction of the cement and the enamel (Waldron 2009). In Elephantidae, these two tooth-building materials form distinctive lamellae that are diagnostic of individual species. The development of caries is a multifactorial process that requires a bacterial film (plaque), the presence of a fermentable carbohydrate, and the production of acid (Bowen 1972). The bacterial film is largely composed of streptococci and lactobacilli, which metabolize fermentable carbohydrates, producing weak organic acids (Takahashi and Nyvad 2008). These latter are responsible for the drop in local pH, which in turn causes the demineralization of the tissues of the tooth.

The moderate degree of tooth destruction relative to the original stage of caries development (usually visible as a brown spot) suggests that the process had been going on for some time. Because the prevalence of caries increases with age (López et al. 2017), one can indirectly infer that the animal was of adult age. This is also confirmed by the degree of wear on the occlusal surface of the tooth.

Another case of caries was found in our study of the bear maxilla from the Kadzielnia site (MUZ.PIG 39.II.12). Here, the cavity affects M2 and the CT scan revealed a hypodense area around the apex of the tooth root, which is consistent with an abscess at the caudal root (Lobprise 2021). Such a dental lesion can be interpreted as an apical abscess of the dental root; this is frequently observed in modern dogs (Jahromi and Mehrshad 2010).

4.5 | Congenital Anomaly and Inherited Disorders

Abnormal tooth formation is a variety of dental anomaly; though given that they may have a genetic basis, we distinguish them here as a separate subcategory, according to the classification of Bartosiewicz and Gal (2013).

Changes in plate shapes, like those observed in the mammoth individual from the Ławy site and unknown locality (MZ VIII/Vm 861 and 862: Hrynowiecka et al. 2018; MZ VIII/Vm 76), are tooth anomalies. According to Kubiak (1965), the deformation of individual plates in mammoths is caused by developmental disorders and occurs during ontogenetic development. A role is also played by pressure on individual teeth in the sequence, as in the Elephantidae tooth replacement is horizontal. Other example of such anomalies with an S-shaped plate (specimen ZZS MF/671/64) is known from Poland, as reported by Kubiak (1965).

Tooth anomalies in fossil elephants are not attributed to the woolly mammoth (*M. primigenius*), which confirms they were also found in the steppe elephant (*Mammuthus trogontherii*), and the forest elephant (*Palaeoloxodon* [*Elephas*] *antiquus*) (Kubiak 1965). The diversity of tooth deformities in Elephantidae led to the creation of a classification of developmental anomalies of teeth by Kubiak (1965), based on the cause of the deformation. Teeth with alterations resulting from developmental disturbances fall into the first group, whereas teeth with abnormally shaped occlusal surfaces make up the second group. Teeth with tumors and protuberances make up the third group, and finally, teeth with evidence of metabolic disorders make up the fourth group. The fifth group include teeth that display any other deformities.

4.6 | Other Lesions

Not every pathological lesion in faunal materials can be unambiguously linked to a disease entity or to an event that caused the injury. An example of this is provided by the elk antlers from Chlewice, which display plausible draining sinuses that open as holes in the furcation area, as a consequence of purulent inflammation in the antler. There are several possible explanations for this condition, ranging from a hunting injury, to fighting between individuals, to a local infection that resulted in an abscess during antler development. Because elk, like other cervids, generally avoid fighting when their antlers are covered with velvet, we assume that the event that led to abscess development was accidental. Such large draining sinuses in the furcation area between the tines have previously been recognized in red deer and have been interpreted as the result of purulent inflammation due to a fracture (Kierdorf, Kierdorf, and Konjević 2013). Similarly, the causes of the draining sinus in the elk antler from Chlewice may lie in the accumulation of pus or blood, kept under the periosteum for some time before either draining through the velvet or being released by velvet shedding (Kierdorf, Kierdorf, and Konjević 2013). The drainage of pus or blood is demonstrated by the presence of a shallow furrow. Regardless of the cause, signs of regeneration indicate that the animal survived.

An unusual lesion on bones can be seen in the curled marks on the vertebral arch of a woolly rhinoceros (MUZ.PIG 1451.II.1-2) from the Szczęśliwickie Lake site, which may be related to the presence of parasites during the animal's lifetime, taphonomic aspects or may represent an imprint of blood vessels, which raises the issue of equifinality in references to their identification. Parasites in the skeleton—the part of human and animal bodies most resistant to posthumous destruction—are less frequently observed than those in soft tissues. They also do not show any specific symptoms on medical imaging (Arkun 2004). It therefore appears that these marks are impressions related to blood vessels or to postmortem modifications, rather than to the presence of a parasite. The texture of these marks led us to employ high-resolution photography, which showed it to be due to the sediment filling that partly covers the marks. Thus, the texture is not diagnostic for identifying the origin of marks. At this stage, any attempt to infer a causal agent would be merely speculative; this can be done in future using a broader range of samples with such marks.

5 | Conclusions

This paper provides the first overview of the generalized data of paleoecological investigation at various sites in Poland, using paleontological and veterinary approaches to the study of paleopathology of large mammals. The review of individual cases of pathological lesions on Pleistocene and early Holocene remains has shown that they involve woolly rhinoceros, woolly mammoth, large bovids, giant deer, elk, and bears.

The classification of Bartosiewicz and Gal (2013) suggests that the cases of pathology found in this study represent the following categories: traumatic lesions, inflammatory disease, arthropathies, diseases associated with the environment, dental anomalies and oral pathology, and inherited anomalies. Many pathologies from a range of epochs in the Holocene can be seen as resulting from direct or indirect human interference with the health of domestic animals, such as crowding, malnutrition, and physical abuse. With the exception of possible hunting injuries, focus on the human factor is generally lacking in paleontological studies. Large and strong species, such as the woolly rhinoceros and the woolly mammoth, can sustain larger or smaller lesions for sufficiently long for them to be manifest on their skeletons.

Because the remains represent various species and because pathological evidence is not common in fossil records, this work makes a significant contribution to our knowledge of the condition of megafauna in the past.

Author Contributions

Kamilla Pawłowska: conceptualization, methodology, investigation, data curation, writing – original draft, writing – review and editing, funding acquisition, supervision, resources, project administration, visualization. **Aleksander Chrószcz**: methodology, data analysis, writing – editing. **Dominik Poradowski**: methodology, data analysis, writing – editing. **Dominika Kubiak-Nowak**: CT study. **Wojciech Borawski**: CT study.

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data will also be publicly available in the repository.

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