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The resilience of an injured Early Pleistocene *Lynx* from Taurida cave (Crimea)

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ABSTRACT

The present work describes for a first time a fused fracture of the metacarpals of the medium-sized felid, *Lynx issiodorensis*, the putative ancestor of all Eurasian extant lynx species. The studied remains, four metacarpals from the same individual, were unearthed from the Early Pleistocene of the Taurida cave (Crimean Peninsula) and studied through computed tomography. These remains exhibit pronounced signs of osteopathology, namely, fracture with displacement of the fifth metacarpal bone fused with the formation of callus and deformation of the bone itself. The pathological process is spread to adjacent metacarpal bones. The likely cause of the injury could be an unsuccessful hunt or an awkward landing from a height. After the injury and in the process of healing the fracture, the studied individual survived with clearly limited hunting abilities.

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Introduction

Bone pathologies in palaeontological remains are a rare find, as noted by Greer et al. (1977). Among carnivorous mammals, such pathologies have been documented in various families, including Canidae (Janssens et al. 2016; Sazelova et al. 2020), Ursidae (Capasso 1998; Chrószcz et al. 2014), Hyaenidae (Rothschild and Rothschild 1994), and Felidae (Balisi et al. 2021). Notably, investigations into extinct felids, particularly from the Late Pleistocene period, have been more usually documented thanks to the abundance of remains of this specific unit of the fossil record (Heald 1986; Brown et al. 2017).

Analysis of Late Pleistocene fossil feline remains has revealed various pathologies, with a focus on cranial injuries attributed to interspecific struggle among lions (Diedrich and Zak 2006; Diedrich 2011b; Rothschild and Diedrich 2012). Conversely, the skeletal injuries in Late Pleistocene saber-toothed cats are predominantly attributed to intraspecific agonistic interactions (Antón 2013; Chimento et al. 2019). Additionally, bone pathologies associated with hunting behaviour have been documented in saber-toothed cats (Argant 2004; Antón 2013; Salesa et al. 2014; Brown et al. 2017; Rabe et al. 2022). However, descriptions of bone pathologies in fossil lynxes are notably absent from existing literature.

This paper presents the findings of a study focused on the metacarpal bones of *Lynx issiodorensis* affected by pathological processes, recovered from the late Early Pleistocene deposits of the Taurida cave in Crimea.

Materials and methods

Location of the Taurida cave

Taurida cave was discovered in Crimea in 2018, being located about 15 km east of Simferopol city (45°02´37´´N, 34°17´09´´E) at the Crimean Peninsula (Figure 1A). Taurida cave is located on the northern macroslope of the Crimean Mountains in the interfluves of the Beshterek and Fundukla rivers at an altitude of 320–340 m above sea level. The cave was formed in nummulite limestones of the Simferopol stage (Middle Eocene) and its total length is ca. 2.5 km (Figure 1B).

Throughout the Pleistocene, the cave was a den of different ancient predators for a long time (Lavrov et al. 2021a, 2021b). The surveyed area of excavation and most of the unearthed fossil remains are concentrated at a distance of no more than 250–260 m from the natural entrance to the cave.

The bone-bearing layer is represented by red-brown loose loams of subaerial genesis (so-called terra rossa). The faunal list of large mammals includes *Canis* sp., *Vulpes alopecoides*, *Ursus etruscus*, *Pachycrocuta brevirostris*, *Chasmaporthetes lunensis*, *Homotherium crenatidens*, *Megantereon ardroveri*, *Lynx issiodorensis*, *Archidiskodon meridionalis*, two taxa of stenonid horses, *Elasmotherium* sp., *Stephanorhinus* sp., *Paracamelus gigas*, *Arvernoceros verestchagini*, *Leptobos* sp., *Bison* (*Eobison*) sp., *Megalovis latifrons*, *Gazellospira torticornis*, *Soergelia minor*, *Pontoceros ambiguus*, *Ovis gracilis*, and *Tavridia gromovi* (Lopatin et al. 2019; Vislobokova et al. 2019, 2020; Gimranov et al. 2020, 2021, 2023c; Lavrov et al. 2020, 2021a, 2021b, 2022a, 2022b; Vislobokova 2022, 2023a, 2023b, 2023c). The recovered small mammals include *Erinaceus sp.*, *Beremendia fissidens*, *Crocidura kornfeldi*, *Rhinolophus macrorhinus cimmerius*, *R. mehelyi scythotauricus*, *Eptesicus nilssonii varangus*, *E. praeglacialis*, *Plecotus macrobullaris sarmaticus*, *Hypolagus brachygnathus*, *Lepus* sp., *Spermophilus nogaici*, *Hystrix* (*Acanthion*) *vinogradovi*, *H. (H.) refossa*, *Sicista* sp., *Apodemus* sp., *Allocricetus ehiki*, *Cricetus* sp., *Clethrionomys* sp., *Ellobius kujalnikensis*, *Lagurodon arankae*, *Mimomys* sp., *Allophaiomys deucalion*, *Mustela palerminea*, and *M. strandi* (Lopatin 2019a, 2019b, 2019c, 2021, 2022, 2023a, 2023b, 2023c, 2024; Lopatin and Tesakov 2021; Gimranov et al. 2023a, 2023b).

All of the listed species are included in the Psekupsian (=Odessan) Faunal Assemblage of Eastern Europe, which correlates with the Late Villafranchian of Western Europe (zones MNQ18–MNQ19) (Lopatin et al. 2019). The revised Quaternary time scale (Gibbard et al. 2010) for chronological references is used in this article.

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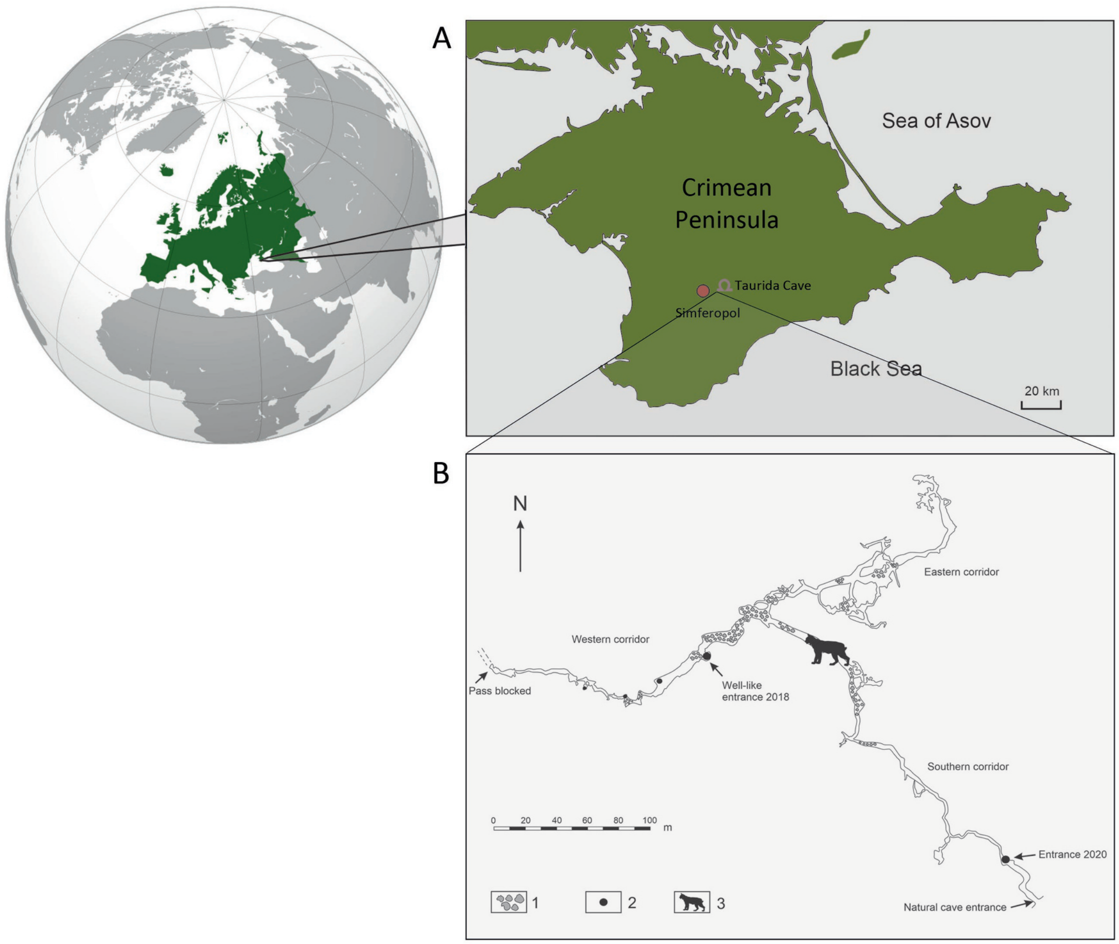

Figure 1. The Taurida locality; A - geographical location of the Taurida cave within Europe and later within the Crimean Peninsula. B - topographic map of the Taurida cave. Legend: (1) landslide-block deposits; (2) large, vertical wells of aggregate deposition close to the surface; (3) finding of *Lynx issiodorensis* remains.

Lynx issiodorensis from Taurida cave

Lynx issiodorensis was presumably the ancestor of the living Eurasian and Iberian lynxes, *Lynx lynx* and *Lynx pardinus* (Kurtén 1978). It differs from *L. lynx* in the absence of the metaconid–talonid complex of m1, the combined position of the foramen lacerum posterior and hypoglossal nerve foramen (for. hypoglossus), opening into a unified sinus (Mecozzi et al. 2021). The presence of a short tail and tassels on the ears is assumed, as in all lynxes (Kurtén 1978). Judging by the size of the skull, as in large modern *L. lynx* (condylobasal skull length up to 152 mm), the basis of the diet of the Issoire lynx could be small and medium-sized ungulates (Melovski et al. 2020), up to a mass of 200 kg (Geptner and Sludsky 1972), small mammals and birds.

In 2020, remains of *Lynx issiodorensis* were found in the southern gallery of the cave in a bone-bearing layer formed in the upper part of variegated loams (Oksinenko and Lavrov 2021). They included skull fragments, long limb bones, vertebrae, and ribs (Lavrov et al. 2021). The minimum number of individuals (MNI) represented by the skeletal remains of this species is seven. Most of the lynx bones were concentrated at a distance of 170–250 m from the excavated natural entrance to the cave but were also found in the entrance part of the Southern corridor in 2021–2022.

We studied the metacarpal bones of the right forelimb McII (specimen PIN, no. 5644/341a), McIII (specimen PIN, no. 5644/341b), McIV (specimen PIN, no. 5644/341c), McV (specimen PIN, no. 5644/341d), found in anatomical order and apparently belonging to the same individual (Figures 2A, B and 3A). The material is housed at the Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN), Moscow, Russia. Computed tomography was performed using a Siemens Somatom Go Up tomograph (Veterinary Hospital Skolkovo Vet, Moscow Region, Odintsovo District, Zarechye Work Settlement). The RadiAnt DICOM Viewer software (v. 2023.1; Medixant, Poznan, Poland) was used to work with the resulting slices. The study used comparative anatomical collections of the PIN and Zoological Museum of Moscow State University (ZMMU).

Results

The studied metacarpals have complete epiphyseal fusion, i.e. they correspond to an adult individual. There are no traces of seams of fusion of epiphyses with the diaphysis. The observed deformation of the bone tissue mainly affected the diaphysis, leaving the articular surfaces of the proximal parts and the distal articular heads unchanged (Figures 2 and 3).

Unfortunately, McI was not found in the up-to-date performed surveys. McII is close to normal morphology in appearance displaying slender and straight morphology with few dorsopalmar curvature. Minor exostoses are observed only on the dorsal side in the proximal part of the bone (Figures 2 and 3). Figure 4B shows the absence of obvious exostoses on McII.

The diaphysis of McIII is clearly pathological (Figures 2 and 3), the secondary growth of bone tissue is observed in both the palmar

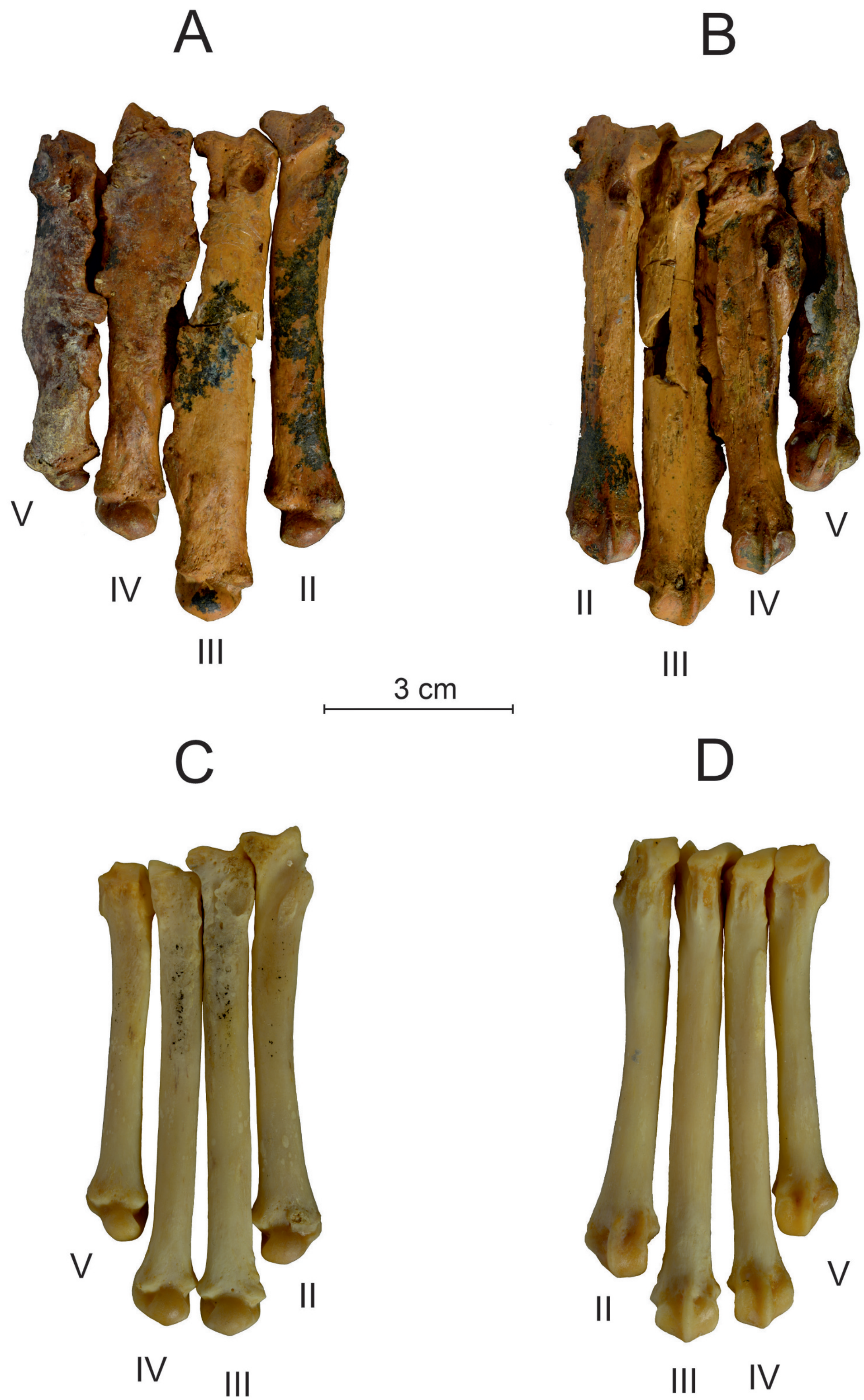

Figure 2. Metacarpal bones of the right forelimb of the studied L*ynx issiodorensis* (specimens PIN, nos. 5644/341a–d) (A, B) and extant *L. lynx* (specimen ZMMU, no. S-200993) without pathology (C, D) in the anatomical position; A, C – anterior view; B, D – posterior view.

and dorsal sides, forming a ridge on the lateral side. In Figure 4D, A periosteal reaction as a dense-elliptical reaction type is clearly visible, in the proximal part it marks a fringed outline. The cortical layer of the bone is clearly visible throughout almost the entire length of the periosteal reaction (Figure 4D).

Observed hyperplasia on the McIV diaphysis is strong and directed medially and laterally (Figures 2, 3 , and 4E). Hyperplasia is also clearly visible from the palmar and dorsal sides of McIV (Figure 2). Figure 4F shows a significant amount of periosteal reaction, most pronounced in the proximal part of the bone.

Figure 3. Metacarpal bones II–V of the right forelimb of lynxes from medial and lateral view; a – studied *L. issiodorensis* (specimens PIN, nos. 5644/341a–d), B – extant *L. lynx* (specimen ZMMU, no. S-200993). For each metacarpal bone, the medial view is shown on the left, and the lateral view on the right.

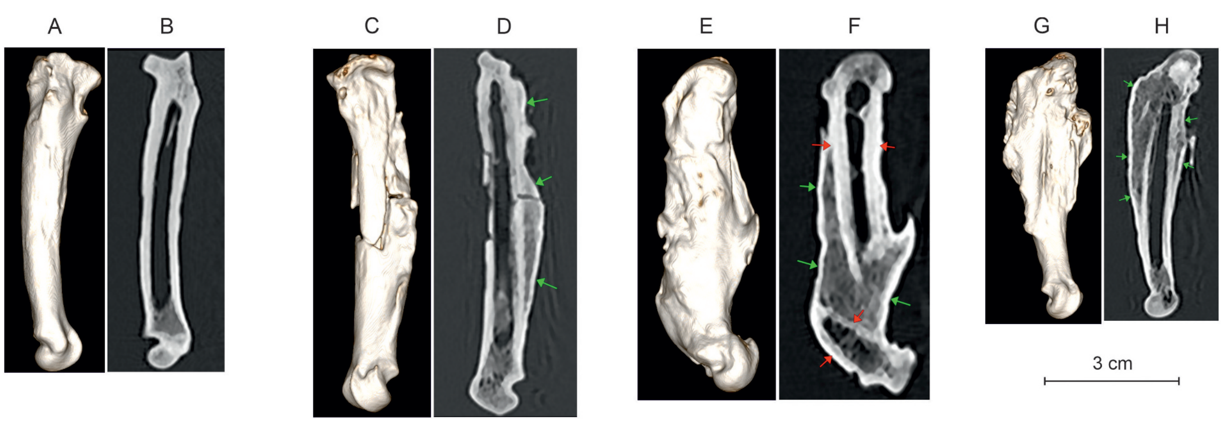

Figure 4. Computed tomography images of metacarpal bones of the studied L*ynx issiodorensis* (specimens PIN, nos. 5644/341a–d). A, B – McII; C, D – McIII; E, F – McIV; G, H – McV. A, C, E, G images is 3D models; B, D, F, H – CT-slices, green arrows indicate the periosteal reaction, red indicate the contours of the cortical bone.

McV is the most severely affected specimen by the pathological process, the proximal part of the bone is curved towards McIV and not parallel to it. In Figure 4H the cortical bone is well differentiated, the contours are intermittent, between them the volume of bone tissue is clearly different in structure, but with clear even boundaries. Since *L. issiodorensis* is mostly similar in body size to *L. lynx*, we compared the main linear parameters of two lynxes (Table 1), it is clearly visible that the pathological McV is shorter than the normal one without pathologies.

Table 1. Measurements of the metacarpal bones of *Lynx issiodorensis* (specimens PIN, nos. 5644/341a–d) with pathology and the extant *L. lynx* (specimen ZMMU, no. S-200993) without pathology. Abbreviations: H dist, distal anteroposterior diameter; H prox, proximal anteroposterior diameter; L, proximodistal diameter; W dist, distal mediolateral diameter; W prox, proximal mediolateral diameter.

Measurements	McII	McIII	McIV	McV
Lynx issiodorensis	5644/341a	5644/341b	5644/341c	5644/341d
specimens PIN, nos. 5644/341a–d				
L	69.1	77.3	69.5	56.8
W dist	12.5	12.3	11.1	11.9
H dist	10.3	10.7	10.3	10.3
W prox	13.0	13.5	11.9	11.7
H prox	16.7	15.7	17.8	12.0
Lynx lynx				
specimen ZMMU, no. S-200993				
L	69.1	78.1	74.0	61.3
W dist	11.2	10.9	10.2	10.2
H dist	10.0	10.2	9.8	9.6
W prox	9.7	11.1	9.6	10.5
H prox	13.9	12.1	12.1	10.2

Discussion

Possible origin of Taurida felid pathologies

Currently, there is no complete and well-established classification of palaeopathological conditions of bone tissue (Stevanović et al. 2015). According to the views of modern veterinary medicine, the pathologies of the skeletal tissue of extant animals are the result of the impact on the body of various factors, and they can be conditionally divided into several groups: (1) dystrophic diseases, often associated with metabolic disorders (rickets, osteoporosis, osteomalacia, osteodystrophy, etc.) and hormonal imbalance (hyperparathyroidism, growth hormone deficiency, etc.); (2) benign tumours (osteomas, osteochondromas, ossifying fibroma and fibrous dysplasia) and malignant (osteosarcoma, hemangiomas, hemangiosarcomas); (3) non-infectious inflammation (osteoarthritis) and infectious, caused by bacteria, fungi (Craig et al. 2016); (4) injuries (fractures, bruises, damage to the ligamentous apparatus).

Theoretically, any of these four groups of pathological factors could be the origin of the bone tissue palaeopathology observed on the metacarpals of the *L. issiodorensis* from Taurida cave (Figures 2–4). However, most of the aforementioned pathologic factors can be excluded based on their diagnoses (Craig et al. 2016). Firstly, diseases associated with metabolic disorders or hormonal imbalance were excluded, since there are no extensions of the bone-brain spaces, there is no atrophy of compact and spongy bone tissue characteristic of osteoporosis (Figure 4). Epiphyseal parts are not deformed. Their deformation is observed during osteomalacia (Craig et al. 2016).

A chondrosarcoma can be also excluded, could be identified on the basis of cartilage cells and not preserved in fossils or osteochondrome, which develops mainly on flat bones (pelvis, scapula) or vertebrae (Gorshkov et al. 2019).

In general, bone tumours are extremely rare in modern domestic animals, only 2–4% of the total number of tumours, and for the most part they occurred in dogs (Baker and Brotherwell 1980). Currently, reliably confirmed cases of osteosarcoma in fossil animals are known for amphibians (Gubin et al. 2000, 2001), dinosaurs (Haridy et al. 2019; Rothschild et al. 2020), artiodactyls (Conkling 1990 cited by Capasso 2005; Capasso and di Tota 1996) etc. The felid metacarpal bones from the Taurida cave did not reveal CT signs of bone tissue destruction, no evident signs of bone tissue absence characteristic of neoplasms growth are shown (Figure 4).

Osteoarthrosis (degenerative osteoarthritis) can also be rejected. It is believed that this is a conventional disease of draft animals, horses and cattle (Bartosiewicz et al. 1997; Cupere et al. 2000; Fabiš 2004; Stevanović et al. 2015). Nevertheless, it is known not only in draft cattle but also in wild animals. It mainly affects large carnivore mammals, e.g. ursids *Melursus ursinus*, *Helarctos malayanus* and *Tremarctos ornatus*, and the mustelid *Gulo gulo* (Greer et al. 1977; Chrószcz et al. 2014). Factors associated with the advent of osteoarthrosis include individuals of advanced age and individual body weight of more than 25 kg (Greer et al. 1977; Rothschild and Martin 2003; Barbosa et al. 2017). In large Felidae, osteoarthrosis is extremely rare (Hawksley et al. 1980; Rothschild et al. 1998; Rothschild and Martin 2003; Diedrich and Rathgeber 2012; Rabe et al. 2022). Therefore, the presence of peripheral exostosis on the McII in *L. issiodorensis* is unlikely to be related to osteoarthrosis. Also, on the articular surfaces of the metacarpal bones, there are no extension and linear-grooves characteristic of osteoarthrosis.

Other non-specific inflammation could be the possible origin of the Taurida remains palaeopathologies such as periostitis and osteomyelitis. The first affects the periosteum, the second also applies to the compact and spongy substance of the bone. Among the fossils, osteomyelitis is well known (Noddle 1974; Baker and Brothwell 1980; Barbosa et al. 2013, 2017a, 2017b; Janssens et al. 2016; García et al. 2017; Shelton et al. 2017; Xing et al. 2018; Aureliano et al. 2020; de Cerff et al. 2021; Luna et al. 2023). Osteomyelitis is characterised by the destruction of bone tissue and the presence of sequesters (necrotic fragments of the bone), and in the case of chronic osteomyelitis, the formation of a fistulous canal. No signs of necrotic isolated fragments of bone are observed in Figure 4F, neither inflammation of the fistulous canal. In addition, osteomyelitis in cats is rare (Harasen and Little 2012).

The largest percentage among the problems with the musculoskeletal system in domestic cats *Felis catus* are associated with fractures. The most common fractures correspond to the mandibular and facial skeleton ones (Harasen and Little 2012). In the wild, living large carnivorans normally display fractures of long bones, mainly because of anthropogenic origin (García 2000; Argyros and Roth 2016). In fossil felines, bone pathologies are associated with injuries sustained during interspecies antagonistic competition but rarely associated with fractures (Diedrich and Zak 2006; Diedrich 2011b, 2011a; Rothschild and Diedrich 2012).

Fractures of the metacarpal and metatarsal bones are generally quite rare. Thus, in domestic cats, they represent only 3.3% of all fractures (Fitzpatrick et al. 2011; Kulendra 2014). There is a known fossil specimen of saber-etoothed felid *Promegantereon ogygia* that demonstrates fracture and abnormal healing of the metatarsal (Salesa et al. 2006) and a third metacarpal of *Machairodus aphanistus* probably affected by osteosclerosis (Salesa et al. 2024) both from the Miocene locality Batallones-1 (Iberian Peninsula).

Nevertheless, based on the above-mentioned comparisons, we believe that the most probable cause for the studied trauma sign was a fracture that was further healed (Figures 2–4). The pathological process displayed by the adjacent McII–IV bones could be associated with trauma without a clear violation of the integrity of these bones. At the same time, a periosteal reaction without lysis in the area of inflammation of the adjacent soft tissues cannot be excluded.

Fracture as case study

Depending on the criterion, fractures are classified (1) according to the type of skin penetration the skin by bone fragments (open/compound and closed); (2) according to the location of the bone defect (diaphyseal, metaphyseal, epiphyseal); (3) according to the shape of the bone defect line (oblique, transverse, spiral, comminuted) or (4) according to the direction of the bone defect line (greenstick fracture and displaced fracture), on its turn fracture repair consists of four overlapping processes: inflammation, soft callus formation, hard callus formation, and remodelling (Schindeler et al. 2008; Waldron 2009; Haschek et al. 2010; Craig et al. 2016).

First, an acute inflammatory reaction is caused by mediators released from the haematoma and from necrotic tissues that form during fracture and circulatory disorders. At the second stage, the haematoma and thrombus are replaced by fibrovascular tissue with the formation of soft callus (fibrous cartilage) as a result of endochondral ossification. The third stage is the formation of hard callus. This stage of primary bone formation is the most active period of osteogenesis. The hard callus is often irregular and insufficiently reconstructed. Due to the formation of callus, the ends of the fracture are firmly fused, and the fracture site is stabilised. The fourth and final phase involves replacing the hard callus with mature lamellar bone and reshaping it to its original bone shape, this final period may take several months or years (Schindeler et al. 2008; Craig et al. 2016). The healing process is not always successful. Formation of new bone and resorption of dead bone may be difficult in the case of a comminuted fracture, a fracture with displacement, or infection of the fracture. In the latter case, a new bone at the border between healthy and diseased is formed, and the organism is trying to isolate the infected area. In this situation, extensive calluses form (Craig et al. 2016). Precisely, this is the process that we observed on the metacarpal specimens from the Taurida cave. The fracture on the studied *Lynx* specimens went through three stages and entered the stage of remodelling.

A disease-associated fracture on the metacarpus of *L. issiodorensis* is here ruled out because there are clear signs of fracture consolidation (pathological fractures due to tumours do not consolidate due to the ongoing destruction process). In addition, pathological fractures usually occur in the late stages of bone tumour development. At this time, other associated signs are already evident, and severe pain is usually present, limiting the use of the limb. It is also worth noting that distal limb tumours are rare in extant and extinct felids. And as a rule, these are tumours of the fingers (Poirier and Steffen 2009; Harasen and Little 2012). It is also important to note that if we assume a primary tumour of one of the diaphyses of the metacarpal bones, then when a certain volume is reached, it would cause deformation of the adjacent bones. In fact, the other three studied metacarpals are parallel to each other. The fossil *Lynx* from the Taurida cave suffered a fifth toe fracture, which initially could not cause severe lameness, but the involvement of adjacent metacarpal bones in the inflammatory process could lead to complications and worsening lameness.

The reason for the fracture of the fifth metacarpal bone in the fossil *Lynx* could be an unsuccessful hunt. *L. issiodorensis* is close in size to the modern Eurasian lynx, had a large skull and a well-developed temporal muscle – m. temporalis (Kurtén 1978). The diet of even a smaller extant *L. lynx balcanicus* in Bulgaria consists of 35% ungulates, such as *Capreolus capreolus* and *Ovis gmelini* (Melovski et al. 2020). It is likely that *L. issiodorensis* also prey on ungulates, such as *Ovis gracilis* or *Tavridia gromovi*. A fracture of the metacarpal bones could have occurred in an unsuccessful attempt to block the blow of the defending victim's horns with the paw. An alternative version of the causes of the fracture may be an unsuccessful landing when jumping from a height (tree or cliff).

It is known that extant large terrestrial predators, including lynxes, adapt to normal life with fractures of long bones of the limbs (and even with their loss-amputations) and are able to hunt and breed for a long time (García 2000; Salesa et al. 2006; Scott et al. 2015). It is likely that the *L. issiodorensis*, after receiving a fracture and during its healing learned how to adapt its dietary behaviours and survived for a moderate time interval.

Conclusions

We conducted a study on four metacarpals belonging to the medium-sized felid *Lynx issiodorensis*, excavated from the Early Pleistocene deposits of the Taurida cave in Crimea. These specimens exhibit clear palaeopathological conditions, likely resulting in a prolonged impairment of hunting abilities for the affected individual.

Our analysis suggests that a displaced oblique fracture observed on metacarpal V (McV) could have initiated the pathological condition in the studied specimen. Furthermore, other metacarpals, particularly McIII and McIV, also show distinct bone growth reactions. Through computed tomographic imaging, we observed initial stages of bone remodelling, indicating a considerable period since the occurrence of the fracture. This includes phases such as inflammation, soft callus formation, and hard callus formation, suggesting that the individual had already progressed beyond these stages.

Our findings align with previous observations on living felids, where scholars have noted a complete return to normal life in extant specimens following complete fracture healing and adaptation of hunting strategies. Thus, our study underscores the resilience of fossil species, akin to their extant counterparts, in overcoming such challenges and adapting to their environment.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Availability of data and material

All relevant data that support the findings of this study are available from the Corresponding Author (joan.madurellmalapeira@unifi.it), upon reasonable request.

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