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An injured lion from Kanegra (Slovenia): CT evidence of survival after severe juvenile forelimb trauma in a MIS6 Eurasian lion

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ABSTRACT

Traumatic limb injuries can be lethal for large predators, yet well documented fossil cases showing severe postcranial trauma with demonstrable long-term survival are extremely rare in extinct lions. We report a pathologically remodelled right humerus (MGGC 22655) from the Kanegra sinkhole (Istria, northern Adriatic), providing the first evidence of a juvenile cave lion surviving a complete forelimb fracture into adulthood. Direct U/Th dating on one associated lion mandible (MGGC 22648) places it in the MIS 6, making it one of the earliest securely dated palaeopathological records for the cave lion lineage. Clinical CT (0.8 mm slices, 0.33 mm resolution) and macroscopic examination reveal a long spiral fracture of the diaphysis, with malunion, overlap and rotational displacement of the shaft, marked shortening, and a hypertrophied deltoid crest. A dense, smoothly marginated circumferential callus and localised cortical thickening along the helical fracture trace document advanced remodelling and robust union, while the absence of sequestrum, involucrum and cloacae allows a purely traumatic etiology to be established. Complete remodelling of the fracture, minimal early arthrosis at the joint and experimental data on age-related healing collectively indicate that the injury occurred before full skeletal maturity, most likely during late juvenile development. Fully fused epiphyses and later degenerative changes show that the individual survived to advanced age despite altered limb geometry and reduced mobility during growth.

This CT-based case provides unprecedented osteopathological evidence that juvenile Eurasian lions could recover from major forelimb trauma and reach adulthood, demonstrating high individual resilience and supplying a critical datapoint for quantifying injury tolerance, survival, and life history strategies in extinct large carnivores.

1. Introduction

Injuries can significantly affect an individual's overall fitness. In predators, such injuries reduce hunting efficiency, constrain prey selection, and limit effective habitat use (Schaller, 1972; Mukherjee and Heithaus, 2013; Harvey et al., 2024). Bone fractures compromise the mechanical stability of the whole body, and the healing process involves progressive phases of recovery: the immediate consequence of the trauma is the damage of blood vessels and the formation of a hematoma, followed by neovascularisation and the formation of a soft fibrovascular

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tissue. Fibrocartilage forms to furnish temporary stability to the bone, and the callus is progressively transformed into woven bone. At this stage, mineralised bone matrix and lamellar bone substitute the woven bone as the final step of the healing process and the callus is ultimately reabsorbed. Bone healing requires time to restore a functional structure (Li and Stocum, 2014); during this period, while the body responds to trauma by stabilising the injured area, the animal experiences a period of intense physiological stress and heightened risk of mortality. Large predators are thought to be particularly vulnerable to such injuries because they require substantial food intake to sustain their body mass and because their overall fitness depends on the continuous maintenance of high performance. This study examines the fossil collection of Eurasian lion remains from Kanegra (Cà Negra in Italian) (Anelli, 1933), housed in the *Collezione di Geologia 'Museo Giovanni Capellini'* (hereafter MGGC) in Bologna, Italy, focusing on the healing process of an injured humerus and the effects of bone remodelling after the trauma. Using clinical computed tomography (clinical CT), we characterise the internal structure, fracture morphology and degree of healing of this element, allowing us to exclude chronic osteomyelitis and to infer the timing and approximate age at which the injury occurred. We discuss the timing and impact of the injury on the animal's growth and assess the potential palaeo-ecological implications of such events in extinct lions, including the conditions that enabled prolonged survival following a severe forelimb fracture in an individual that likely sustained the injury during late juvenile development.

2. Materials and methods

2.1. Clinical CT protocol and diagnostic criteria for fossil long bone trauma

Computed tomography (CT) is now a standard tool for investigating pathologies and traumas in fossil skeletal remains. It has been applied mainly to cranial and dental material, with postcranial diagnoses still comparatively rare (Iurino and Sardella, 2015; Tong et al., 2020; Balisi et al., 2021). CT permits non-destructive, three-dimensional assessment of cortical and trabecular bone, fracture planes, callus morphology and marrow-space changes, and in palaeopathology it complements gross inspection by revealing diagnostic internal patterns (e.g. fracture helicity, periosteal new bone, sequestra) and by guiding targeted histology (Carlson et al., 2003; Cnudde and Boone, 2013). Studies on diverse fossil taxa, including non-avian dinosaurs, show that internal lesion morphology—patterns of new bone, cortical breach and internal organisation—can constrain etiology even in the absence of soft tissues (Hamm et al., 2020). Image quality and interpretability, however, depend on X-ray attenuation contrast and can be compromised by diagenetic mineralisation, beam-hardening and partial-volume effects, necessitating careful acquisition and reconstruction protocols (Ketcham and Carlson, 2001; Cnudde and Boone, 2013; Heřmanová et al., 2020). Resolution must also match the question: clinical scanners are well-suited to large bones and gross pathology, whereas micro-CT is required for micro-cracks and early woven callus (Cnudde and Boone, 2013). Within this framework, we use clinical CT to investigate the traumatised lion humerus from Kanegra, characterising fracture morphology, healing stage and remodelling to reconstruct the injury and its implications for the life history of this Eurasian lion.

The tomographic analysis was carried out using a Philips Incisive CT (Computed Tomography) scanner, originally acquired for applications in precision medicine and medical education and currently housed in the Anatomy Center of the Department of Biomedical and Neuromotor Sciences at the University of Bologna, which also hosts another collection of the University Museum Network (SMA), the "Luigi Cattaneo" Anatomical Wax Collection (Marvi et al., 2024). The scan was acquired at 140 KeV with 300 mA, with the specimen positioned vertically to minimise artefacts and image noise. Images were reconstructed with a proprietary AI-based denoising system, with a "soft" and a "sharp" kernel. 2D Images are displayed with the sharp kernel, and 3D modelling and visualisation was performed on the soft kernel series. Slice thickness was 0.8 mm, with a spatial resolution of 0.33 mm. Cinematic rendering was performed using MeVisLab, and 3D modelling with 3DSlicer (Fedorov et al., 2012).

2.2. Eurasian lion material from Kanegra

The fossil material of Eurasian lion from Kanegra hosted at the MGGC consists of 23 specimens, including teeth and hemimandibles (MGGC 22653, 22656, 22646, 22648) and parts of the postcranium (vertebrae – MGGC 22645, MGGC 22647, humeral fragments and one left ulna – MGGC 22654, MGGC 22652, one scapula – MGGC 22579, one femur – MGGC 23201, and metapodials – MGGC 22658). The present contribution focuses on specimen MGGC 22655, a right humerus with evident features related to a traumatic event. The minimum number of individuals (MNI) for the Kanegra deposit was estimated on the basis of the number of left lower carnassial teeth completely erupted and the presence of a very small, non-ossified humeral epiphysis.

For the purposes of this study, we assign the material to Eurasian lion. Even though the authors are convinced that *Panthera fossilis* (von Reichenau, 1906) and *Panthera spelaea* (Goldfuss, 1810) should be recognised at the species level, the chronological frame and the available skeletal elements from Kanegra do not allow such taxonomic resolution, and the two species are grouped together here. By the term "extinct lions" we refer to all lion populations on all continents, excluding *Panthera leo*. Measurements were taken using a manual calliper with an accuracy of 0.5 mm.

2.3. U-Th chronological framework

U-Th dating was performed on selected carbonate crusts of fossil bones. A chipped subsample of 0.1-0.2 g was gently crushed in segments and ultrasonicated with pure deionised water 3-4 times until no visible powder or detrital material remained and then dried at 70 °C on a class-100 laminar-flow bench in a class-10,000 clean room (Shen et al., 2008). Finally, a subsample of 17-70 mg was picked for U-Th chemistry (Shen et al., 2003). Determination of uranium and thorium isotopic compositions and contents were conducted on a multi-collector inductively coupled plasma mass spectrometer (MC-ICPMS), Thermo Fisher NEPTUNE, housed at the Department of Geosciences, National Taiwan University (Shen et al., 2012). Decay constants used for age calculation are 2.8215 x 10-6 a^{-1} for ^{234}U from Hu et al. (2025) and others available in Cheng et al. (2013). The corrected U-Th ages are relative to AD 1950.

3. The Kanegra sinkhole: site history, stratigraphy and lion assemblage context

The Kanegra quarry (Fig. 1), situated in the northern Sicciole Valley between Piran and Cape Savudrija (Red Istria; Italian: Punta Salvore), was discovered accidently in 1930 following a quarry explosion. In the 1930s, Franco Anelli (1899–1977), a prominent Italian speleologist, produced the first, preliminary classification of the fossil vertebrates recovered from the quarry (Anelli, 1933). As the site no longer exists — owing to decades of extensive and uninterrupted mining in the area — their description, stratigraphic occurrence and age are crucial for improving our knowledge of this fossiliferous but historically understudied locality. At the beginning of the Second World War, the faunal collection was transferred to the University of Bologna to prevent possible destruction. In 1961, in the context of political reconciliation between Italy and Slovenia (Yugoslavia at the time), eleven crates still containing fossil vertebrates were returned to Ljubljana and entrusted to Prof. Ernst Mayr. After a preliminary assessment a few years ago, this material was found to be unavailable both at the Slovenian Museum of Natural History in Ljubljana and at the Notranjski Muzej in Postojna (Matija (Matej) Križnar and Slavko Polak, pers. comm.) and is therefore

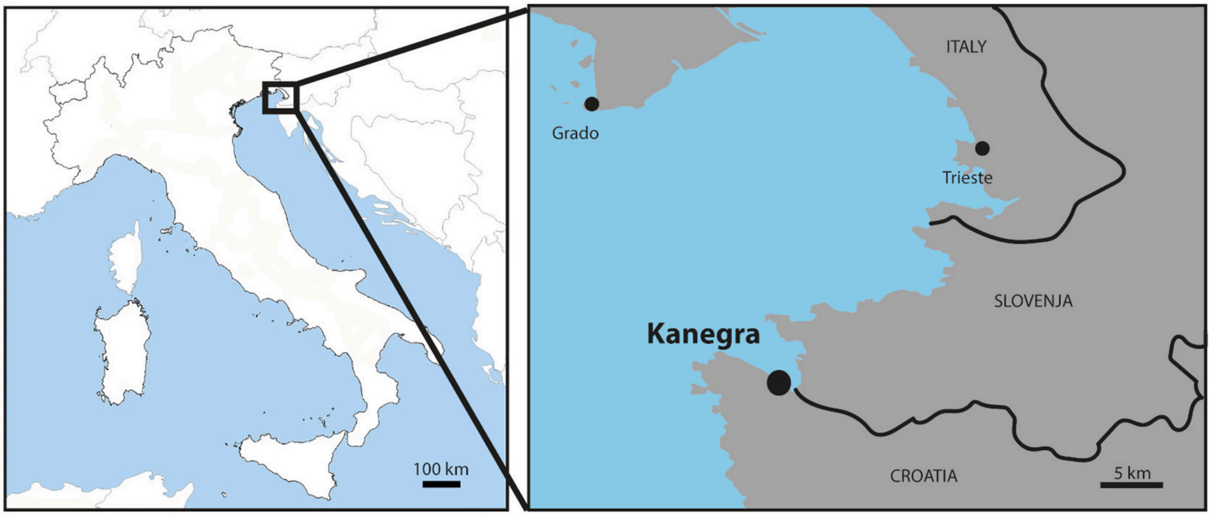

Fig. 1. Kanegra location map.

presumed to have been completely lost. A recent revision of the material still housed in Bologna has produced a comprehensive reappraisal of the Kanegra collection presented here. In parallel, a re-evaluation of the geological and taphonomic data has allowed the recognition of multiple fossil horizons within the original sinkhole sequence. Anelli proposed the first stratigraphic subdivision of the deposits based on field observations (Fig. 2), recognising (from the lower beds upwards) five units:

1. Lower level: ca. 4 m of boulders, rounded pebbles and red clay;
2. Ossiferous horizon: ca. 3.7–3.8 m of incoherent limestone breccia containing heavily oxidised vertebrate remains;
3. Clayey level: ca. 4 m of red–orange clay, barren of vertebrate fossils but containing some carbonised plant fragments;
4. Limestone rubble level: ca. 2 m of breccia preserving bones of domestic animals, micromammals, fish vertebrae, shell fragments and ceramic sherds;
5. Calcitic breccia: ca. 3.5 m of light coloured breccias with calcitic cement, containing human bones, ceramic fragments and shells of *Pomatias elegans*.

By comparing the Bologna collection with Anelli's stratigraphy, the fossil elements in the collection are assigned to at least two levels: the bone-rich (2nd) horizon and the limestone-rubble (4th) level. Bones from the 2nd horizon are typically encrusted in a reddish, clay-rich matrix, frequently with carbonate concretions that are difficult to remove, whereas elements attributed to the 4th horizon display a greyish colour and generally lack carbonate encrustation. Both the pathological humerus MGGC 22655 and the dated lion mandible MGGC

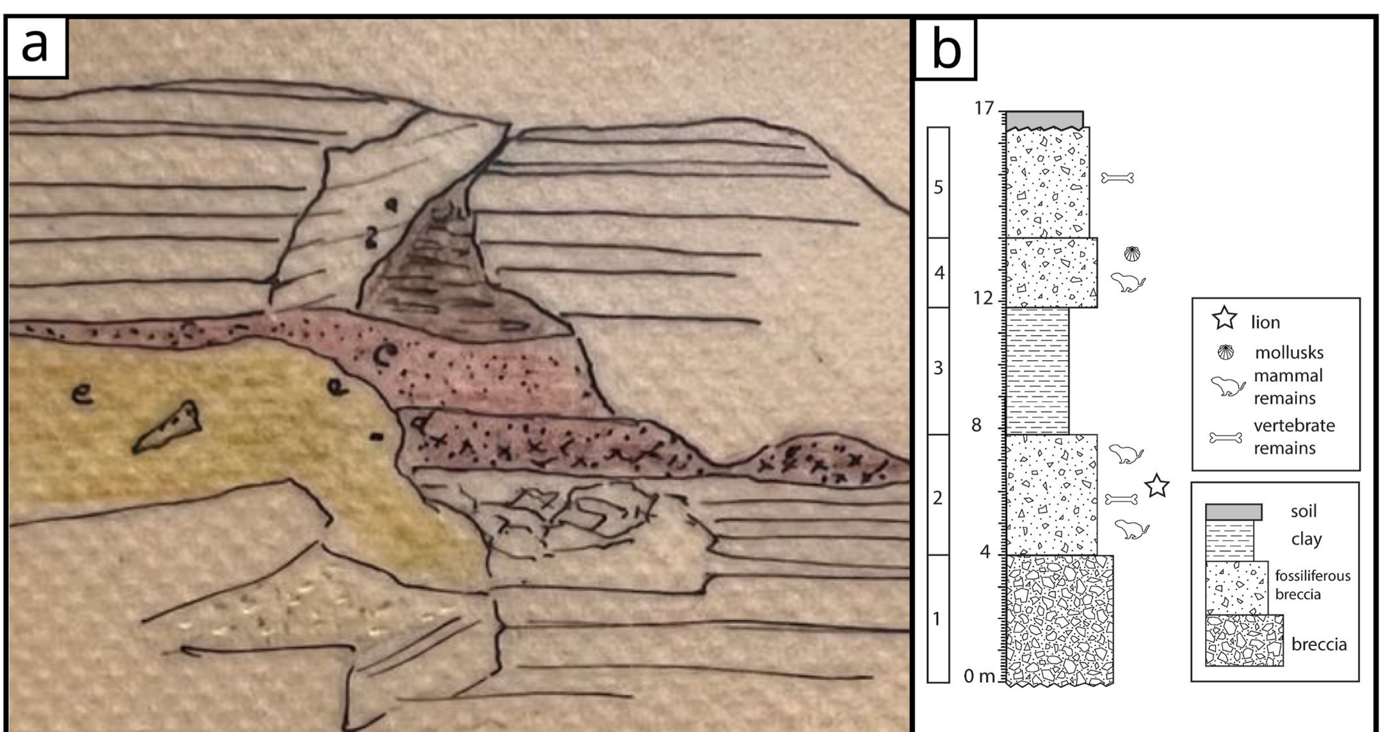

Fig. 2. A. Anelli's 1930 stratigraphic sketch from field notebook (MGGC archives) B. Stratigraphic log of Kanegra sinkhole.

22648 derive from the ossiferous 2nd horizon, providing a common stratigraphic framework for interpreting the age and palaeoenvironmental context of the Kanegra lions. Overall, the Kanegra faunal assemblage is similar to that of numerous other Pleistocene Istrian karst-cave sites, such as Šandalja I and II (Malez, 1972, 1974, 2001), Marlera I, Romualdova pećina (Janković et al., 2016) and Hijenska pećina (Piculjan, 2012). These comparative sites are crucial for constraining the chronological position and faunal context of the Kanegra assemblage, including the lion material described in this study.

4. Trauma and disease in modern and extinct lions: current osteopathological evidence

In extant *Panthera leo*, fractures tend to occur more frequently in the hindlimbs (Nielsen and Bishop, 1953; Kirberger et al., 2006), whereas skeletal alterations are often associated with captivity and ageing (Terra Rossi de Barros et al., 2024) and/or pathological conditions (Viljoen et al., 2015). In extinct lions, traumas and pathologies can only be diagnosed from the skeletons. Injuries have been documented mostly on the cranial region (Diedrich, 2005, 2008a), typically from bites and interpreted as evidence of interspecific conflicts, such as those with cave hyenas, *Crocuta crocuta spelaea* (Goldfuss, 1823) or cave bears, *Ursus spelaeus* (Rosenmüller, 1794). Intraspecific aggressions are less documented (Turner and Antón, 1997; Diedrich and Žák, 2006; Diedrich, 2008b, 2011b, 2021) and have been interpreted as resulting from competition for carcasses or access to shelters (Stiner, 1994; Diedrich, 2005, 2008b, 2010, 2011b; Diedrich and Žák, 2006; Rothschild and Diedrich, 2012). Traumas resulting from conflicts with humans are also documented (Dogandžić, 2023; Russo et al., 2023; Abrams et al., 2025). Sclerosing osteomyelitis and various dental abnormalities such as broken or missing teeth, periodontitis, and congenital malformations are also commonly reported (Beebe and Hulland, 1988; Van Valkenburgh and Hertel, 1993).

Injuries in the postcranium have been reported from both limb and vertebral elements in cave lion, particularly in specimens showing other age-related changes (e.g. arthrosis; Koenigswald and Schmitt, 1987; Diedrich, 2005, 2010, 2011b; Diedrich and Rathgeber, 2012). In the American relative, *Panthera atrox* (Leidy, 1853), a higher frequency of pathological changes has been reported, possibly linked to scavenging behaviour and advanced age (Martin and Gilbert, 1978; Van Valkenburgh and Hertel, 1993; Rothschild and Martin, 2003). No pathologies have yet been documented for *Panthera fossilis* (Blasco et al., 2010), likely reflecting the scarcity of available specimens. Overall, well-documented cases of severe postcranial trauma with clear evidence of long-term survival remain rare in extinct lions, particularly for juvenile individuals (Rothschild and Diedrich, 2012).

An animal's ability to survive and heal is closely linked to several factors: ease of access to food, immune system efficiency, population density of competitors, and, in social species, the presence of caregiving or tolerance among conspecifics. The latter is strictly related to social behaviour; understanding healing processes in extinct animals can therefore provide valuable insights into their behavioural ecology. Modern lions, *Panthera leo* (Linnaeus, 1758) are exceptional among felids in forming stable social groups with reciprocal tolerance among adult conspecifics. However, injured, weak or elderly individuals are generally not actively provisioned by pride members (Mosser and Packer, 2009). For extinct lions, such behaviours remain speculative, and many aspects of their social ecology are still poorly understood (Nedoluzhko et al., 2024). The wall paintings of the Chauvet Cave, depicting a probable group of lions stalking prey, have been interpreted by some authors as evidence of possible social behaviour in the cave lion, and remain an isolated, and debated, line of evidence; comparable depictions are scarce in other Palaeolithic artworks, including the Lion-Man of Hohlenstein-Stadel and additional anthropomorphic or zoomorphic artefacts (Delporte, 1993; Clottes and Azéma, 2005; Kind et al., 2014; Hussain and Floss, 2015, but see Diedrich and Rathgeber, 2012; Wolf et al., 2020; Sigari et al., 2024). Osteopathological evidence of survival after major trauma therefore represents an independent line of data with which to explore life history and potential social strategies in these extinct large felids albeit indirectly and with important caveats regarding sampling and taphonomic bias.

5. Results

5.1. Age and stratigraphic context

U–Th analyses of carbonate crusts on the lion mandible MGGC 22648 (unit 2) yielded ages of 164 ± 42 ka (2σ). After correction for initial ^{230}Th, these ages cluster within Marine Isotope Stage 6 (MIS 6; ca. 191–130 ka). We interpret it as a close minimum estimate for the time of bone burial, with no evidence for significant open-system behaviour in the dated crust. MGGC 22648 and the pathological humerus MGGC 22655 share the same reddish, clay-rich, carbonate-encrusted matrix characteristic of the ossiferous breccia of unit 2, and no internal subdivision of this unit has been recognised in the field record. We therefore infer that MGGC 22655 belongs to the same MIS 6 lion assemblage as MGGC 22648. In this framework, the Kanegra lions represent a late Middle Pleistocene population close to the *Panthera fossilis*–*P. spelaea* turnover, and MGGC 22655 constitutes one of the earliest securely dated cases of severe postcranial pathology in the cave lion lineage.

5.2. Pathological morphology and CT characterisation

All lion specimens from Kanegra are not anatomically connected. The collection is dominated by fragmentary mandibular elements bearing teeth, while the postcranial material is limited and generally small in size. The size variation of the four molars allows to estimate the sex of probably at least two females and two males (Turner, 1984) (Fig. 3). No other specimen in the collection shows direct evidence of fracture, while stress might be visible on some of the teeth. The minimum number of individuals (MNI), inferred by the amount of fully erupted left lower first molars (m1s), is three. The small size of one proximal humeral epiphysis in the Kanegra collection supports the presence of at least one additional very young individual.

The complete humerus (MGGC 22655) is heavily modified in its thickness and shape. This specimen shows a supracondyloid foramen on the medial-distal portion of the bone, typical of Felidae and some species of mustelids. Distally, the lateral condyle is short and rounded, while the lateral epicondyle is conical and positioned medially on the shaft, oriented transversely to the diaphysis (Fig. 4). All epiphyses are fully ossified, and no growth lines are visible on the bone surface. The size of the bone is considerably affected by the trauma, and its measurements are therefore unsuitable for comparative purposes. The total length of the humerus measures 328 mm (Table 1); the bone is shortened, as a direct result of malunion and partial overlap of the two fractured

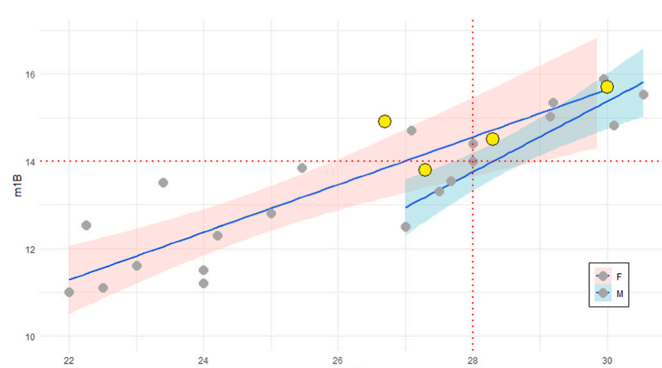

Fig. 3. Sex estimation for the m1s of Kanegra. The specimens used for the comparison are listed in Suppl. Mat.

Fig. 4. Orthophoto of the humerus MGGC 22655: cranial (a), caudal (b), lateral (c) and medial (d). A healthy modern lion humerus is represented in grey for comparison (e − not in scale).

Table 1
Measures of the specimen 22655. *in correspondence of the developed deltoid crest.

Humerus 22655	mm
Total length (gl)	328
Proximal breadth (bp)	83
Proximal depth (dp)	113
Depth of the humeral head	79.5
Distal breadth (bd)	98
Diameter under the humeral head	66
Diameter at the midpoint*	107
Distal trochlea breath	70
Olecranon fossa breadth	37

segments. The middle shaft is also significantly remodelled, and the deltoid crest is anteriorly projected and markedly hypertrophied, heavily altering the whole aspect of the bone. Despite this deformation, the fracture appears to have fully healed. The cortical surface exhibits pronounced vascularisation and branching of blood vessels, particularly around the fracture site, with additional vascular impressions along the anterodistal portion of the diaphysis.

CT examination identifies a transverse fracture at the midshaft of the diaphysis, stabilised by a small metallic wire loop. Distally, the spongy bone exhibits the onset of a long oblique, spiral fracture. A helical low-attenuation line with adjacent cortical thickening and an external callus is evident. The callus is dense and smoothly contoured, with rounding and sclerosis of the original fracture margins and partial reconstitution of the cortical shell, features consistent with advanced healing and a remodelled rather than an early woven callus. No evidence of sequestrum, involucrum, cloaca, or lamellated periosteal reaction extending beyond the remodelled callus is observed. Based on these features, chronic osteomyelitis can be excluded. Patchy trabecular rarefaction and minor cortical irregularities are present at the metaphyseal ends and are interpreted as post-depositional or taphonomic alterations rather than pathological changes. Radiographic screening suggests pseudoarthrosis or a healed fracture that consolidated with partial rotational displacement of the shaft, resulting in misalignment of the proximal and distal epiphyses and a corresponding lateral deviation of the forelimb. On the sagittal plane, two localised areas of cortical thickening are visible, compatible with spiral fracture remodelling. The humeral head appears smoothed, indicating early arthrosis, while the trabecular network within the metaphysis is less dense than expected, suggesting a localised inflammatory process that affected the surrounding bone tissue (Fig. 5).

6. Discussion

We examined the complete collection of lion remains from Kanegra housed in Bologna, currently comprising a minimum of four individuals: one very young and three adults. Based on m1 size variation, the assemblage includes two females and two males. The overall morphology and size of the relatively gracile skeletal elements suggest that the Kanegra lions most likely belong to *P. spelaea*. U–Th dating of carbonate crusts on the associated mandible MGGC 22648 places the Kanegra lion assemblage in MIS 6 (late Middle Pleistocene), and—given the shared lithological context within unit 2—provides a robust chronological framework for the pathological humerus MGGC 22655 as an early representative of the cave lion lineage.

Lions first dispersed into Europe around one million years ago, with *Panthera fossilis* documented in a few localities (Madurell-Malapeira et al., 2024a, 2024b). By approximately 700 ka, the species had achieved a geographically widespread distribution (Sala, 1990; Argant et al., 2007; Hankó and Korsós, 2007; Blasco et al., 2010; Sabol, 2014; Argant, 2024). Later, *Panthera spelaea* replaced this first representative of the group (Lewis et al., 2010; Sotnikova and Foronova, 2013; Sherani et al., 2023; Iannucci et al., 2024; Puzachenko et al., 2024; Madurell-Malapeira et al., 2024a). The two species are estimated to have genetically diverged between ~2.9 and 0.6 Ma (Burger et al., 2004; Barnett et al., 2016; Stanton et al., 2020). Across the chronological interval spanning the Middle–Late Pleistocene boundary, the fossil record of extinct lions is sparse, leading to an ongoing and unresolved debate among palaeontologists regarding their speciation and taxonomic classification (Argant and Brugal, 2017; De Manuel et al., 2020; Persico, 2021; Prat-Vericat et al., 2022; Riquelme Cantal et al., 2024). In particular, the timing and mechanism of the turnover remain debated due to overlapping morphology, population contractions, size variation,

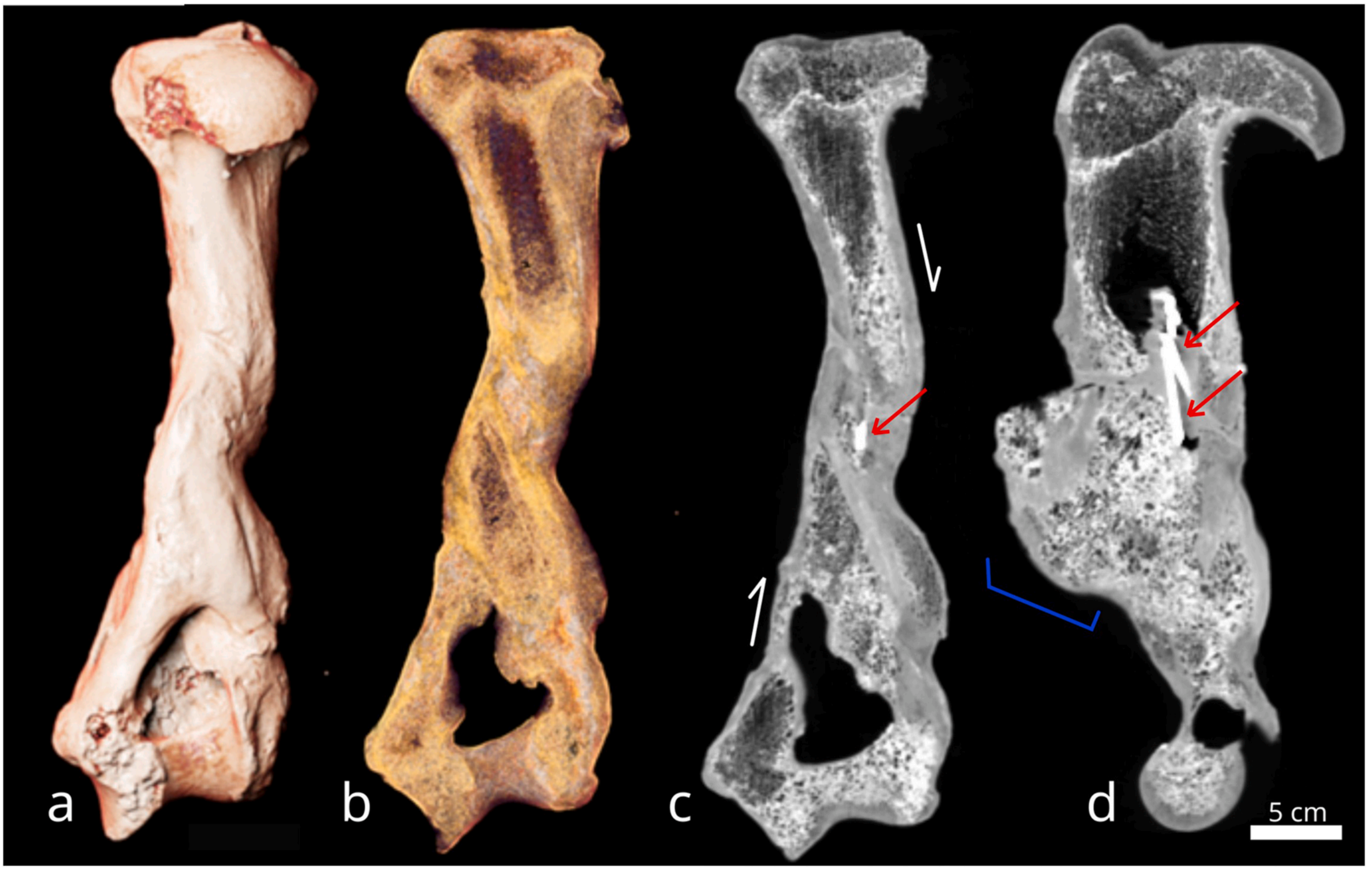

Fig. 5. CT results for the humerus MGGC 22655. (a) Three-dimensional rendering of the specimen. (b) Mid-sagittal CT slice showing internal structure and fracture remodelling. (c) Mid-sagittal slice with white arrows indicating the direction of torsional deformation. (d) Mid-lateral slice highlighting the hypertrophied development of the deltoid process (blue). Red arrows indicate the stabilising metallic clip. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

and sexual dimorphism (Turner, 1984; Stuart and Lister, 2011; Marciszak et al., 2014; Marciszak and Gornig, 2024; Puzachenko et al., 2024). Beyond the lack of a clear taxonomic framework and the discontinuity of the fossil record, the small number of described skeletal remains has resulted in very few specimens preserving postcranial pathologies or traumatic lesions. This limitation restricts the robustness of interpretations and hinders reliable comparisons among extinct lion populations.

We focus our attention on the injured humerus MGGC 22655. The bone is shortened relative to the expected length due to malunion and overlap, with malrotation of the shaft inferred from epiphyseal misalignment; cortical hypertrophy near the deltoid insertion indicates adaptive remodelling under altered loading. These observations are congruent with the gross and metric description (shortening due to overlap) and with CT evidence of a fully healed fracture. Spiral fractures in long bones reflect torsional loading; on CT they are recognised as helically oriented lucent lines that may traverse cortex and cancellous bone. The presence of a circumferential, dense, smoothly marginated callus bridging the defect is a hallmark of union and remodelling on CT. Together, the helical fracture trace and mature bridging callus indicate a torsional injury with subsequent long-term survival and robust healing (Perlepe et al., 2019). Well documented CT signs of chronic osteomyelitis in long bones include sequestrum (devitalised fragment with a lucent rim), involucrum (reactive sheath of bone) and cortical cloacae. The absence of these features in the Kanegra humerus supports a traumatic rather than infective etiology and excludes an infective superposition (Desimpel et al., 2017). A small metallic wire loop present at the mid-diaphysis (a historical stabilisation-restoration) could generate beam-hardening artefacts, yet the callus architecture and fracture helicity remained interpretable at the chosen settings. Given the ~0.33 mm pixel size and 0.8 mm slice thickness, sub-millimetre histological features (e.g. early intramedullary woven callus, fine vascular channels) lie below reliable resolution; micro-CT would be necessary to investigate such details, albeit with the caveat regarding potential dose effects on collagen if future geochemical analyses are planned (Cnudde and Boone, 2013; Duval et al., 2025). The CT appearance of the healed fracture is highly comparable to that illustrated by Mubarak et al. (2006) for paediatric femoral shaft fractures treated with casts, particularly in terms of callus distribution and alignment.

Most pathologies described in extinct lions involve the cranial region and are interpreted as consequences of conflicts and dental disease (Beebe and Hulland, 1988; Van Valkenburgh and Hertel, 1993; Stiner, 1994; Turner and Antón, 1997; Diedrich, 2005, 2008a, 2008b, 2010, 2011b; Diedrich and Žák, 2006; Rothschild and Diedrich, 2012), whereas injuries and traumas affecting the postcranium are rarely reported. A single humeral pathology in an adult cave lioness has been described at Neumark-Nord Lake 1 (Eemian, central Germany; Diedrich, 2011a). This bone exhibits exostosis at the deltoid tuberosity, associated with enlarged distal humeral foramina, arthritis and traumatic lesions in other regions of the skeleton. The overall condition of this articulated skeleton has been interpreted as the result of chronic stress and localised calcification at the tendon insertion. To our knowledge, no other humeral pathologies have been reported for Eurasian lions.

In fact, postcranial traumas are rarely reported in extinct carnivores. Evidence of a healed fracture in *Lynx issiodorensis* (Croizet and Jobert, 1828) has been reported by Serdyuk et al. (2024): in this case, the trauma on the fifth metacarpal caused an extended infection, with the secondary bone growth on the adjacent bones. Postcranial fractures in

Smilodon fatalis (Leidy, 1869) and *Aenocyon dirus* (Leidy, 1858) from Rancho La Brea have been interpreted as reflecting differences in social behaviour and hunting strategies between the two species (McCall et al., 2003; Brown et al., 2017). A displaced fracture has been reported in *Canis chihliensis* Zdansky, 1924 (Nihewan Basin, Early Pleistocene): the right tibia (IVPP V18139.20) shows similarities with the humerus described here (shortened bone, remodelled callus, possible torsion, increased vascularisation) (Tong et al., 2020). Given the severity of the trauma, the authors suggested the presence of social behaviour in *C. chihliensis*.

Assuming the trauma in our specimen MGGC 22655 was confined to the humerus within the postcranium, the Kanegra lion likely did not experience any long-term debilitating impairment. A lateral torsion above the elbow, combined with a general shortening of the forelimb, was likely evident in life, visibly affecting gait and reducing overall mobility. The supracondylar foramen was not impacted by the trauma, suggesting that the median nerve and brachial artery remained functional, allowing normal flexion of the paw and maintaining adequate peripheral blood circulation. The deltoid tuberosity was disrupted by the fracture but subsequently compensated by hypertrophic remodelling of the bone surface, with the deltoid process displaced slightly distally along the diaphysis. Despite this alteration, the deltoid muscle attachment appears to have been efficiently reorganised, enabling the animal to retain normal forelimb posture, shoulder alignment and functional strength. Given the complete remodelling of the bone, with little to no evidence of chronic periosteal degeneration or arthrosis, the injury likely occurred while the bone was still developing and retained some plasticity, allowing functional recovery during growth. Gruber et al. (2006) summarise evidence that increasing age is associated with slower fracture healing and higher risks of delayed union and non-union in long bones, linking age-related biological changes (e.g. reduced vascularity and progenitor cell function) to longer time-to-union and lower healing success rates (Foulke et al., 2016).

On this basis, we propose that the individual likely was injured before full skeletal maturity, and most likely during late juvenile development. At this stage, the animal was therefore most likely still dependent on its mother but had begun accompanying the pride on hunts. In modern lions, this corresponds to an age when cubs remain vulnerable to infanticide by incoming males. At this developmental stage, bone tissue is still porous and rapidly growing, which may have facilitated a faster recovery than would occur in adults. The individual evidently survived to an advanced age, as indicated by the complete ossification of the epiphyses and arthritic changes. Arthrosis is a degenerative condition commonly associated with ageing, prior trauma or repetitive mechanical stress. Together, these features imply that the individual lived well beyond independence and reached sexual maturity. Despite the early trauma, its overall fitness and capacity to survive within a putative pride were likely not significantly compromised.

Osteological data on putative social behaviour in extinct lions remain scarce. The main iconographic evidence invoked for group hunting is the lion panel in Chauvet Cave (Clottes and Azéma, 2005). This interpretation is debated, and comparable depictions are rare in other Palaeolithic art (Delporte, 1993; Diedrich and Rathgeber, 2012; Kind et al., 2014; Hussain and Floss, 2015; Sigari et al., 2024). In this context, well-documented cases of survival after major trauma provide an independent, albeit indirect, line of evidence for assessing life history and potential social strategies in cave lions. Modern lions (*Panthera leo*) are unusual among felids in forming stable social groups with reciprocal tolerance among adults, yet severely injured adults are generally not provisioned and typically recover, if at all, through solitary retreat, fasting and wound care by licking (Mosser and Packer, 2009). Reports of sustained care for severely injured cubs are very rare and not reported in the scientific literature. These observations suggest that, even in a social felid, survival after major limb trauma does not necessarily imply active provisioning by conspecifics. In specimen MGGC 22655, the humeral fracture resulted in forelimb shortening and torsion that would have altered gait and reduced mobility, at least during healing. Nevertheless, the preserved morphology indicates that major muscle attachments and neurovascular structures remained functional and that effective forelimb use was ultimately regained. The individual survived a late juvenile injury and reached advanced age, attaining skeletal maturity and developing arthrosis. Since juvenile individuals are less likely to survive periods of feast and famine, we can neither confirm nor reject the hypothesis that the young lion had access to food during the healing process — either as part of a pride or due to environmental conditions of resource abundance that may have reduced intraspecific aggression and competition, thereby ensuring sufficient food intake for full recovery. This demonstrates that at least some Middle Pleistocene Eurasian lions could recover from severe forelimb trauma and maintain sufficient function for long-term survival and probable reproduction.

We therefore interpret MGGC 22655 primarily as evidence of marked individual resilience and favourable ecological conditions (e.g. adequate prey availability) rather than as direct proof of cooperative care. Both solitary and group-living scenarios remain compatible with the observed healing. However, the case provides an important datapoint showing that cave lions were capable of enduring substantial musculoskeletal impairment, a factor that should be incorporated into future discussions of their hunting ecology and social flexibility.

7. Conclusion

The fossil assemblage from Kanegra in Croatia represents one of the few European collections and probably the oldest fossil providing direct evidence of traumatic postcranial pathology in cave lion. The completely remodelled humeral fracture in MGGC 22655 documents the survival of an individual that sustained a severe forelimb injury during late juvenile development but despite this lived to advanced age. This is, to our knowledge, the first reported case of a juvenile cave lion surviving a complete forelimb fracture into adulthood, indicating that, despite altered limb geometry and reduced mobility during growth, functional strength and hunting ability were ultimately regained. By combining macroscopic description with clinical CT, this study provides a detailed, non-destructive characterisation of fracture morphology, healing stage and remodelling in an extinct lion, and robustly excludes chronic osteomyelitis as an alternative diagnosis. Beyond its individual narrative, this case offers new insight into life history, resilience and the biomechanical tolerance of extinct lions, showing that juveniles could recover from major limb trauma and still reach reproductive age. Prolonged survival following such an injury, in a large (mostly) ambush predator living under Pleistocene climatic and resource fluctuations, also constrains plausible social and ecological scenarios for cave lions. More broadly, this rare integration of osteopathological, stratigraphic and taphonomic data provides a comparative framework for assessing stress, injury, survival strategies and potential social dynamics in extinct large carnivores and highlights the value of CT-based palaeopathology for refining behavioural and ecological inferences from fragmentary fossil records.

CRediT authorship contribution statement

Elena Ghezzo: Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Michela Contessi:** Conceptualization, Data curation, Investigation, Methodology, Resources, Validation, Writing – original draft, Writing – review & editing. **Giulio Vara:** Data curation, Formal analysis, Methodology, Software, Writing – original draft, Writing – review & editing. **Elisa Lodolo:** Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Stefano Ratti:** Data curation, Investigation, Methodology, Software, Writing – original draft, Writing – review & editing. **Paul J. Funston:** Investigation, Writing – original draft, Writing – review & editing. **Chuan-Chou Shen:** Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review

& editing. **Chun-Yuan Huang:** Data curation, Funding acquisition, Methodology, Writing – original draft, Writing – review & editing. **Jo De Waele:** Methodology, Resources, Validation, Writing – original draft, Writing – review & editing. **Federico Fanti:** Conceptualization, Data curation, Investigation, Validation, Writing – original draft, Writing – review & editing.

Declaration of competing interest

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

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