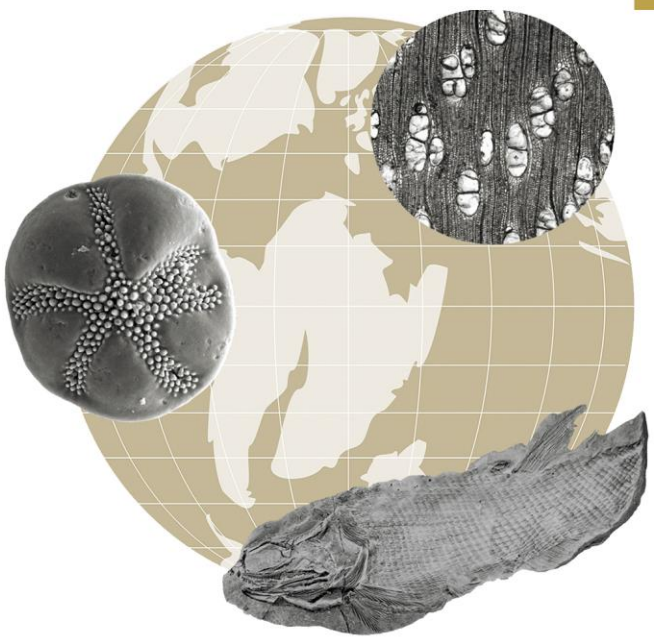
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# Evidence of bone infection in the Middle Jurassic ophthalmosaurid *Mollesaurus periallus* (Ichthyosauria) from Patagonia, Argentina

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Running Header: Mitidieri *et al*.: Bone infection in *Mollesaurus periallus*.

Short Description: This study documents bone infection in *Mollesaurus periallus*, providing new insights into disease and paleobiology in Jurassic ichthyosaurs.

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**Abstract.** Skeletal pathologies preserved in fossil vertebrates provide direct evidence of disease processes and host responses, offering valuable insights into the biology and survival of extinct organisms. Here, we describe pathological lesions affecting the holotype of the ophthalmosaurid ichthyosaur *Mollesaurus periallus* from the early Bajocian Los Molles Formation (Neuquén Basin, Patagonia, Argentina). Based on a macroscopic analysis, the right stapes and some rib fragments exhibit cortical disruption, exposed trabecular bone, and periosteal reactive bone growth. A computed tomography (CT) of the ribs further revealed internal cavities and localized areas of reduced bone density. Combined macroscopic and tomographic evidence is consistent with an infectious process affecting the stapes, whereas the lesions in the rib fragments are most compatible with an osteomyelitis-like infection. This study represents the first documented infectious skeletal pathology in a Jurassic ichthyosaur from the Neuquén Basin and expands the currently limited knowledge of infectious skeletal pathologies in Ophthalmosauridae.

**Keywords.** Marine reptile, Paleopathology, Ichthyosaur, Bajocian.

**Resumen.** EVIDENCIA DE INFECCIÓN ÓSEA EN EL OFTALMOSÁURIDO DEL JURÁSICO MEDIO *MOLLESAURUS PERIALLUS* (ICHTHYOSAURIA) DE LA PATAGONIA, ARGENTINA. Las patologías esqueléticas preservadas en vertebrados fósiles proporcionan evidencia directa de procesos patológicos y de las respuestas del hospedador, ofreciendo valiosos aportes sobre la biología y supervivencia de organismos extintos. En este trabajo, describimos lesiones patológicas que afectan al holotipo del ictiosaurio oftalmosáurido *Mollesaurus periallus*, procedente de la Formación Los Molles del Bajociano temprano (Cuenca Neuquina, Patagonia,

Argentina). Sobre la base de un análisis macroscópico, el stapes derecho y algunos fragmentos de costillas presentan disrupción cortical, exposición del hueso trabecular y crecimiento óseo reactivo periostal. Una tomografía computarizada (TC) de las costillas reveló además cavidades internas y áreas localizadas de menor densidad ósea. La evidencia macroscópica y tomográfica combinada es consistente con un proceso infeccioso que afecta al stapes, mientras que las lesiones en los fragmentos de costilla son más compatibles con una infección similar a la osteomielitis. Este estudio representa el primer registro documentado de una patología esquelética infecciosa en un ictiosaurio jurásico de la Cuenca Neuquina y amplía el conocimiento actualmente limitado sobre las patologías esqueléticas infecciosas en Ophthalmosauridae.

**Palabras clave.** Reptil marino, Paleopatología, Ictiosaurio, Bajociano.

## INTRODUCTION

Ichthyosaurs were among the most successful marine reptiles of the Mesozoic, ranging from the Early Triassic (early Olenekian, ~250 Ma) to the Late Cretaceous (late Cenomanian, ~94 Ma) (McGowan & Motani, 2003; Fischer *et al*., 2016; Kear *et al*., 2023; Meyerkort *et al*., 2025). Following the end-Permian mass extinction, they underwent a rapid evolutionary radiation and acquired numerous anatomical and physiological adaptations to a fully aquatic lifestyle, including a streamlined body, enlarged eyes, and efficient swimming capabilities (Maisch & Matzke, 2000; Motani, 2005; Kelley & Pyenson, 2015). Among them, Ophthalmosauridae became the dominant ichthyosaur clade during the Middle and Late Jurassic, achieving a nearly global distribution and occupying a wide range of marine environments (Fernández & Campos, 2015; Moon, 2019).

Paleopathology provides direct evidence of injuries and diseases of extinct organisms (Rothschild *et al*., 2023) and has become an essential tool for reconstructing vertebrate paleobiology. Many pathological conditions produce characteristic modifications to bone tissue that can persist in the fossil record. As a result, fossil skeletons may retain diagnostic signatures of biological processes that affected individuals during life (Rothschild *et al*., 2023). These pathological features facilitate a differential diagnosis, providing insights into behavior, ecology, biomechanics, and survival following injury or disease (Moodie, 1918; Rothschild & Martin, 1993, 2006; Rothschild *et al*., 2023). Previous studies in extinct vertebrates have interpreted healed bite marks as evidence of failed predation or intraspecific aggression (*e.g.*, Tanke & Currie, 1998; Zammit & Kear, 2011; Benoit *et al*., 2021; Herrera *et al*., 2026), whereas fractures, vertebral fusions, avascular necrosis, and other skeletal pathologies have been used to infer locomotor stresses, diving behavior, and responses to traumatic injury

(*e.g.*, Bell & Coria, 2013; Pardo-Pérez *et al*., 2019, 2020; Talevi *et al*., 2019, 2021; Cruzado-Caballero *et al*., 2021, 2023; Rothschild *et al*., 2023; Baiano *et al*., 2024; Mitidieri *et al*., 2025).

Skeletal pathologies are well documented in ichthyosaurs. Previous studies have reported traumatic injuries, healed fractures, bite marks, avascular necrosis, vertebral abnormalities, ankylosis, and infectious conditions affecting the jaws, ribs, girdles, vertebrae, and appendicular skeleton (Kear, 2002; Zammit & Kear, 2011; Rothschild *et al*., 2012; Maxwell *et al*., 2019; Pardo-Pérez *et al*., 2018a, 2018b, 2019, 2020). These studies have demonstrated that skeletal pathologies constitute an important source of information on ichthyosaurs behavior, locomotion, interactions with predators or conspecifics, and the ability of individuals to survive severe injuries or chronic disease. Moreover, they highlight that even historically well-known specimens may preserve previously unrecognized pathological features warranting renewed investigation.

The ophthalmosaurid *Mollesaurus periallus* Fernández, 1999, from the early Bajocian Los Molles Formation in the province of Neuquén, Argentina, represents an important taxon for understanding the early evolution of the clade. Previous studies focused on its anatomy and bone histology demonstrated an unusually compact rib cortex compared with other parvipelvian ichthyosaurs, suggesting that not all derived ichthyosaurs were adapted for sustained high-speed swimming (Talevi & Fernández, 2012). However, despite the detailed anatomical and histological study of this specimen, pathological modifications affecting the skeleton have never been investigated. Consequently, whether this historically important specimen preserves evidence of disease has remained unknown.

We describe previously unrecognized pathological lesions affecting the holotype of *Mollesaurus periallus*. We integrate detailed macroscopic observations with

computed tomography to characterize these lesions, evaluate their differential diagnosis, and discuss their paleobiological significance.

**Institutional abbreviation.** MOZ-PV, Museo Olsacher Zapala - Paleovertebrados, Zapala, Neuquén, Argentina.

## Geological setting

The first major marine transgression recorded in the Neuquén Basin occurred during the Early Jurassic and is represented by the Los Molles Formation (Weaver, 1931). In the Chacaico Sur area (Fig. 1A, B), the upper part of the formation is exposed and consists predominantly of dark shales and marls interbedded with sandstones (Gasparini, 1997). These deposits are interpreted as offshore, pelagic-dominated sediments, with sandstone layers attributed to storm-induced orbital and gravitational flows (Spalletti *et al*., 1994; Zavala, 1996; Franzese *et al*., 2007).

The age of the fossil-bearing interval has traditionally been assigned to the early Bajocian based on invertebrate fauna (Westermann & Riccardi, 1979; Riccardi *et al*., 1994; Spalletti *et al*., 1994). More recently, Chaumeil Rodríguez *et al*. (2025) confirmed an early Bajocian age (Subzone NJT10a) based on calcareous nannofossil analysis. The low diversity and abundance of the assemblage suggest shallow marine conditions linked to the onset of a regressive phase (Chaumeil Rodríguez *et al*., 2025).

[Insert Figure 1 here. Figure intended for two-column width.]

# MATERIAL AND METHODS

## Specimen examined for pathological analysis

The holotype of *Mollesaurus periallus* (MOZ-PV 2282) was recovered from the Middle Jurassic of the Chacaico Sur area (Los Molles Formation, early Bajocian) in the province of Neuquén, Argentina (Fernández, 1999).

It consists of an incomplete and partially articulated skeleton containing the skull, parts of the vertebral column and associated ribs of an adult specimen (Fig. 2) (Fernández, 1999). The identification of this specimen as an adult is supported by the ontogenetic fusion of the sutures between the vertebral centra and their neural arches (Fernández, 1999). This interpretation is further supported by rib histology, which shows extensive secondary remodeling reaching the cortical region (Talevi & Fernández, 2012).

[Insert Figure 2 here. Figure intended for two-column width.]

The right stapes, still articulated with the skull, and rib fragments of the specimen MOZ-PV 2282 were selected based on macroscopically observed pathological features. These elements are the only skeletal remains exhibiting macroscopic abnormalities consistent with pathological modification.

**Methodology**

The pathological elements of *Mollesaurus periallus* (MOZ-PV 2282) were examined through detailed macroanatomical observations. Particular attention was paid to distinguishing pathological lesions from post-mortem damage by evaluating cortical continuity, reactive bone formation, surface texture, and the spatial relationship between cortical destruction and surrounding bone. Differential diagnosis followed the comparative criteria proposed by Thompson (2017), Jacobson & Garner (2020), Rothschild *et al*. (2023), and Cornille *et al*. (2025), emphasizing lesion morphology, cortical destruction, periosteal reaction, and internal architecture. Histological sampling

was not performed because destructive analysis of the holotype was not authorized by the museum curatorial staff. The rib fragments were therefore investigated using computed tomography (CT) as a non-destructive approach to evaluate their internal morphology and improve a differential diagnosis. The CT was carried out at Clínica Moguillansky (Neuquén, Argentina) using a GE BrightSpeed CT scanner with 16 detector rows. The acquisition protocol employed a tube voltage of 120 kV. Additionally, standard volumetric reconstructions (STD) at 1.2 mm and bone reconstructions (BONE) at 0.625 mm were obtained. The stapes could not be scanned because the articulated skull exceeded the size limitations of the available CT scanner.

## RESULTS

### Stapes

The right stapes of *Mollesaurus periallus* (MOZ-PV 2282) is a robust and well-ossified element (Fig. 3A). Its broad proximal portion bears an articular surface for contact with the basioccipital and opisthotic, while the narrower distal portion preserves the facet for articulation with the quadrate (Fig. 3A).

In MOZ-PV 2282, the pathological alterations are restricted to the distal portion of the stapes, particularly around the quadrate articulation. This region exhibits an irregular cortical surface associated with localized periosteal reactive bone growth (Fig. 3B). This reactive tissue forms a roughened external texture that contrasts with the normally smooth cortical bone of non-pathological stapes. Adjacent to this area, portions of the cortical layer are disrupted, exposing underlying trabecular bone (Fig. 3C–D). The margins surrounding the exposed trabecular bone are bordered by a thin rim of periosteal reactive bone, indicating an active osseous response rather than post-

mortem or taphonomic alteration (Fig. 3D). Since only the right stapes is preserved, it is not possible to determine whether the left stapes exhibited the same pathological signs.

[Insert Figure 3 here. Figure intended for two-column width.]

**Rib fragments**

Non-pathological ribs of *Mollesaurus periallus* (MOZ-PV 2282) are characterized by a ventrally swollen and dorso-ventrally expanded morphology, with a sharp ridge extending from the capitulum along the main axis (Fig. 4). In addition, the posterior surface bears a deep groove, and the cortex is smooth and compact (Fig. 4). The rib fragments analyzed here show an unusual arrangement, consisting of two transversely overlapping fragments (Fig. 5A). However, this overlap is not related to a pathological process, but rather resulted from post-mortem displacement and diagenetic compression. The longer fragment preserves part of the proximal portion and an incomplete distal end, whereas the shorter fragment corresponds to the distal portion of a second rib. Due to the absence of diagnostic anatomical landmarks, both elements are regarded as indeterminate ribs.

[Insert Figure 4 here. Figure intended for two-column width.]

The pathological region of the rib fragments is characterized by irregular cortical disruption, exposed trabecular bone, and localized periosteal reactive bone growth (Fig. 5B). The cortical surface is markedly irregular, with areas of bone loss exposing the underlying trabecular tissue (Fig. 5B). Multiple cavities with irregular margins are present on the bone surface and communicate with the exposed trabecular bone (Fig. 5C–E). These cavities vary in size and shape and are distributed throughout the affected region. Around these areas, a thin rim of periosteal reactive bone growth forms slightly elevated surfaces (Fig. 5D–E).

[Insert Figure 5 here. Figure intended for two-column width.]

Computed tomography scans reveal the internal morphology of the lesions observed on the external surface of the rib fragments, corresponding to the cavities described above (Fig. 6). Additionally, the scans show localized areas of decreased bone density relative to the adjacent unaffected bone, represented by darker grey regions compared with the higher-density appearance of the surrounding normal bone (Fig. 6B–C). The lesions affect both the external cortical surface and the internal architecture of the ribs.

[Insert Figure 6 here. Figure intended for two-column width.]

## DISCUSSION

### Stapes pathology

The pathological alterations observed in the stapes are most consistent with a localized infectious process. Macroscopically, the bone exhibits periosteal reactive bone growth associated with cortical disruption and exposure of the underlying trabecular bone. These features are consistent with an inflammatory response, a pattern commonly reported in infectious skeletal lesions of extant reptiles and fossil vertebrates (Divers & Mader, 2005; Rothschild & Martin, 2006; González, 2019; Rothschild *et al*., 2023; Cornille *et al*., 2025). Because only external morphology is available, the lesion is more conservatively interpreted as an infectious bone pathology rather than assigned to a specific infectious condition. The absence of tomographic or histological data precludes a confident differential diagnosis among infectious bone pathologies, such as osteomyelitis, osteitis, and periostitis (Anné *et al*., 2015; Rothschild *et al*., 2023).

The available evidence is insufficient to determine the route by which the infection reached the stapes, and therefore the origin of the lesion remains uncertain.

Observations from extant reptiles suggest two plausible mechanisms. In turtles, crocodilians, and squamates, inflammatory diseases affecting the middle-ear commonly originate from ascending bacterial infections through the Eustachian tube and frequently induce localized inflammatory changes in adjacent cranial bones (Divers & Stahl, 2019; Jacobson & Garner, 2020). Alternatively, infections affecting cranial bones may result from local extension of adjacent soft-tissue infections or from hematogenous dissemination originating at distant infectious foci (*e.g.*, Divers & Mader, 2005; González, 2019; Jacobson & Garner, 2020; Cornille *et al.*, 2025). Accordingly, both localized middle-ear infection and hematogenous dissemination remain plausible pathways by which the infection could have reached the stapes. However, the available evidence does not allow discrimination between these alternatives.

Finally, the stapes provides structural support to the braincase, articulating medially with the basioccipital and opisthotic, and laterally with the quadrate (McGowan, 1973; Kear, 2005). Although its functional role in ichthyosaurs remains poorly understood and the auditory capabilities of this group are still incompletely known, the stapes may have functioned as an inertial element in the detection of low-frequency sounds (Hetherington, 2008; Sobral *et al.*, 2016). Under this hypothesis, the pathological alteration of the stapes in MOZ-PV 2282 could potentially have interfered with sound transmission. Nevertheless, given the limited understanding of ichthyosaur auditory function, the magnitude and functional consequences of such an effect cannot be directly assessed in fossil material.

**Rib fragments pathology**

The pathological rib fragments provide more robust evidence for an infectious bone disease owing to the integration of macroscopic observations and computed

tomography. Among infectious bone diseases, such as osteitis, periostitis, and osteomyelitis, the last one provides the closest match to the pathological features observed in the rib fragments. Osteitis and periostitis were considered during the differential diagnosis but are regarded as less consistent with the observed evidence. Osteitis primarily involves inflammation and remodeling of cortical bone, whereas periostitis is generally characterized by reactive periosteal bone deposition with comparatively limited cortical destruction (Rothschild & Martin, 2006; Rothschild *et al*., 2023). Neither condition typically produces the combination of features documented in the pathological rib fragments. On the other hand, osteomyelitis is characterized by bone destruction and reactive new bone formation, commonly associated with bacterial, fungal, viral, or protozoal infections (Townsend & Koç, 2023). The condition may affect the medullary cavity, cortical bone, periosteum, and adjacent soft tissues (Jorge *et al*., 2010), and in severe cases may result in extensive skeletal damage and systemic complications such as sepsis (Smith *et al*., 2006). Common features associated with osteomyelitis include involucrum (*i.e*., reactive periosteal bone surrounding infected tissue), sequestrum (*i.e*., necrotic bone separated from healthy tissue), cloacae (*i.e*., openings that allow drainage of infectious material), and periosteal reaction induced by inflammation (Divers & Mader, 2005).

The affected elements of MOZ-PV 2282 exhibit extensive cortical disruption associated with periosteal reactive bone growth and exposure of trabecular bone. Computed tomography additionally reveals multiple internal cavities and localized areas of reduced bone density within the surrounding bone. The internal cavities identified through computed tomography may represent cloaca-like structures associated with a destructive process, potentially related to osteomyelitis (Rothschild *et al*., 2023). In extant reptiles, osseous cloacae function as drainage pathways for inflammatory

exudates during infection (Huchzermeyer & Cooper, 2000; Rothschild *et al*., 2023). Reptiles typically produce caseous or granulomatous inflammatory material rather than the liquid purulent exudate commonly observed in mammals (Huchzermeyer & Cooper, 2000; Divers & Stahl, 2019; Jacobson & Garner, 2020). In addition, the surrounding areas of reduced bone density may represent regions of bone resorption associated with inflammatory processes (Divers & Mader, 2005).

Finally, the precise cause of the rib infection cannot be established. Previous studies have shown that the ribs, jaws, and pectoral girdle represent some of the skeletal regions most frequently affected by traumatic and infectious lesions in Jurassic ichthyosaurs, probably reflecting injuries sustained during intra- or interspecific interactions, failed predation attempts, or accidental trauma (*e.g*., Pardo-Pérez *et al*., 2018a, 2019, 2020). Because the postcranial region of MOZ-PV 2282 is incompletely preserved, the presence of additional lesions cannot be evaluated, precluding confirmation or exclusion of a traumatic origin. Direct trauma to the ribs followed by a subsequent infection remains a plausible explanation for the observed pathology.

**General diagnosis and paleobiological implications of MOZ-PV 2282**

The infectious lesions documented in MOZ-PV 2282 expand the currently known spectrum of skeletal infections in ichthyosaurs. Infectious bone diseases have previously been reported in several ichthyosaur taxa, including *Stenopterygius* Jaekel, 1911, *Cymbospondylus buchseri* Sander, 1989, and *Hauffiopteryx typicus* von Huene, 1931, affecting the jaws, pectoral girdle, ribs, and gastralia (Pardo-Pérez *et al*., 2018a, 2019, 2020). In these cases, the morphology and spatial distribution of the lesions suggest that the infections originated from penetrating traumatic events —potentially related to intra- or interspecific interactions, failed predation attempts, or accidental

injuries— before spreading through the medullary cavity or along the periosteal surface (*e.g.*, Pardo-Pérez *et al.*, 2018a, 2019, 2020).

The pathological evidence documented in MOZ-PV 2282 suggests that the individual experienced at least two localized infectious bone lesions affecting two anatomically distinct and distant regions of the skeleton. Although both lesions exhibit evidence of inflammatory response, the available data do not demonstrate that they originated through the same pathogenic pathway. The stapes lesion is more conservatively interpreted as an infectious bone pathology because only external morphological evidence is available, whereas the rib lesion most plausibly represents an osteomyelitis-like infection based on the combined macroscopic and tomographic evidence. Because no additional skeletal elements exhibit pathological alterations, hematogenous dissemination between these anatomically distant sites appears less parsimonious, although it cannot be completely excluded. The extensive reactive bone growth indicates that the individual survived for an extended period during the course of the infection. This prolonged survival suggests that bone formation remained active despite sustained physiological stress (Divers & Mader, 2005).

Finally, the present specimen broadens this spectrum by documenting infectious pathology affecting both cranial and postcranial skeleton in an ophthalmosaurid. More importantly, it demonstrates that well-known specimens that have already been studied anatomically and histologically may still preserve previously unrecognized pathological evidence. Re-examination of museum collections therefore represents an important source of new paleobiological information, allowing the pathological record to be expanded without requiring the discovery of additional specimens.

## CONCLUSION

The pathological alterations documented in the holotype of *Mollesaurus periallus* (MOZ-PV 2282) constitute the first paleopathological record for a Jurassic ichthyosaur from the Neuquén Basin and expand the currently limited evidence of infectious bone disease in Ophthalmosauridae. Macroscopic observations indicate that both the stapes and rib fragments were affected by localized infectious lesions, whereas the integration of computed tomography with external morphology allowed a more robust diagnosis of an osteomyelitis-like infection in the ribs. The occurrence of infectious lesions in anatomically distinct skeletal regions, together with the extensive reactive bone growth, indicates that the individual survived long enough to develop an osseous response. Overall, this study contributes to our understanding of the diversity, diagnosis, and palaeobiological significance of infectious skeletal pathologies in extinct marine reptiles.

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**Figure captions**

**Figure 1. A,** Location map of the Chacaico Sur area, in the province of Neuquén, Argentina (modified from Chaumeil Rodríguez *et al*., 2025). **B,** Satellite image of the Chacaico Sur area (obtained from Google Earth; Image © 2026 Airbus).

**Figure 2.** *Mollesaurus periallus* (MOZ-PV 2282), skeleton in right lateral view. Scale bar equals 10 cm.

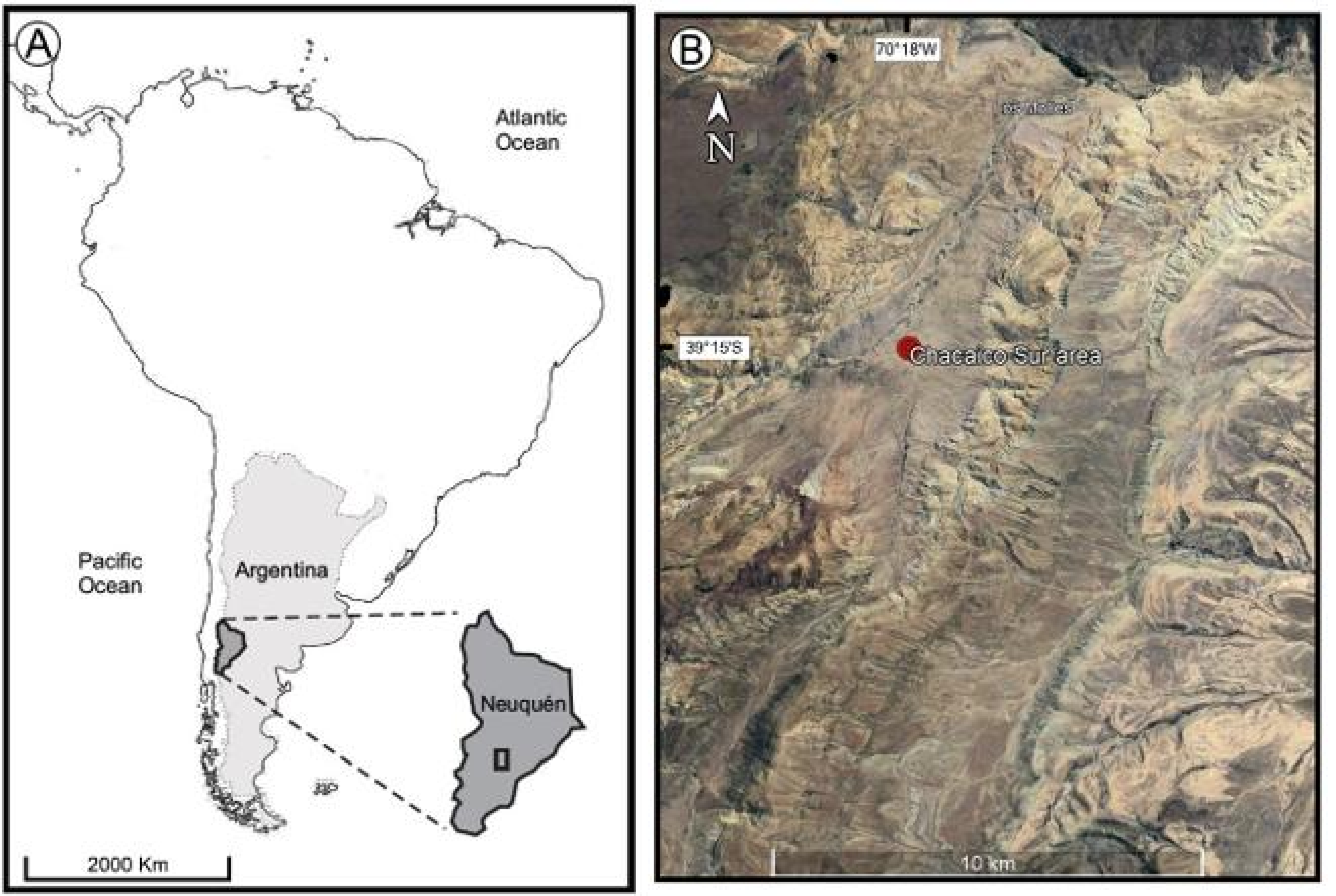
**Figure 3.** Right stapes of *Mollesaurus periallus* (MOZ-PV 2282). **A,** Posterior view. **B,** Distal portion in anterior view. The dashed line shows localized periosteal reactive bone growth. **C,** Ventral view. The red box indicates cortical disruption and exposure of the underlying trabecular bone. **D,** Detailed view of the exposed trabecular bone. Asterisks indicate the periosteal reactive bone growth. Abbreviations: Fb, facet for the basioccipital; Fo, facet for the opisthotic; Fq, facet for the quadrate; Tb, trabecular bone. Scale bars equal 3 cm (**A, C**), 1 cm (**B**), 0.5 cm (**D**).

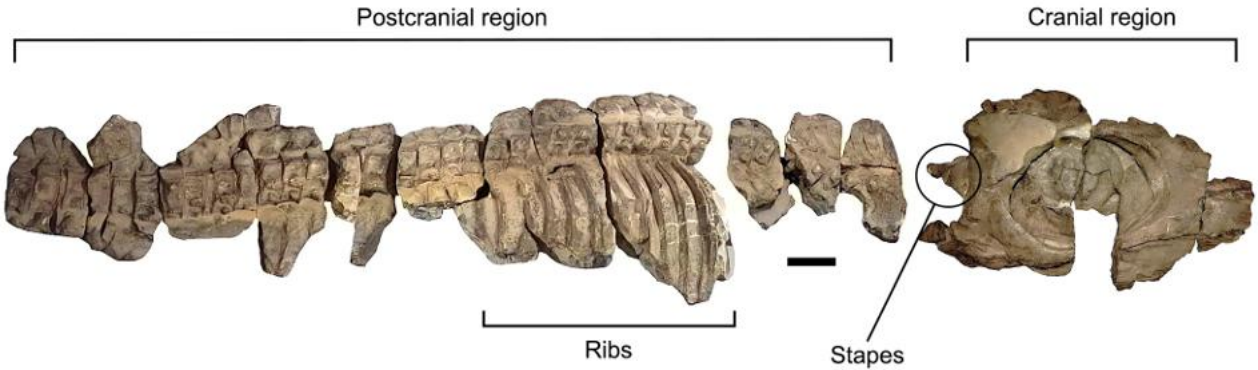
**Figure 4.** Non-pathological rib from the anterior region of *Mollesaurus periallus* (MOZ-PV 2282) in anterior (**A**) and posterior (**B**) views (modified from Talevi & Fernández, 2012). The black arrow points towards the distal region. Abbreviations: Cp, capitulum; Gr, grooves; Ri, ridge; Tu, tuberculum. Scale bar equals 8 cm.

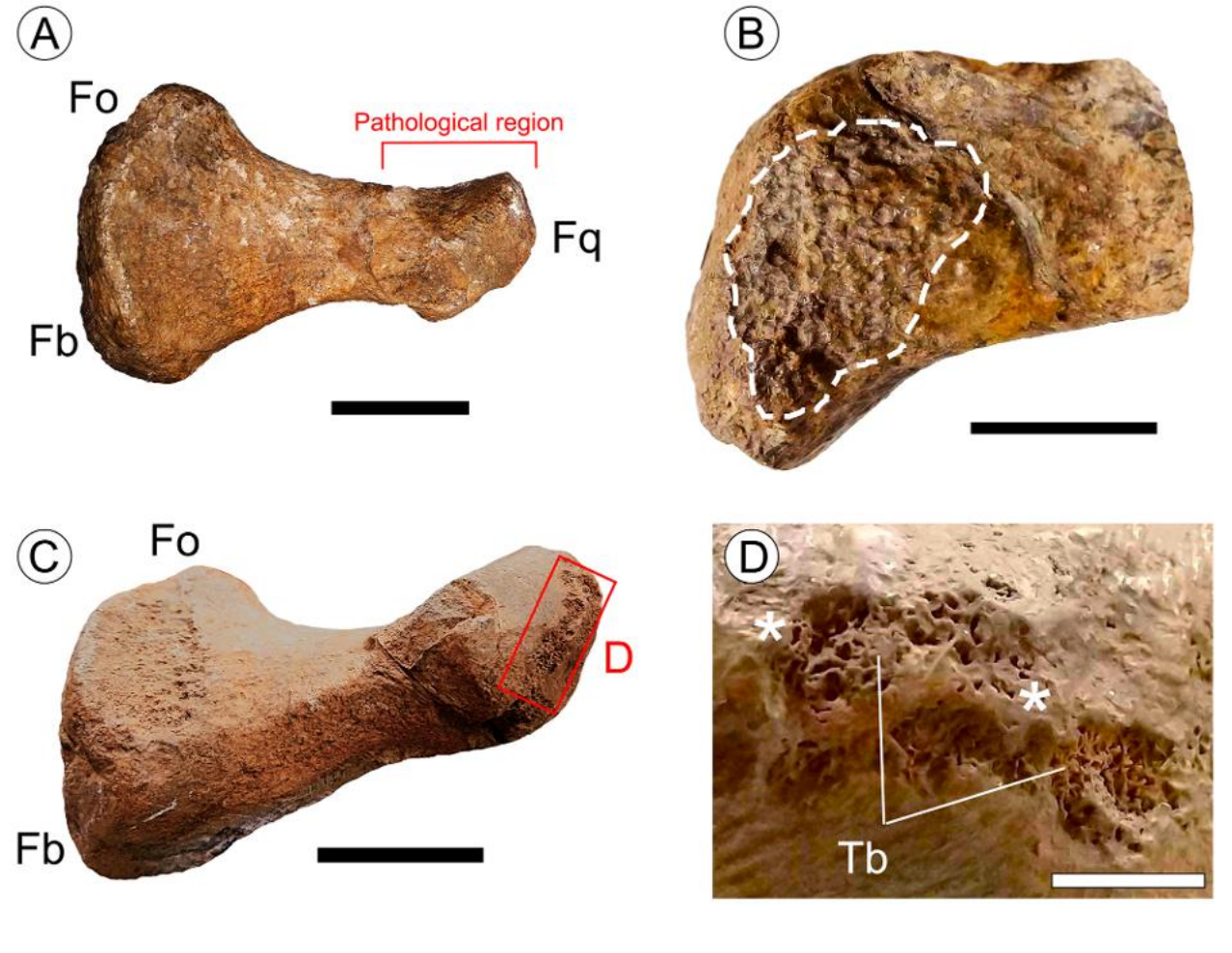
**Figure 5.** Pathological rib fragments of *Mollesaurus periallus* (MOZ-PV 2282) in anterior (**A**) and dorsal (**B**) views. The red boxes in (**B**) indicate pathological regions. **C–E,** Detailed views of the pathological regions showing exposed trabecular bone and cavities. Asterisks indicate the periosteal reactive bone growth. Abbreviations: Cv, cavity; Tb, trabecular bone. Scale bars equal 4 cm (**A–B**), 1 cm (**C–E**).

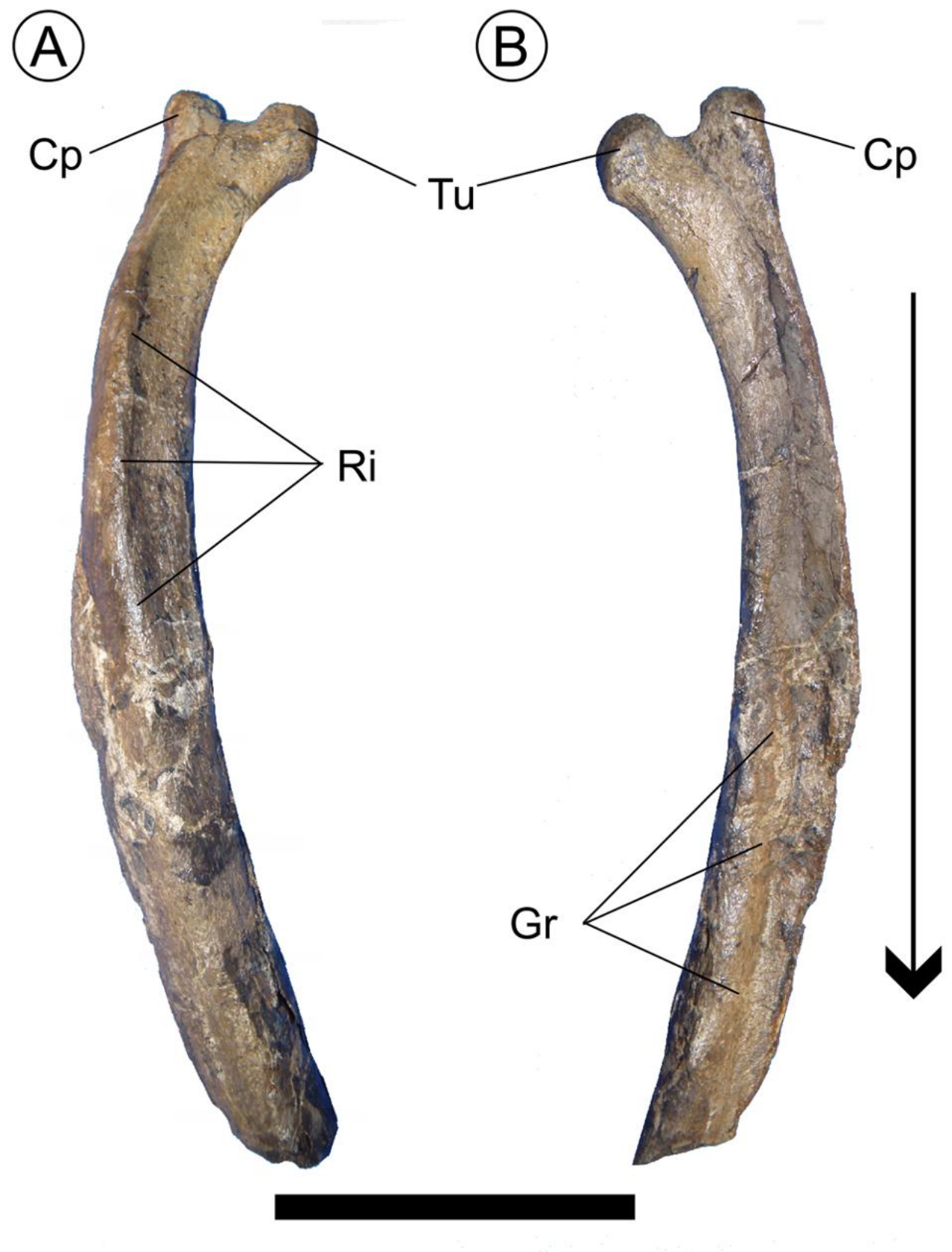
**Figure 6.** Pathological rib fragments of *Mollesaurus periallus* (MOZ-PV 2282). A, Volumetric reconstruction of the rib fragments in anterior view. The dashed lines illustrate where the images **B** and **C** were taken. **B–C,** Pathological regions in dorsal

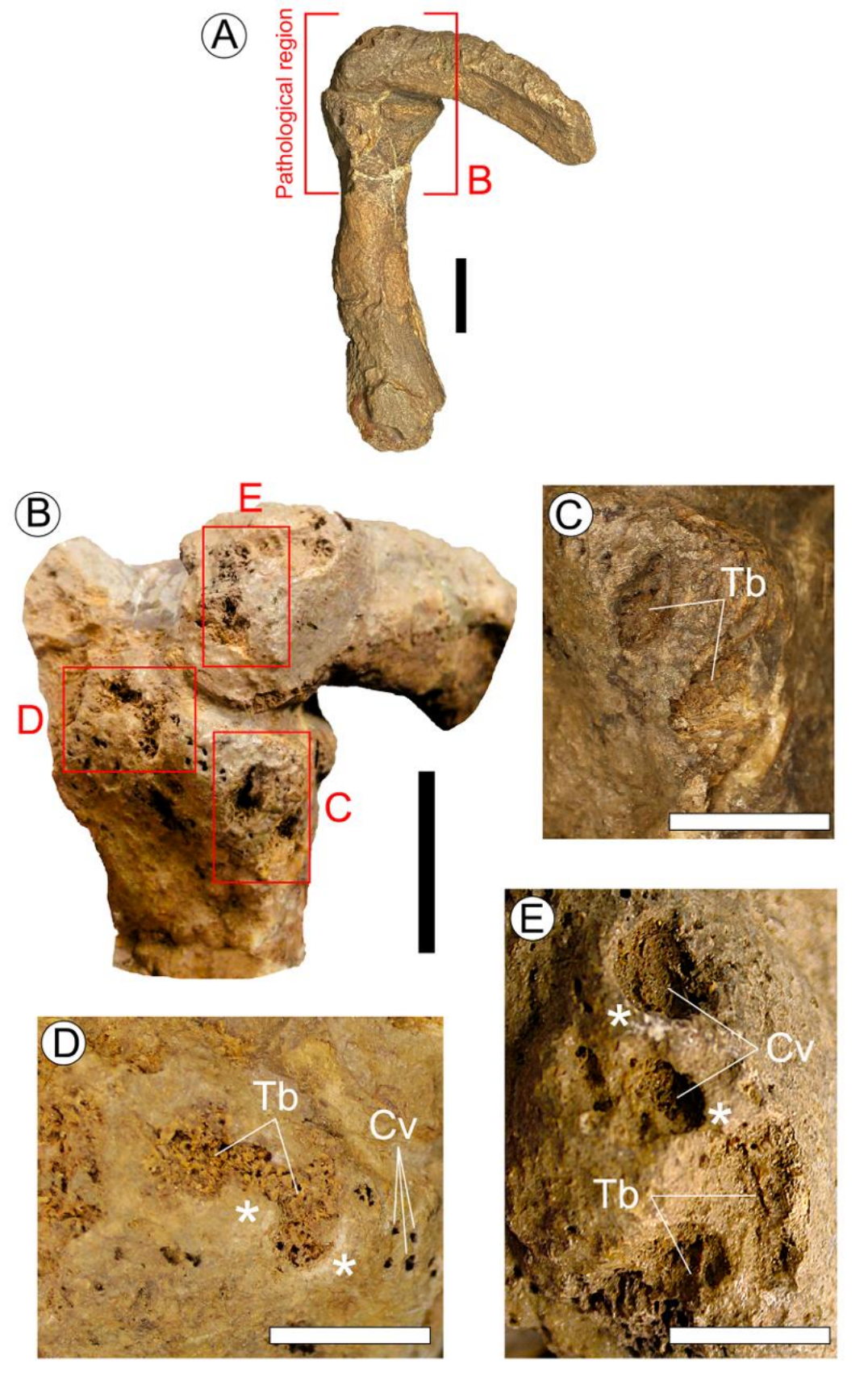
548 view. The red arrows indicate internal cavities within the bone, surrounded by areas of
549 reduced bone density. Asterisks indicate the periosteal reactive bone growth. The white
550 arrow points towards the distal region. Scale bars equal 4 cm (**A**), 2 cm (**B–C**).

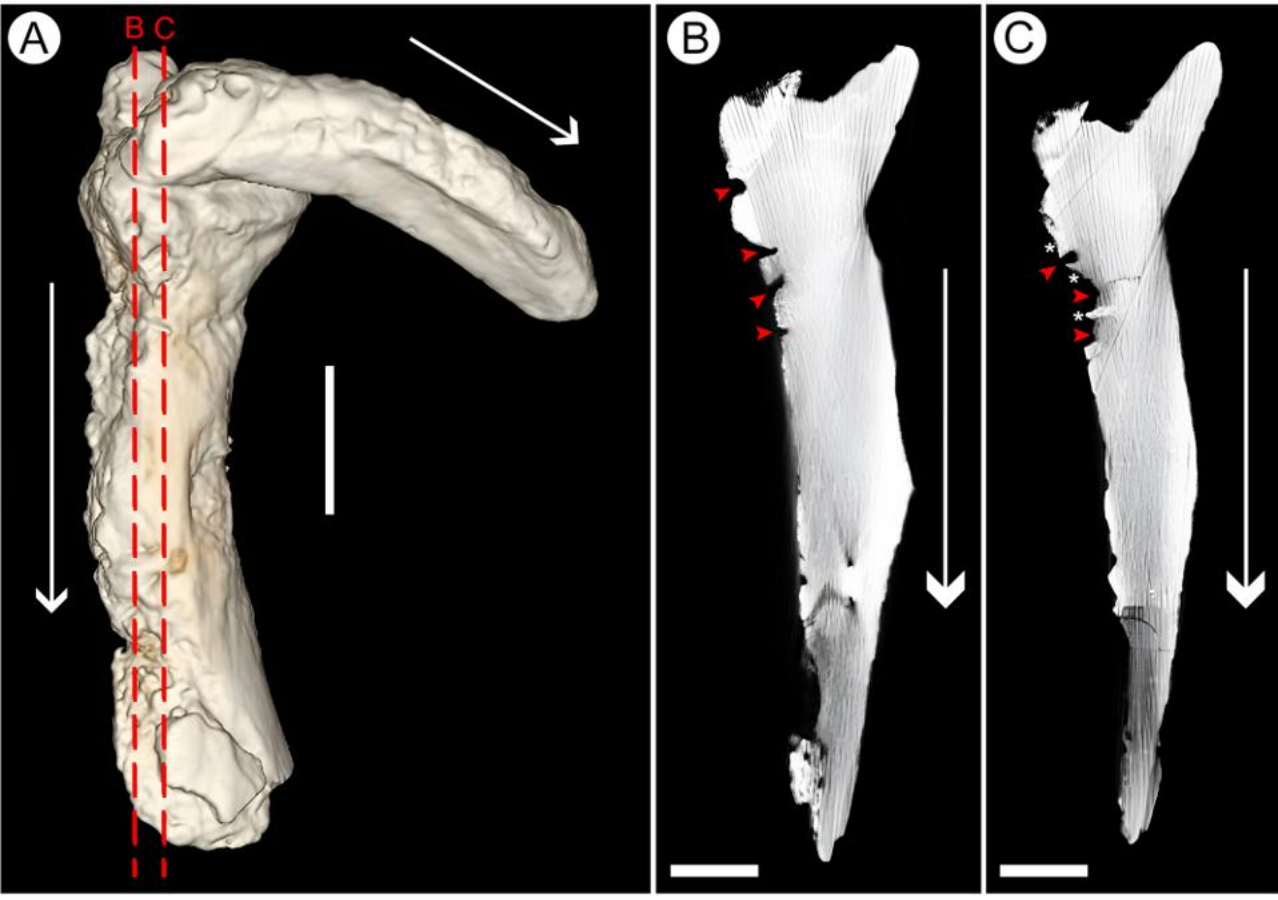

A
Atlantic
Ocean
Pacific
Ocean
Argentina
Neuquén
2000 Km
B
70°18'W
N
39°15'S
Chacaico Sur area
10 km


Postcranial region
Cranial region
Ribs
Stapes


A
Fo
Pathological region
Fq
Fb
B
C
Fo
D
Fb
D
*
*
Tb


A
B
Cp
Tu
Cp
Ri
Gr


A
Pathological region
B
B
E
D
C
C
Tb
D
Tb
Cv
*
*
E
*
Cv
*
Tb


A
B C
B
C