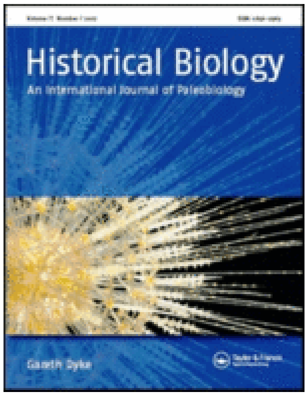

A limping dinosaur in the Late Jurassic: Pathologies in the pes of the neornithischian Othnielosaurus consors from the Morrison Formation (Upper Jurassic, USA)

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A limping dinosaur in the Late Jurassic: Pathologies in the pes of the neornithischian *Othnielosaurus consors* from the Morrison Formation (Upper Jurassic, USA)

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A limping dinosaur in t~~-~~he Late Jurassic: Pathologies in the pes of the neornithischian *Othnielosaurus consors* from the Morrison Formation

The study of palaeopathology provides valuable information about injury and behaviour in extinct organisms. Appendicular pathologies are ~~of particular~~ interesting as they directly affect mobility and therefore the ability of an animal to survive. Here, the injuries recorded in the left pes of the neornithischian *Othnielosaurus consors* are described. The implications of these injuries in its behaviour are also discussed. *Othnielosaurus* shows pathological features in all its pes digits, with three types of pathologies have been identified: calcium pyrophosphate deposition disease (CPPD), and pilon and impact fractures. Calcium pyrophosphate deposition disease is visible on the articular surface of phalange II-3 as a small osseous plaque. ~~The~~ A pilon fracture is~~,~~ evidenced by the grow~~ing~~th of ~~a~~ callous tissue o~~i~~n the shaft of the phalange I-1 and demonstrates healing~~ed~~ before death. The impact fractures are identified as a focal subsidence on the articular surfaces of phalanges III-1 and IV-4, which are partially healed. Perhaps the suite of palaeopathologies encountered would generate pain and discomfort when walking, which probably resulted in a limp that would have impacted on its lifestyle. Finally, the fact that the fractures are in different stages of healing would suggest that impact fractures could have contributed to the death of the individual.

Keywords: Impact fracture, Pilon fracture, CPPD, Jurassic, Ornithischia

~~Subject classification codes: include these here if the journal requires them~~

Introduction

Palaeopathology studies the presence of injuries and their appearance in the fossil record (Rothschild and Martin 2006). This provides valuable information about the behaviour, environmental interactions and lifestyles of ancient organisms (see Rothschild et al. 2012; Kappelman et al. 2016 for tetrapod examples). It is relatively common to find traumas or other pathologies in Mesozoic dinosaur bones (see Arbour and Currie 2011; Peterson and Vittore 2012 and references therein). For instance, the presence of impact fractures in theropods (Rothschild 2009) can reveal that hunting is also dangerous for the hunter, or the particular facial lesions in specimens of *Triceratops* may demonstrate the effects of periodic intraspecific combats (Farke et al. 2009). In bipedal dinosaurs, the fracture record is not as abundant in theropods (Rothschild and Martin 2006; Anné et al. 2015) as in ornithopods (diverse clade of bipedal herbivorous ornithischians that includes ‘hypsilophodontids’ and iguanodontians, such as dryosaurids, camptosaurids basal iguanodontoids and hadrosaurids; Gilmore 1912; Blows 1989; Norman et al. 2004; Butler et al. 2008; Witzmann et al. 2008; Straigth et al. 2009; Butler and Barrett, 2012; Tanke and Rothschild 2014; Ramírez-Velasco et al. 2017; Herne et al. 2018), pachycephalosaurids (Peterson and Vittore 2012) or ceratopsians (Rothschild and Martin 2006; ~~; ;~~ Hedrick et al. 2016~~;~~). Furthermore, the presence of fractures in associated pedal elements is even scarcer, and they are principally reported in the clade Hadrosauridae (Rothschild and Tanke 2006; Tanke and Rothschild 2014).

Fractures, such as a broken bone, cartilage or both (Waldron 2008), are a useful type of pathology from which to infer behaviour (Rothschild and Martin 2006; Arbour and Currie 2011; Rothschild et al. 2012; Kappelman et al. 2016). According to Rothschild and Martin (2006) the factors affecting occurrence of a fracture relate to the nature of the force (magnitude, direction, loading rate, and duration) and the osseous area of distribution of that force (density, fatigue strength, resilience, and elasticity). Depending on the relationship between these factors, there are several types of fracture: oblique (which can be closed or displaced), transverse, greenstick, spiral, ~~comminute,~~ compression, impact, and stress (Rothschild and Martin 2006).

The presence of fractures in dinosaur tends to be more abundant in the axial skeleton and proximal areas of the body (Rothschild and Martin 2006; Arbour and

Currie 2011; Peterson and Vittore 2012; Hearn and Williams 2019). Although it is common to find pedal elements in the tetrapod fossil record, they are not usually preserved together after death, so it is difficult to find a complete pes. Autopodia tend to separate into their individual components during the early *post-mortem* stage and are easily transported by water currents. (Voorhies 1969; Conybeare and Haynes 1983; Hill and Behrensmeyer 1984).

While primary osteoarthritis is extremely rare in dinosaurs (Rothschild 1990), a form of crystalline arthritis, calcium pyrophosphate deposition disease (CPPD, a rheumatic~~ologic~~ disease which is thought to be secondary to abnormal accumulation of calcium pyrophosphate dihydrate crystals within joint soft tissues) has been identified. CPPD typically is recognized by chondrocalcinosis or pseudogout (Jacobson et al. 2008; Rothschild 2005, 2007; Rothschild and Bruno 2009; Rothschild et al. 2013). The former is recognized as calcification on joint surfaces, while the latter is the term used when inflammation is present. The presence of calcified sheet deposition on articular surfaces is definitive for the diagnosis (Rothschild and Martin 2006). This disease is common in mammals (Barbosa et al. 2014; Rothschild 2005), dinosaurs (Anné et al. 2015), including birds (Angel 2007) and other reptiles (Rothschild 2010;~~ ;;;~~ Rothschild and Martin 2006; Rothschild et al. 2013).

Here we present the pathological record of the almost complete left pes of the neornithischian *Othnielosaurus consors* (YPM VP 1882; Fig. 1) from the Upper Jurassic Morrison Formation of Wyoming (USA). The main goals of the present paper are: (1) to describe the injuries registered in the left pes YPM VP 1882; and (2) to hypothesize on the possible implications of these injuries in the behaviour of *Othnielosaurus consors*.

Specimen studied and Taxonomic assignment

YPM VP 1882 includes at least two partial skeletons discovered by O. C. Marsh in 1879 (Marsh 1894) at W. H. Reed's YPM Quarry 7 "Three Trees Quarry" in Como Bluff, Albany County, Wyoming, USA (Ostrom and McIntosh 1966:53; map in fig. 3). The stratigraphic position of the type locality is given by Bakker et al. (1990, fig. 1 left). The material was found in a green-grey mudstone of the Brushy Member or upper member of the Morrison Formation (Galton 1983).

In YPM VP 1882, the neural arches and centra of the vertebrae are fused (Carpenter and Galton 2018), so it might be considered that the material belongs to osteologically subadult or adult individuals. Based on skeletal measurements, *Othnielosaurus* was a small dinosaur, about 1.5 m in length.

Following Galton, "the proximal phalanges of digits II and IV should be transposed and when this is done the fourth digit is no longer unusually elongate" (see Galton 1983, p. 224, fig. 6Z). Recently, Carpenter and Galton (2018) illustrated the left pes of YPM VP 1882 (erroneously labelled by them as 1822) in anterior and posterior views. Here, we have reordered the pedal elements according to the recommendations of Dieudonné et al. (2016), and identify new assignments: i.e., Phalanx II-2 of Carpenter and Galton (2018, fig. 18) is considered here as III-3 due to its symmetry and its arrangement with the phalanx III-2. Phalanx II-1 of Carpenter and Galton (2018)is regarded here as belonging to digit IV, as IV-1, taking into account the lateral asymmetry and the ventral development of its proximal area. On the other hand, phalanges III-3 and IV-1 by Carpenter and Galton (2018) were not found in the collections when the visit was made, but a new unpublished phalanx is identified there that would correspond by its medial asymmetry and proximal shape with phalanx II-1 (see Fig. 1).

YPM VP 1882 was originally referred to *Laosaurus consors* by Marsh (1894, 1896). This assignment was followed by subsequent authors (e.g., Gilmore 1925;

Ostrom and McIntosh 1966; Galton and Jensen 1973). Galton (1977, 1981, 1983) proposed that *L. consors* is referable to *Othniela rex* , but subsequentlyreassigned YPM VP 1882 to the new genus *Othnielosaurus* as *O. consors* (Galton, 2007). In a recent paper, Carpenter and Galton (2018) considered *Nanosaurus agilis* as senior synonym of *Othnielosaurus consors* and *Othnielia rex* (also *Drinker nisti* , named by Bakker et al. 1990), all taxa based on fossil remains from the Upper Jurassic Morrison Formation of western USA. Until consensus is reached, we prefer to assign provisionally YPM VP 1882to *Othnielosaurus consors*.

Othnielosaurus (formerly under the names *Laosaurus*, *Nanosaurus* or *Othnielia*) has classically been considered to be an ornithopod (e.g., Marsh 1894, 1896; Gilmore 1925), and commonly classified among the hypsilophodontids (i.e., Galton 1977, 1983; Sues and Norman 1990). Currently, Hypsilophodontidae appears to represent a paraphyletic grade of basal neornithischian and basal ornithopod taxa (Norman et al. 2004; Butler et al. 2008). Norman et al. (2004) regarded *Othnielia* as a basal euornithopod less derived than *Hypsilophodon* (see Galton 2007). However, recent phylogenetic analyses place *Othnielosaurus* outside of Ornithopoda as a non-cerapodan, basal neornithischian (e.g., Butler et al. 2008; Han et al. 2012; Boyd 2015).

In summary, the taxonomic status of *Othnielosaurus consors* is currently under debate. It could be a valid taxon or a junior synonym of *Nanosaurus agilis*. Its phylogenetic position is problematical as well: Long considered as ornithopod, the most recent analyses support that it represents a basal neornithischian.

Institutional Abbreviations.

YPM VP, Yale Peabody Museum of Natural History, Division of Vertebrate Paleontology, Yale University, New Haven, Connecticut, USA.

Description and Pathological diagnoses

YPM VP 1882 includes an almost complete left pes of *Othnielosaurus consors* (Fig. 1). Nearly all the metatarsals and phalanges are preserved, except for the proximal part of metatarsal I and the phalanges I-2 and II-2. The morphology of both the metatarsals and the phalanges is similar to that of other basal ornithischians or basal ornithopods (Norman 2004; Norman et al. 2004). The pes shows pathological features in all digits (Fig. 1), as described below.

Pedal phalanx I-1

Phalanx I-1 exhibits considerable growth of pathological bone covering some two-thirds of the element and an oblique displacement of the distal half of the phalanx which is angulated dorsomedially. These two factors indicate an old transverse fracture through the diaphysis (Fig. 1 a1-a3, Fig. 2 a). This growth increases the mediolateral width of the diaphysis relative to unmodified elements (phalanx II-1 to IV-1). The ~~callus~~callous tissues do not reach the proximal and distal ends where both articular surfaces maintain their original shape and texture. The surface of the ~~callus~~callous has a slightly irregular texture, as is common in fractured bone, and its maximum growth is around the middle of the phalanx. The abnormal growth increases the width of the phalanx to 18.4 mm at the central shaft (phalanx II-1, the most similar, has a normal width of 12.5 mm). Coinciding with the ~~callus~~callous tissues on dorsal and plantar views is a fracture line perpendicular to the axis, located at a mid of the phalangeal shaft (Fig. 1 a1-a2). In dorsal view, it can be observed that the shaft has been pushed up relative to the dorsal and medial sides by compression forces. In plantar view, the absence of correct alignment of the phalanx before healing can be observed, resulting in minor displacement of the axis. Last, there is a pathological rectangular subsidence (marked by a scratched area in Fig. 1 a1-a2.) in the dorsoproximal area of the shaft.

The presence of reactionary bone growths allows refutation of the possibility that the damage resulted from a post-mortem or taphonomic modification.

Pathological diagnosis.

The presence of an external fracture line and callous tissues indicates healing. Minor displacement of the axis as result of the relative upward thrust of the shaft, implies slight shortening of the diaphysis. Both are characteristic of a pilon fracture (a fracture in which the proximal portion of a fractured bone actually penetrates into the distal portion). This is caused by a high-energy impact and as a consequence the force acts along the long axis of the bone and crushing and shortening of the bone occurs (Bourne et al. 1983; Helfet et al. 1994; Haller et al. 2017).

Pedal phalanx II-3

Pedal phalanx II-3 has a small teardrop-shaped calcified plaque (approximately 0.5 cm) situated on the dorsomedial quadrant of the proximal articular surface. It has a sclerotic margin parallel to the articular surface associated with crumbling edges (Fig. 1b, Fig. 2 c). This sheet is absent in the other conserved ungual phalanges (Fig. 2 c-j).

The presence of a calcified sheet, sharply defined, and retention of bone integrity allow refutation of the possibility that the deposit resulted from taphonomic modification.

Pathological diagnosis

The presence of a calcific sheet on the joint surface of the phalanx is compatible with calcium pyrophosphate deposition disease (CPPD). This disease is a variety of a crystalline and erosive arthritis that can be recognize by the presence of calcified sheet deposited, of small size, sharply defined, with characteristic sclerotic margins and retention of underlying bone integrity. When the CPPD affects to the hands and feet, it is characterized by being predominantly marginal in its distribution, affecting 1-2 joints, and tending to have a subchondral distribution in the absence of new bone formation. The affected joints reflect that of the non-erosive component of CPPD (Rothschild and Martin 2006

~~The former is recognized as calcification on joint surfaces, while the latter is the term used when inflammation is present.~~

Pedal phalanges III-1 and IV-4

Structural weakening produced collapse (focal subsidence) of the bone of the proximal articular surfaces (Fig. 1c-d, Fig. 2 f-j). In digit III the area collapse is circular and covers almost all the articular surface. In digit IV, it has a drop-shape and only covers the left half of the surface. Such collapse is absent in the other preserved phalanges (Fig. 2 d-j).

The presence in the area of collapse, of a smooth articular surface without parallel cracks and polygonal fracture patterns (which commonly characterize subaerially exposed and eroded bone surfaces) (Peterson and Vittore 2012), indicates that such damage was not the result of a post-mortem or taphonomic modification.

Pathological diagnosis

Focal subsidence is the loss of bone as a result of inflammation and decreased blood flow. The loss of blood supply is a complication that usually occurs after a fracture, resulting in avascular necrosis and bone collapse and/or reabsorption (Waldron 2008). The~~ articular surface~~ absence of new bone ~~formation ~~on the articular surface and fibrous and disorganized surface texture indicates that it is a partially healed fracture. This appearance contrasts with the foreshortening and splaying that typically result from the plafond or pilon fractures (Bourne et al. 1983; Helfet et al. 1994; Haller et al. 2017). It also differs from the "divot fracture", wherein force applied to a small section of diaphyseal or metaphyseal bone produces an incomplete fracture with displacement of fragments into the medullar cavity (Rose et al. 1988; Resnick 2002). The presence of focal subsidence is characteristic of an impact fracture, in which a portion of articular subchondral bone ~~is ~~has broken free of the metaphysis (Wolfe and Katz 1995; Sullivan et al. 2000; Rothschild et al. 2012).

Differential considerations for impact fractures include osteochondrosis and infectious arthritis. Osteochondrosis defines failure of articular cartilage to transform into subchondral bone during normal development (Resnick 2002). It has the form of focal, sharply defined, deep articular surface depressions, as previously reported in theropod and hadrosaurid phalanges (Bell and Coria 2013; Tanke and Rothschild 2014). In contrast, infectious arthritis typically presents with reactive growth of new bone around the periphery of the lesion, filigree reaction on the bone surface, draining sinuses, and distortion of the underlying bone (Rothschild and Martin 2006). The absence of these signs in YPM VP 1882 suggests that the impact fractures are probably not a result of infectious arthritis.

Implications on behaviour

The record of pathological fractures in dinosaurs is sparse. When present they are predominantly distributed in the axial and appendicular areas (Rothschild and Martin

2006; Arbour and Currie 2011; Peterson and Vittore 2012 and references therein). These authors documented several types of fractures present in dinosaur skeletons, including compound, impact, green-stick and stress fractures. Fractures have implications for behaviour, both in the predator and in the prey, as well as possible intraspecific interactions (Rothschild 2009; Arbour and Currie 2011; Rothschild et al. 2012; Kappelman et al. 2016).

Three different pathologies have been observed in the pes of YPM VP 1882: two types of fractures (pilon and impact) and CPPD, a pathology which may be metabolic, familial or idiopathic in origin (Rothschild and Martin 2006; Rothschild 2010). Pilon fractures were interpreted as caused by impact during a fall (Kappelman et al. 2016), and impact fractures, by relatively low impact contact with the substrate, either by the animal jumping, landing on uneven ground, or during running (Sullivan et al. 2000).

Calcium pyrophosphate deposition disease (CPPD) affects the articular surface of pedal phalanx II-3. Phalanx II-2 is not preserved, so it not possible to know whether the presence of calcification also affected (or not) its articular face. Although this arthropathy was not dangerous to the integrity of *Othnielosaurus*, it likely would increase the discomfort of walking caused by the defects in phalanges III-1 and IV-4.

It is important to note that the fractures present different healing stages. While the pilon fracture is completely healed, the impact fractures are only partially healed. Therefore, we hypothesize that this individual suffered at least two traumatic events of different intensity before death. The first one, which generated the pilon fracture, is related to a high energy impact such as a fall, possibly a consequence of inter- or intraspecific interactions.~~The first was a high energy impact such as a fall, possibly a consequence of several events like a fall or inter- or intraspecific interactions (pilon fracture)~~. Complete healing of the fracture confirms survival of the traumatic event~~,~~ but was insufficient for resorption of the ~~callus~~callous tissues, the last stage of fracture healing (Arbour and Currie 2011; Anné 2014). The second event resulted in at least two unhealed impact fractures in the phalanges III-1 and IV-4, as the result of a low energy impact. Basal ornithischians and basal ornithopods are considered as tetradactyl or tridactyl digitigrade bipedal dinosaurs (Thulborn 1990). Nevertheless, Norman et al. (2004) pointed out that digit I was not long enough to touch the ground during locomotion. In this way, it is possible that the pilon fracture in the phalanx I-1 of YPM VP 1882 may not have significantly affected locomotion (as there was no significant contact of this digit with the ground). This "protected status" would facilitate fracture healing. During the healing period the pathology likely caused discomfort and pain, due to the tendon action of *M. flexor hallucius longus* (Carrano and Hutchinson 2002). In this way, every time *Othnielosaurus* took a step, the tendon would have exerted pressure on the fracture that would likely have resulted in pain and protective behaviour related to use of the injured limb (Hearn and Williams 2019). On the other hand, the impact fractures located in the phalanges III-1 and IV-4, which supported the weight of *Othnielosaurus* on the ground, might had causing chronic pain and, consequently, a limp. Similar cases of pedal pathologies affecting an individual's mobility have been described in the fossil record of dinosaurs, crocodyliforms and mammals, including hominoids (Hanna 2002; Farke and O'Connor 2007; Cabral et al. 2011; Anné et al. 2014; Foth et al. 2015; McCrea et al. 2015; Macdonald and Currie 2018; Hunt et al. 2019). Survival of lesions of weight-bearing bone would have greater consequence for obligate bipeds and evidence of lesions healing in these bones is rare (Hearn and Williams 2019). Pilon fractures likely produced more marked lameness in *Othnielosaurus* than impact fracture. The presence of *Othnielosaurus* pedal pathologies may have contributed to reduced ability to obtain food with subsequent malnutrition, greater susceptibility to other diseases and complications, and higher risk of predation (Cabral et al. 2011; Foth et al. 2015; Gross et al. 1993; Hanna 2002; Hunt et al. 2019).

Conclusions

The results obtained in the analysis of pathologies in the left pes of *Othnielosaurus* indicate that the dinosaur suffered a form of arthritis, which can be metabolic, familial or idiopathic in origin and at least two accidental events during its life. The injuries resulting from both accidents (pilon and impact fractures) were likely painful events and likely resulted in reduction in activity. It is likely that this individual had difficulty walking and did so with a limp. That could have interfered with obtaining food, compromised ability to escape from predators, and increased susceptibility to illness. Finally, the state of incomplete healing of impact fractures indicates that this *Othnielosaurus* did not survive sufficiently long after the injuries for complete healing to occur. It is unclear if these pathologies contributed directly or indirectly (e.g., reducing predator avoidance efficacy) to its death.

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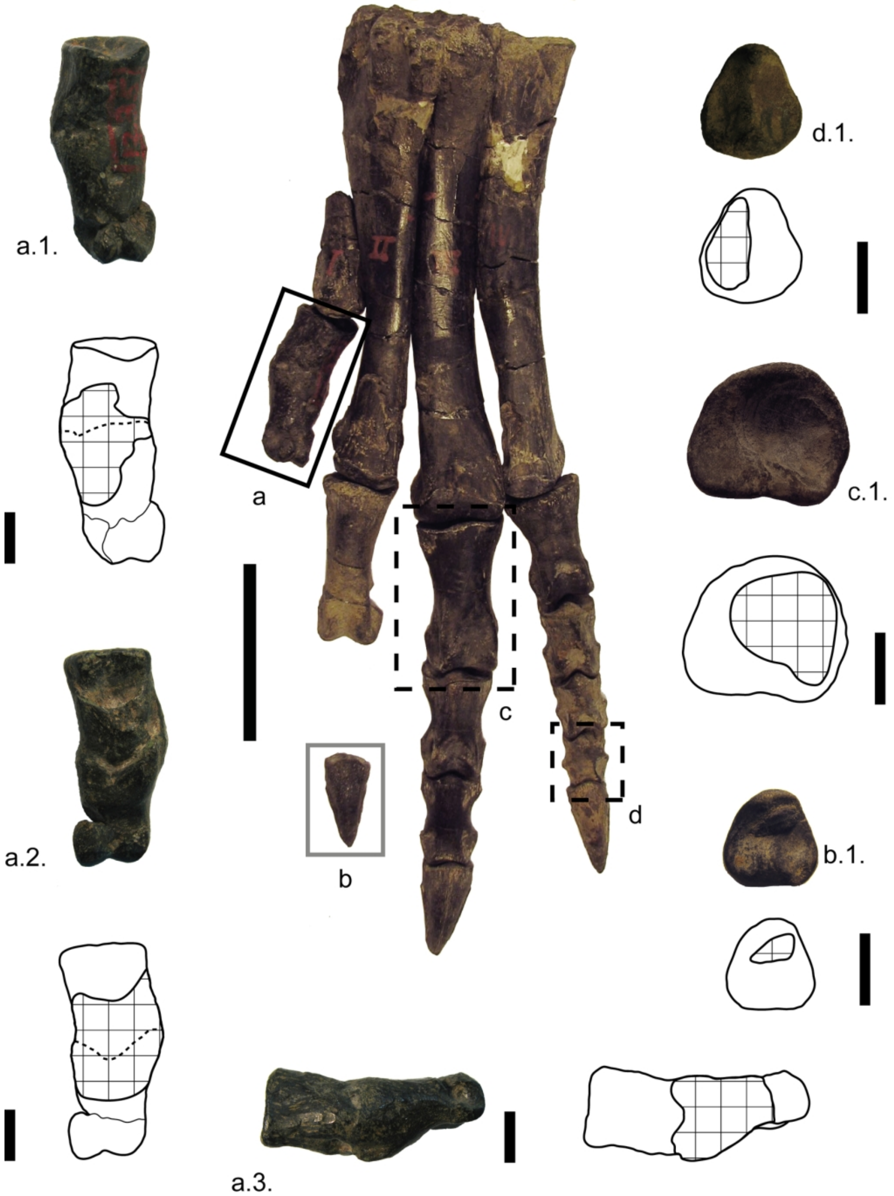
Figure 1. Left pathological pes of *Othnielosaurus* (YPM VP 1882) in dorsal view. (a) Pedal phalanx I-1, (a.1-3) in dorsal, plantar and lateral views respectively; (b) pedal phalanx II-3, (b.1) in proximal view; (c) pedal phalanx III-1, (c.1) in proximal view; (D) pedal phalanx IV-4, (d.1) in proximal view. Black rectangle, pilon fracture; rectangle with dashed line, calcium pyrophosphate deposition disease (CPPD); gray rectangle, impact fracture. Area scratched in the drawing, pathological zone, and the dashed line in the draw A1 indicate the fracture line. Scale bar of the pes = 5 cm. a-d and a.1-d.1 scale bar = 1 cm.

Figure 2. Pathological and healthy phalanges of *Othnielosaurus* (YPM VP 1882). (a) Pedal phalanx I-1, (b) pedal phalanx II-1, (c) pedal phalanx II-3, (d) pedal phalanx III-4, (e), pedal phalanx IV-5, (f) pedal phalanx IV-4, (g) pedal phalanx III-2, (h) pedal phalanx IV-2, (i) pedal phalanx III-1, (j) pedal phalanx II-1. (a, c, f and i), pathological phanlages, (b, d-e, g-h and j) healthy phalanges. (a-b) in lateral view, c-j in proximal views. Scale bar = 1 cm.



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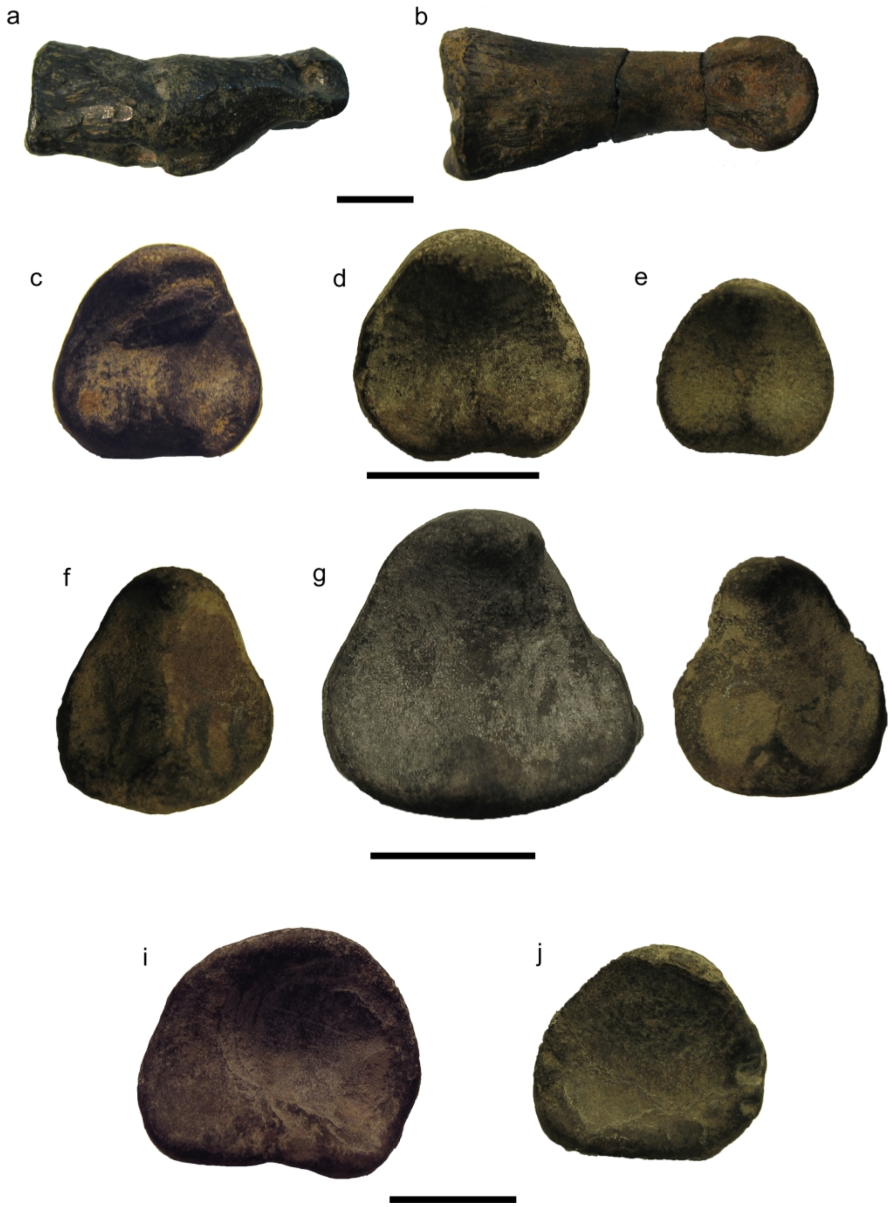

Figure 2. Pathological and healthy phalanges of Othnielosaurus (YPM VP 1882). (a) Pedal phalanx I-1, (b) pedal phalanx II-1, (c) pedal phalanx II-3, (d) pedal phalanx III-4, (e), pedal phalanx IV-5, (f) pedal phalanx IV-4, (g) pedal phalanx III-2, (h) pedal phalanx IV-2, (i) pedal phalanx III-1, (j) pedal phalanx II-1. (a, c, f and i), pathological phanlages, (b, d-e, g-h and j) healthy phalanges. (a-b) in lateral view, c-j in proximal views. Scale bar = 1 cm.

204x271mm (300 x 300 DPI)