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FIRST JURASSIC EVIDENCE OF A POSSIBLE SPINOSAURID PEDAL UNGUAL FROM THE JAISALMER BASIN, INDIA

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Abstract. We describe an isolated, almost complete pedal ungual phalanx from the Middle Jurassic marine carbonate rocks of the Jaisalmer Basin, Rajasthan, north-western India. The ungual bone is triangular shaped, pointed, elongated, asymmetrical, dorsoventrally compressed, ventrally flat, bearing a shallow semi-circular excavation, and almost straight in lateral view. The morphological features, as well as its proportions closely resemble the pedal ungual phalanges of spinosaurid theropods, presently known dominantly from the Cretaceous. The affinity to spinosaurids is supported by bivariate and multivariate analyses. The ungual phalanx is tentatively identified as a basally branching Jurassic spinosaurid under Megalosauroidea. Considering the stratigraphical and geographical provenances, this contribution may represent the oldest record of a spinosaurid.

INTRODUCTION

Jaisalmer Basin has attracted palaeontologists ever since the first report of ammonites recovered from the Mesozoic sediments published by Carter (1861). Oldham (1886) mapped the Mesozoic rocks and recorded the marine invertebrate fossils from the Middle Jurassic Jaisalmer Formation. Many species of marine invertebrate fauna such as brachiopods, echinoderms, ammonites, foraminifers and corals have been described from the Jaisalmer Formation (Blanford 1877; Oldham 1886; Sahni 1955; Sahni & Bhatnagar 1958; Krishna 1979; Singh et al. 1982, 1983; Pandey et al. 2009 as cited in Pandey et al. 2014). However, the vertebrate record of the Jaisalmer Basin is comparatively poor. The earliest record of vertebrate remains is represented by some fragmentary bones from the Middle Jurassic rocks, identified as dinosaurian based on bone histology (Mathur et al. 1985). No serious attempts have been made to search for Jurassic vertebrate fossils for several years. Three decades later, footprints (unfortunately lost), attributed to the theropod ichnotaxa *Eubrontes* cf. *giganteus* Hitchcock, 1836 and *Gralla-*

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tor tenuis Hitchcock, 1858 were reported from the Lower Jurassic marginal marine sediments of the Thaiat Member, Lathi Formation of the Jaisalmer basin (Pieńkowski et al. 2015). Sharma and Singh (2021) described dental remains of European marine hybodonts such as *Strophodus magnus* Agassiz, 1838; *Strophodus medius* Owen, 1869 and *Planohybodus* sp., from the coeval (Bathonian) marine carbonate sediments of the Jaisalmer Basin. Later on, isolated dental remains of a turiasaurian sauropod and a non-coelurosaur averostran theropod were also recorded from the same rocks (Sharma et al. 2022; Sharma et al. 2023), confirming the presence of both herbivorous and carnivorous dinosaurs in the area during the Middle Jurassic. These discoveries were important milestones in the Jurassic vertebrate record of the Jaisalmer Basin. Jaisalmer is emerging as an important site for exploration of the Middle Jurassic vertebrates representing the Tethys coast of Gondwanan India.

In the present study, we describe an isolated ungual phalanx from the Bathonian of the Jaisalmer Formation. The aim of this paper is to identify the specimen and to highlight the taxonomic importance of isolated unguals in a poorly preserved faunal assemblage. The morphometric analyses have been attempted for classifying the isolated ungual and we also tried to explore the palaeogeographic implications of this find.

GEOLOGICAL SETTING

Jaisalmer Basin is one of the largest sedimentary basins of India (Fig. 1A). It originated in response to rifting of the supercontinent Gondwana when a fracture system in the western margin of the Indian plate got activated (Pal et al. 2007). The highly fossiliferous Mesozoic and Cenozoic sedimentary rocks of this basin representing periodic transgression-regression events, are very well documented (Ahmad et al. 2017). The low-dipping Mesozoic sediments are exposed as an arcuate outcrop. The Mesozoic sedimentary succession of the basin is represented by the Lathi, Jaisalmer, Baisakhi, Bhadasar, Pariwar and Habur formations in chronological order (Das Gupta 1975) (Fig. 1B). The Jaisalmer Formation is the most fossiliferous formation of the basin. The marine siliciclastic-carbonate facies of the Jaisalmer Formation is represented by an alternating sequence of fossiliferous limestone/marlstone/lime-mudstone/rudstone and yellow/brown sandstone/siltstone/shale/clay of Middle Jurassic age (Ahmad et al. 2017). Sediments were deposited on a stable shelf with a very low angle depositional slope favouring the development of carbonates (Pal et al. 2007). The marine carbonate rocks of the Jaisalmer Formation, overlying the terrestrial to deltaic sandstone of Lathi Formation and underlying the arenaceous Baisakhi Formation, clearly stand out because of their typical golden yellow colour (Ahmad et al. 2020). The Cretaceous of the Jaisalmer Basin is represented by an arenaceous facies deposited during the regressive phase (Das et al. 2021). Stratigraphically, the Jaisalmer Formation has been splitted into the Hamira, Joyan, Fort, Badabag, Kuldhar and Jajiya members (Kachhara & Jodhawat 1981; Pandey et al. 2014) (Fig. 1B). The bio-stratigraphic age of the Jaisalmer Formation is considered to range from Bajocian to Oxfordian on the basis of nannofossils, corals and ammonites (Pandey et al. 2014).

Rocks of the Badabag Member of Jaisalmer Formation are exposed in the study area (Fig. 1B). The underlying Fort Member is also exposed in the quarry at a depth of 5 to 6 m from the ground surface (Fig. 1C, D). The Fort Member comprises calcareous sandstone along with several beds of oolitic, bioturbated, highly fossiliferous limestone, which is overlain by the Badabag Member. The Badabag Member comprises sandstone, siltstone, and fossiliferous calcareous sandstone, intraformational calcareous conglomerate along with periodic intercalations of limestone, marlstone, lime-mudstone, matrix supported bioclastic rudstone (Pandey et al. 2014; Ahmad et al. 2017). The bioclastic carbonate rudstone bed exposed in the upper part of the quarry, comprised of variegated to red coloured mud clasts along with fossils in a carbonate-siliceous matrix (AS pers. obs.). This bed produced turiasaurian teeth, hollow bone fragments, hybodont dental remains, button-shaped teeth and scales of actinopterygian fish, marine reptile teeth, scutes along with many marine invertebrate fossils and petrified wood (AS pers. obs.) (Fig. 1D). Based on the ammonite stratigraphy, a Bathonian age has been assigned to the Badabag Member (Pandey et al. 2014; Sharma et al. 2022). This age is also corroborated by the presence of Bathonian hybodont *Strophodus magnus* in the rocks exposed in the quarry.

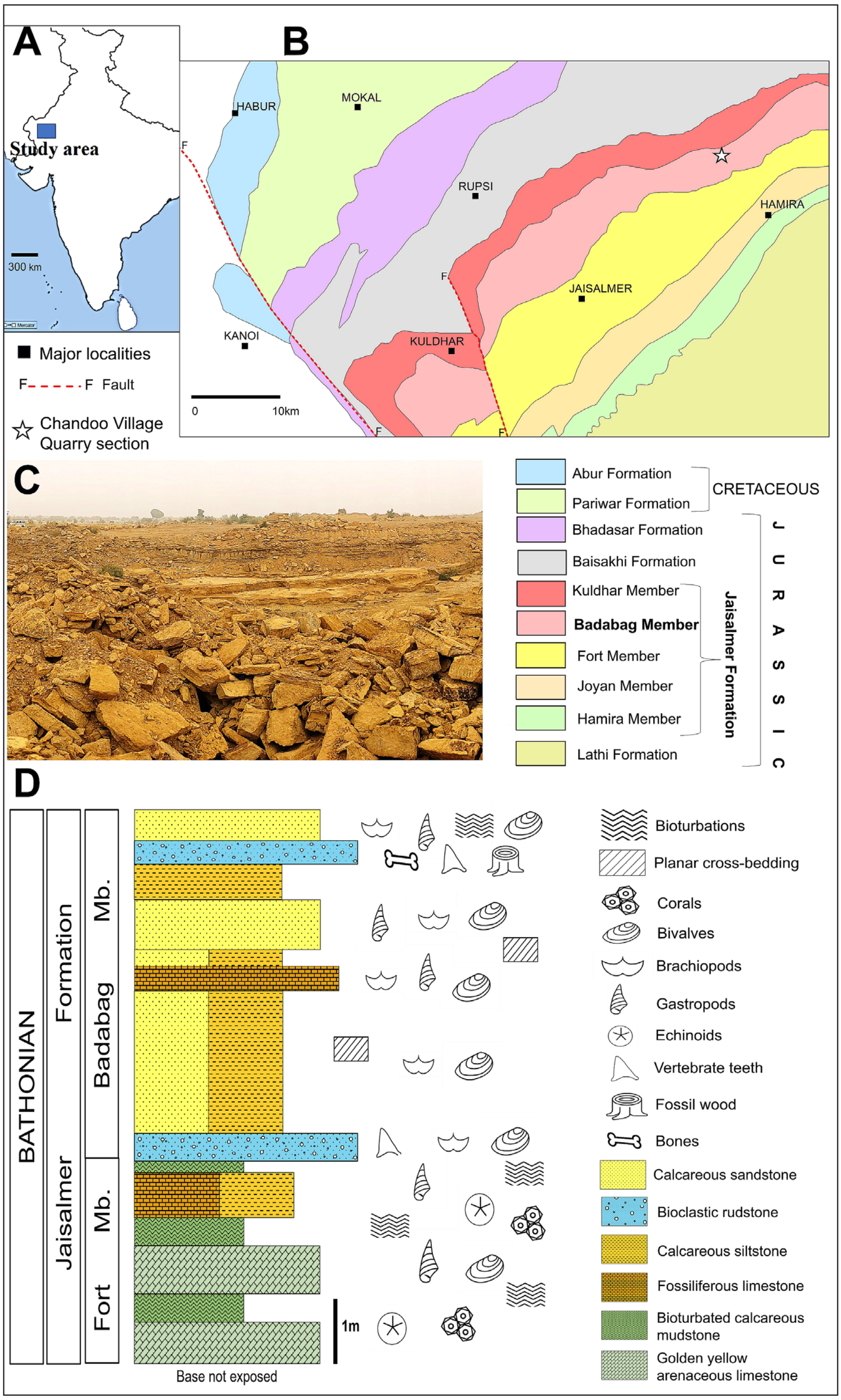

Fig. 1 - A) Location map of the study area; B) Geological map of the Mesozoic rocks of Jaisalmer Basin, Rajasthan, India (modified after Das Gupta 1975; Sharma et al., 2022); Chandoo Village Quarry Section (CVQS) is marked as a star; C) Litho-section of Chandoo Village Quarry Section (modified after Sharma et al. 2022), showing vertebrate fossils bearing bioclastic rudstone horizons. Abbreviations: Mb, Member.

Abbreviations:

Institutional abbreviations—**AAOD**, Australian Age of Dinosaur Museum of Natural History, Australia; **BSC**, Birla Science Centre, Hyderabad, India; **FSAC**, Faculté des Sciences Aïn Chock (University of Casablanca), Casablanca, Morocco; **GSI**, **WR,** Geological Survey of India, Western Region, Jaipur, Rajasthan, India; **MACN**, Museo Argentino De Ciencias Naturales “Bernardino Rivadavia”, Argentina; **MEF**, Museo Paleontológico Egidio Feruglio, Argentina; **MFN**, Museum für Naturkunde, Berlin; **MSNM,** Museo di Storia Naturale di Milano, Italy; **MPCM**, Museo Paleontologico Citadino di Monfalcone, Italy; **MPM,** Museo Padre Molina, Río Gallegos, Argentina; **UACH**, Universidad Austral de Chile; **UC OBA**: Department of Organismal Biology and Anatomy, University of Chicago, Chicago; **USNM**: National Museum of Natural History, Smithsonian Institution, Washington; **YPM**: Peabody Museum of Natural History, Yale University.

Other Abbreviations—**CVQS**, Chandoo Village Quarry Section; **JAIS**, Jaisalmer; **RAJ**, Rajasthan; **SM**, Strategic Minerals; **WR**, Western Region.

MATERIAL AND METHOD

The ungual phalanx bone (Fig. 2) was surface collected by the first author (AS) in a newly excavated building stone quarry near Chandoo (Charu) Village, located 23 km NE of Jaisalmer town and 500 m south of Chandoo village, on the Jethwai-Kanod road (Fig. 1B, C). The specimen is registered as RAJ/JAIS/CVQS002. The specimen is housed in the GSI, WR, Jaipur, Rajasthan under the custody of the Director, SM-I Division. The specimen was measured with a digital calliper. The measurements were rounded off to the nearest tenth of a millimetre. The specimen was photographed with Canon 50D using Canon EF 100 mm f/2.8 macro lens in proximal, lateral, medial, distal, ventral, and dorsal views. All photographs were processed using Adobe Photoshop 23.1.0 and IrfanView version 4.60.

The ungual specimen is extensively compared with the unguals of many dinosaurs as shown in Fig. 3. We have accessed the following original (and casts of original) dinosaur specimens for direct comparisons with RAJ/JAIS/CVQS002: *Australovenator wintonensis* Hocknull et al., 2009 (AODF 604 in AAOD), *Kotasaurus yamanpalliensis* Yadagiri, 1988 (exhibited at BSC), *Spinosaurus* sp. (MPCM 13574; cast in MACN), *Talenkauen santacrucensis* Novas et al., 2004 (MPM) and *Tyrannotitan chubutensis* Novas et al., 2005 (MEF). Photographs of *Camptosaurus dispar* Marsh, 1879 (USNM 4277) and *Tenontosaurus tilletti* Ostrom, 1970 (YPM VP 5460) were kindly facilitated by Karen Moreno (UACH). Photographs of cast of pedal unguals of *Afrovenator abakensis* Sereno et al., 1994 (MNN TIG1=UC OBA 1) are provided by Tyler Keillor (UC) along with some unpublished illustrations by Paul Sereno (UC). Photographs of pedal unguals of *Dysalotosaurus lettowvorbecki* Virchow, 1919 (MB-R 1465) are provided by Daniela Schwarz (MFN), and of *Spinosaurus aegyptiacus* Stromer, 1915 (FSAC-KK11888) by Cristiano Dal Sasso (MSNM).

Morphometric analyses. To check the role of morphometrics in the classification, quantitative analyses were performed on forty-three ungual specimens of different dinosaurs. The following measurements have been used in the analyses - ML, Maximum proximo-distal Length (distance between proximal end to distal end); PMD, Proximal Mediolateral Diameter (mediolateral width of the proximal articular surface); PDD, Proximal Dorsoventral Diameter (dorsoventral height of the proximal articular surface); Angle of curvature of the ventral surface. The following ratios were calculated: EI (Elongation Index = ML/PMD) and CI (Compression Index = PDD/PMD). For most of the dinosaurs, these measurements were obtained from the previously published datasets, especially the dataset modified after Mateus & Estraviz-López (2022), originally modified from Maganuco & Dal Sasso (2018). We added some additional taxa for refining the morphometric characterization of our ungual. The specimen from which the measurements were taken for each taxon has been specified. In the case of taxa for which there are published measurements of several specimens, only the relatively more complete specimens were considered. In some cases, estimated measurements have been taken for bones with a very small part not preserved, so that the measurements are quite close to the complete specimen with a difference of hardly 1-2 mm. Some measurements were made on scaled photographs of the specimens or from the casts of the specimens. The data for angle of curvature of the ventral surface are taken from Hone & Holtz (2021) and also measured from the scaled, published photographs using the methodology of Hone & Holtz (2021). Statistical comparisons of various unguals were conducted using the software PAST v4.03 (Hammer et al. 2001) for analysis. Both bivariate (Elongation Index vs Compression Index) as well as multivariate (Discriminant Functional Analysis) analyses were attempted (Supp_File_2, Supp_File_3 & Supp_File_4).

The dataset modified after Mateus & Estraviz-López (2022), originally modified from Maganuco & Dal Sasso (2018) and Hone and Holtz (2021) is used in quantitative analysis (plots in Fig. 4, 5). Correct value of the Compression Index of specimen MSNM V 6894 is included in the database as also pointed by De França et al. (2021). This dataset includes six morphometric measurements of 43 ungual specimens. The data generated and analysed in the contribution is available in Supp_File_1.

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA Owen, 1842
THEROPODA Marsh, 1881
Tetanurae Gauthier, 1986
Megalosauroidea Fitzinger, 1843
?Spinosauridae Stromer, 1915

Gen. and sp. indet.

Referred Material: RAJ/JAIS/CVQS002 is an isolated theropod pedal ungual (Fig. 2).

Locality: Building stone quarry near Chandoo (Charu) Village located 23 km NE of Jaisalmer town and 500 m south of Chandoo village on Jethwai-Kanod road. (Fig. 1).

Stratigraphic Horizon and Age: Badabag Member, Jaisalmer Formation, Bathonian, Middle Jurassic (Fig. 1).

Description. The specimen RAJ/JAIS/CVQS002 is an almost complete ungual phalanx, nicely preserved except that both the proximal and the distal tips are missing, and all the edges are not sharp but slightly abraded. Traces of yellowish coloured carbonate sediment, subangular quartz grains and iron stains are observed in the vascular grooves and the articular surface of the bone. It is identified as a pedal, rather than a manual ungual, because it is dorsoventrally depressed, almost straight in lateral aspect, and with the ventral surface almost flat. The pedal ungual is identified as not belonging to digit III because it is asymmetrical in dorsal view and curved to one of its sides. The bone is asymmetrical in both dorsal and ventral views, a condition more compatible with collateral digits II and IV. In proximal view, it is more similar to pedal ungual IV of some theropods, having broader proximal surface (e.g., *Allosaurus*, Madsen 1976; *Sinraptor*, Currie & Zhao 1993; and abelisaurids, Novas & Bandyopadhyay 2001). The specimen RAJ/JAIS/CVQS002 resembles the pedal ungual of digit IV of specimen FSAC-KK11888 (Ibrahim et al. 2014) in dorsal view, which is curved medially towards digit III. The unguals of digit IV usually curve towards digit III. We, therefore, suggest that the Indian specimen belongs to the fourth pedal digit of the left pes of a theropod (Fig. 6B, C). Therefore, the lateral surface of the Indian ungual is convex in dorsal view, and the medial surface is slightly concave.

The specimen RAJ/JAIS/CVQS002 shares the long and slender profile and conical distal tip with theropods. The ungual measures 58.7 mm in proximo-distal length, but we estimate it to be at least 64 mm when complete. In a general aspect, the ungual is dorsoventrally shallow (17.2 mm), mediolaterally wide (24 mm), slightly curved (angle of curvature of the ventral surface is 168°), resulting in a slightly subtriangular shaped contour in mid-cross-section. The ungual is elongated and slightly curved with a flat ventral surface having a broken distal tip that is acuminate forming a sharp triangle in dorsal view (Fig. 2A). Though broken, the distal tip is not blunt and looks sharp (Fig. 2A, F). The dorsal margin of the ungual is continuously curved from the proximal to distal end forming an angle of almost 45° with ventral surface towards the distal tip (Fig. 2B, C). The ungual is well preserved, exhibiting details of its outer surface, which is copiously perforated by tiny foramina. As seen on the articular surface, the bone is slightly porous even internally (spongy bone) (Fig. 2E).

The extensor tubercle (proximodorsal lip) is present. The base of proximodorsal lip is robust and overhangs the proximal articular surface, but the rest of the lip is eroded (Fig 2). The proximal articular surface is ovoid, being transversely wider than dorsoventrally deep. A faint, dorsoventral keel separates the lateral and medial concavities for the articulation with the distal condyles of the pre-ungual phalanx (not preserved). The lateral articular concavity is slightly larger than the medial one (Fig 2E).

Vascular grooves are well-defined on the medial and lateral surfaces and limited with a sharp dorsal margin (Fig. 2B, C). They are deep and show a row of foramina at the bottom of the grooves. The vascular groove on the medial surface is deeper than the one on the lateral surface. The vascular grooves extend for most of the ungual length, except in the proximal third of the bone, where the grooves curve ventrally thus interrupting the proximal projection of the ventral edges. Because the distal tip of the ungual is broken, it is not possible to check the distal extension of the grooves, but it is expected that they reached the tip, as it occurs in other dinosaurs. The vascular grooves are located at mid-height of both lateral and medial surfaces, lacking signs of asymmetry. In dorsal view (as well as in the ventral view) it becomes evident that the external margin is convex, whereas the medial one is slightly concave (Fig. 2A, D). The vascular grooves on both the medial and lateral surfaces are bounded by collateral shelves towards the ventral margin, forming a platform profusely decorated with striations and foramina (Fig. 2A). The margins of the collateral shelves are abraded.

The ventral surface of the ungual is weakly curved. A semi-circular, shallow depression (flexor fossa) is observed on the proximal half of the ventral surface. This depression is traversed by four low

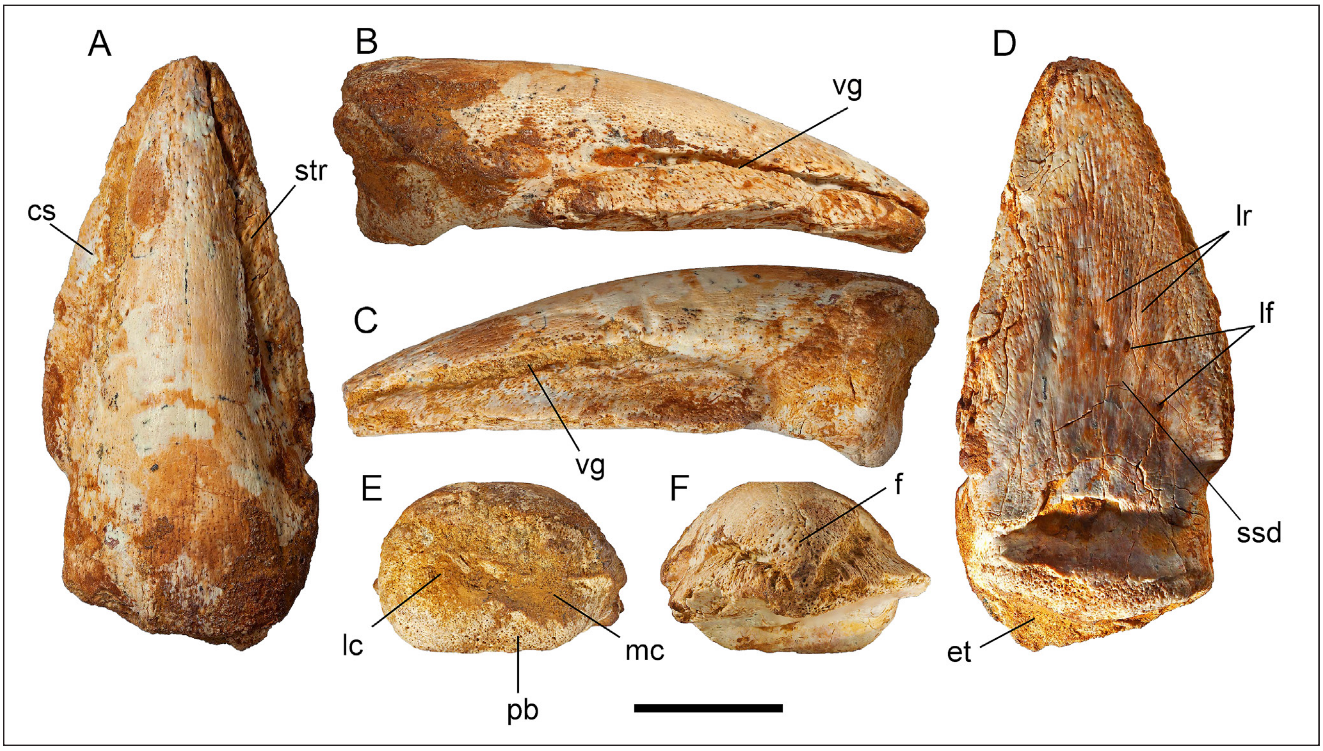

Fig. 2 - Pedal ungual phalanx from the Bathonian of Jaisalmer Basin, India. Specimen RAJ/JAIS/CVQS002 in A) dorsal; B) medial; C) lateral; D) ventral; E) proximal; F) distal views. Abbreviations: cs, collateral shelves; et, extensor tubercle; f, foramina; lc, lateral concavity; lf, large foramina; lr, low ridges; mc, medial concavity; pb, porous bone; ssd, shallow semi-circular depression; str, striations and vg, vascular grooves. Scale bar equals 15 mm.

ridges (Fig. 2D). This region of the ungual sharply contrasts with the periphery of the bone, which is flat and decorated with narrow radial striations (formed by rows of minute foramina). In the transition between the proximo-central region and the periphery of the ungual, there are some unevenly dispersed foramina of large size. Many small fractures are seen on the ventral surface and the collateral shelves because of taphonomic effects (Fig. 2).

Regarding the ontogenetic stage of the specimen, it must be said that some skeletal immaturity is observed on the proximo-articular surface. Tiny pores are observed on the distal tip, collateral shelves and ventral surface, though most of the dorsal surface is comparatively smoother with very tiny pores. The porous texture of bones is also present in archosaur hatchlings, and the degree of porosity decreases gradually with ontogenetic growth (Maganuco & Dal Sasso 2018; De França et al. 2021). The porous texture of the inner bone is revealed on the articular surface, showing incomplete ossification but not as porous as the juvenile spinosaurid specimen MSNM V 6894 (Maganuco & Dal Sasso 2018). Incomplete bone ossification suggests that the Indian specimen may belong to an intermediate stage between a juvenile and a young adult. The asymmetric shape of the ungual indicates that it did not came from the III digit, so this was not the largest ungual in the pes. The animal was still growing and yet to attain its maximum adult size, but it most certainly belonged to a medium to large sized animal (ungual maximum length ≈ 64 mm).

Comparison. The Jurassic was a period of high diversity of reptiles and dinosaurs such as crocodylomorphs, pterosaurs, sauropods, ornithischians and theropods etc. A comparison made with these groups is as follows:

Crocodylomorphs — The unguals in the Middle Jurassic crocodylomorphs, though not described in the literature, are comparatively smaller and thick and not as large and slender as the Indian ungual (Michela Johnson pers. comm. October 2022).

Pterosaurs — The unguals in pterosaurs are more curved, slender and higher than the Indian ungual (Witton 2015).

Sauropodomorphs — A turiasaurian tooth has been described from the same quarry (Sharma et al. 2022), indicating the presence of large sauropods in the area. Direct comparisons have been made with the unguals of the Early Jurassic Indian sauropod *Kotasaurus yamanpalliensis* displayed at the BSC, Hyderabad, India, which are large, robust, transversely compressed, and recurved with a prominent flexor tubercle. The proximal articular surface is asymmetrically biconcave with a prominent vertical ridge (Yadagiri 2001). Sauropod dinosaurs characteristically bear transversely compressed and dorsoventrally deep pedal and manual unguals, which are strongly curved outwards when seen in dorsal view. The ungual here described differs from this pattern, thus dismissing its referral to the sauropodomorphs.

Ornithopods — This clade of ornithischian dinosaurs is well documented in the Jurassic rocks mainly in North America and Asia. They depict a diverse ungual morphology including forms with claw shaped unguals as well as flat hoof shaped ones. As in most dinosaurs, all basal ornithischians have claw-shaped, slightly curved pedal unguals, as present in *Lesothosaurus*, heterodontosaurid *Heterodontosaurus* (Norman et al. 2004; Sereno 2012), hypsilophodontids *Hypsilophodon* (Gilmore 1915), *Parksosaurus* (Parks 1926), *Psittacosaurus* (Colbert 1962: Fig. 29), neornithischian *Othnielosaurus* (Cruzado-Caballero et al. 2021: Fig. 1b), and the basal ornithopods *Dryosaurus* (Galton 1981; Carpenter & Galton 2018), and *Yandusaurus* (He & Cai 1984). All Jurassic ornithopods were mostly small-sized animals. The Late Jurassic taxon *Dryosaurus* had small, claw-like, more recurved pedal unguals. In the Late Jurassic *Draconyx*, the ungual of pedal digit III (Rotatori et al. 2022: Figs. 8, 9) are transversely robust and dorsoventrally deep, being different from RAJ/JAIS/CVQS002. The Late Jurassic taxon *Camptosaurus* (a basal ankylopollexian) was a large animal with distally pointed, large, claw-shaped unguals, but they are shorter, recurved, angled downwards with respect to the articular surface, and transversely narrow (Gilmore 1909: Fig 28, 35; Galton & Powell 1980: Text-figs. 13S, T, U). Unlike specimen RAJ/JAIS/CVQS002, the semi-circular excavation is not present on the ventral surface of the unguals of *Camptosaurus dispar*, specimen USNM 4277 (Fig. 3S2). *Dysalotosaurus* (Janensch 1955, 1961) is the only Jurassic Gondwanan ornithopod reported from the Late Jurassic of Africa and it was a small taxon with small, claw-like, flattened pedal unguals. The vascular grooves are more distally located with a constant thickness from proximal end to distal end as seen in the specimen MBR 1465 (Fig. 3N1). The distal tip is blunt in *Dysalotosaurus*. In comparison the RAJ/JAIS/CVQS002 ungual is bigger, slender with pointed distal tip and the dorsal surface is continuously curved from proximal to distal end. The semi-circular excavation seen in the Indian ungual is absent in *Dysalotosaurus* (Fig. 3N2). In the Early Cretaceous heterodontosaurid *Tianyulong*, the pedal ungual phalanges are small and described as 'transversely compressed and taper to slender tips' by Sereno (2012). An anteriorly displaced flexor tubercle is present in the pedal ungual phalanges of *Tianyulong* (Becerra et al. 2016), unlike the Indian ungual. In the holotype specimen of the Late Cretaceous *Talenkauen santacrucensis* (Rozadilla et al. 2019) from Patagonia, the collateral shelves develop more distally (Fig. 3E2, E3), and the ungual lacks the kidney-shaped fossa on the articular surface present in the Indian specimen. Besides, in *Talenkauen* there exists a pair of longitudinal shallow furrows, on the ventral surface (Fig. 3E3), delimiting the shelves from the rest of the ventral surface. Similar feature is also observed in the ungual of Late Cretaceous *Rhabdodon* (Chanthasit 2010: Fig 4.27, 4.35) which has curved, angled downwards and arrow-shaped pedal unguals (Fig. 3I1, I2, I3). Arrowhead-shaped unguals are also observed in the Late Cretaceous taxon *Thescelosaurus* (Brown et al. 2011) but not present in the Indian ungual. In the Vegagete rhabdodontid (Dieudonné et al. 2016: Fig 10, 11), the unguals are very small, claw-shaped, and dorsoventrally higher than in the specimen from India (Fig. 3J2). The basal Iguanodontian *Tenontosaurus* from Late Cretaceous, has elongated claw-shaped unguals comparable in size to the Indian ungual (Forster 1990). No excavation is seen on the ventral surface of *Tenontosaurus tilletti*, specimen YPM VP 5460 (Fig. 3O1, O2, O3) and the unguals are higher than the Indian specimen. In the Cretaceous *Zalmoxes*, (Weishampel et al. 2003), the ungual of digit IV, is described as long, narrow, arched and pointed at end with two well-developed lateral grooves. It is wider, higher, and more curved than the Indian ungual. In the more derived iguanodontian *Iguanodon*, the pedal unguals are hooflike, dorsoventrally flattened, with a blunt, flattened distal tip (Fig. 3T1, T2, T3), except for the ungual I of manus which is an asymmetrical conical structure (Norman 1986: Figs. 50, 51, 52, 63, 64, 65; Norman 2004). In the Early Cretaceous *Ouranosaurus* (Styracosterna), the unguals are blunt, spade-like, dorsoventrally flattened and look square shaped in dorsal view (Bertozzo et al. 2017: Fig 18).

Among Ornithopoda, there exist taxa with small, claw-shaped recurved unguals (as in the non-iguanodontid euornithopods) as well as blunt, hoof-shaped flat unguals (as in the more derived larger iguanodontids). None of the examined ornithopods have a semi-circular excavation on the ventral surface similar to the specimen RAJ/JAIS/CVQS002. The shape, morphology and proportions of the Indian ungual are different from any of the above listed ornithopods (Fig. 3). Thus, we conclude that RAJ/JAIS/CVQS002 does not belong to the Ornithopoda clade.

Theropods — The specimen RAJ/JAIS/CVQS002 shares the long, slender profile and conical distal tip with theropods, but almost all theropods are characterised by strongly curved unguals, though the pedal unguals are comparatively less curved than manual unguals. The dorsoventrally flattened ungual RAJ/JAIS/CVQS002 certainly differs from the more recurved and dorsoventrally higher pedal unguals of most theropod clades i.e., tetanurans, ceratosaurians, non-spinosaurid megalosauroids, allosauroids. All of these theropod clades have a well-developed flexor tubercle on the ventral surface, whereas the Indian ungual lacks a flexor tubercle and instead has a semi-circular fossa on the ventral surface. Comparisons were made with many theropods such as *Afrovenator* (photo provided by Tyler Keillor), *Australovenator* (Hocknull et al. 2009), *Kileskus* (Averianov et al. 2010), *Majungasaurus* (Carrano 2007), ornithomimids (Brownstein 2017), *Poikilopleuron* (Allain & Chure 2002), *Spectrovenator* (Zaher et al. 2020), spinosaurids (Stromer 1934; Ibrahim et al. 2014; Maganuco & Dal Sasso 2018), and *Tyrannosaurus* (Brochu 2003) etc. in Fig. 3.

Most of the contemporaneous Middle Jurassic theropods (Sharma et al. 2023: Fig. 6) were Laurasian megalosaurids e.g., *Dubreuillosaurus*, *Megalosaurus* and *Poekilopleuron* from the Bathonian of Europe. *Poekilopleuron* from France had more recurved and dorsoventrally higher pedal unguals (Allain & Chure 2002: Text-Fig. 5). The pedal unguals are not preserved in the Bathonian megalosaurids *Dubreuillosaurus*, *Megalosaurus* and in indeterminate averostran *Cruxicheiros* (also from Bathonian of Europe) precluding any comparison with RAJ/JAIS/CVQS002. Other Middle Jurassic theropod taxa from Laurasia are the basally branching Bathonian tyrannosauroids (*Kileskus* from Russia and *Proceratosaurus* from Europe respectively) and the metriacanthosaurids (*Yangchuanosaurus* and *Sinraptor,* from Bathonian-Callovian of China); both clades are known by more recurved, sharp claws. Middle Jurassic theropods record in Gondwana is comparatively poor, represented mostly by fragmented remains i.e., isolated teeth and some fragmentary bones (Maganuco et al. 2005, 2007; Serrano-Martínez et al. 2016; Haddoumi et al. 2016; Prasad & Parmar 2020; Sharma et al. 2023). *Afrovenator* (?Bathonian-Oxfordian) from Northern Africa (Sereno et al. 1994): the only taxon known from the Middle Jurassic Gondwana was a megalosaurid, and it had more recurved and dorsoventrally higher pedal unguals (Fig 3G1, G3). Flat pedal ungual morphology is not observed in the Jurassic theropods, so we tried to compare RAJ/JAIS/CVQS002 to the theropod clades having unguals with similarly flat ventral surface, which are mostly known from the Cretaceous.

Fig. 3 - Comparison of the Indian ungual with the pedal ungual bones of various theropods and ornithischians in different anatomical views. Specimen RAJ/JAIS/CVQS002 in A1) dorsal view; A2) lateral view; A3) ventral view; unguals of *Poikilopleuron bucklandii* in B1) B2 & B3) side views (Allain & Chure 2002); pedal ungual of *Majungasaurus crenatissimus*, in C1) dorsal view; C2) medial view (Carrano 2007); ungual of *Kileskus aristotocus* in D1) side view; D2) articular view (Averianov et al. 2010); ungual of *Talenkauen santacrucensis* in E1) side view; E2) dorsal view; E3) ventral view (Rozadilla et al. 2019); ungual of *Spinosaurus aegyptiacus* (FSAC-KK11888 digit IV-5R) in F1) dorsal view; F2) ventral view; F3) side view (photos provided by Cristiano Dal Sasso); ungual of *Afrovenator abakensis* (MNN TIG1) in G1) side view; G2) dorsal view; G3) articular view (photos provided by Tyler Keillor & Paul Sereno); ungual of Indian abelisaurid in H1) side; H2) dorsal; H3) ventral views (Novas & Bandyopadhyay 2001); ungual of *Rhabdodon* in I1) side; I2) ventral; I3) dorsal views (Chanthasit 2010); ungual of Vegagete rhabdodontid in J1) dorsal; J2) side view (Dieudonné 2016). ungual of '*Spinosaurus* B' in K1) dorsal; K2) side view (Stromer 1934); ungual of *Tyrannosaurus rex* in L1) lateral; L2) dorsal view (Brochu 2003); unguals of *Spectrovenator ragei* in M1) lateral; M2) ventral views (Zaher et al. 2020); ungual of *Dysalotosaurus lettowvorbecki* (MBR 1465) in N1) dorsal; N2) ventral; N3) side views (photos provided by Daniela Schwarz); ungual of *Tenontosaurus tilletti* (YPM VP 5460) in O1) dorsal; O2) ventral; O3)side views (photos provided by Karen Moreno); ungual of juvenile *Spinosaurus* in P1) dorsal; P2) lateral; views (Maganuco & Dal Sasso 2018); ungual of ornithomimid in Q1) medial; Q2) articular views (Brownstein 2017); ungual of *Australovenator wintonensis* in R1) side view; R2) ventral; R3) dorsal views (Hocknull et al. 2009); ungual of *Camptosaurus dispar* (USNM 4277) in S1) dorsal; S2) ventral; S3) side views (photos provided by Karen Moreno); ungual of *Iguanodon* in T1) dorsal; T2) ventral; T3) side views (Posmosanu 2003). Scale bars: J, P (5 mm), A, B, C, D, M, N, Q. T (10 mm), K, O, H, I, F (20 mm), E (30 mm), G, L, R, S (50 mm).

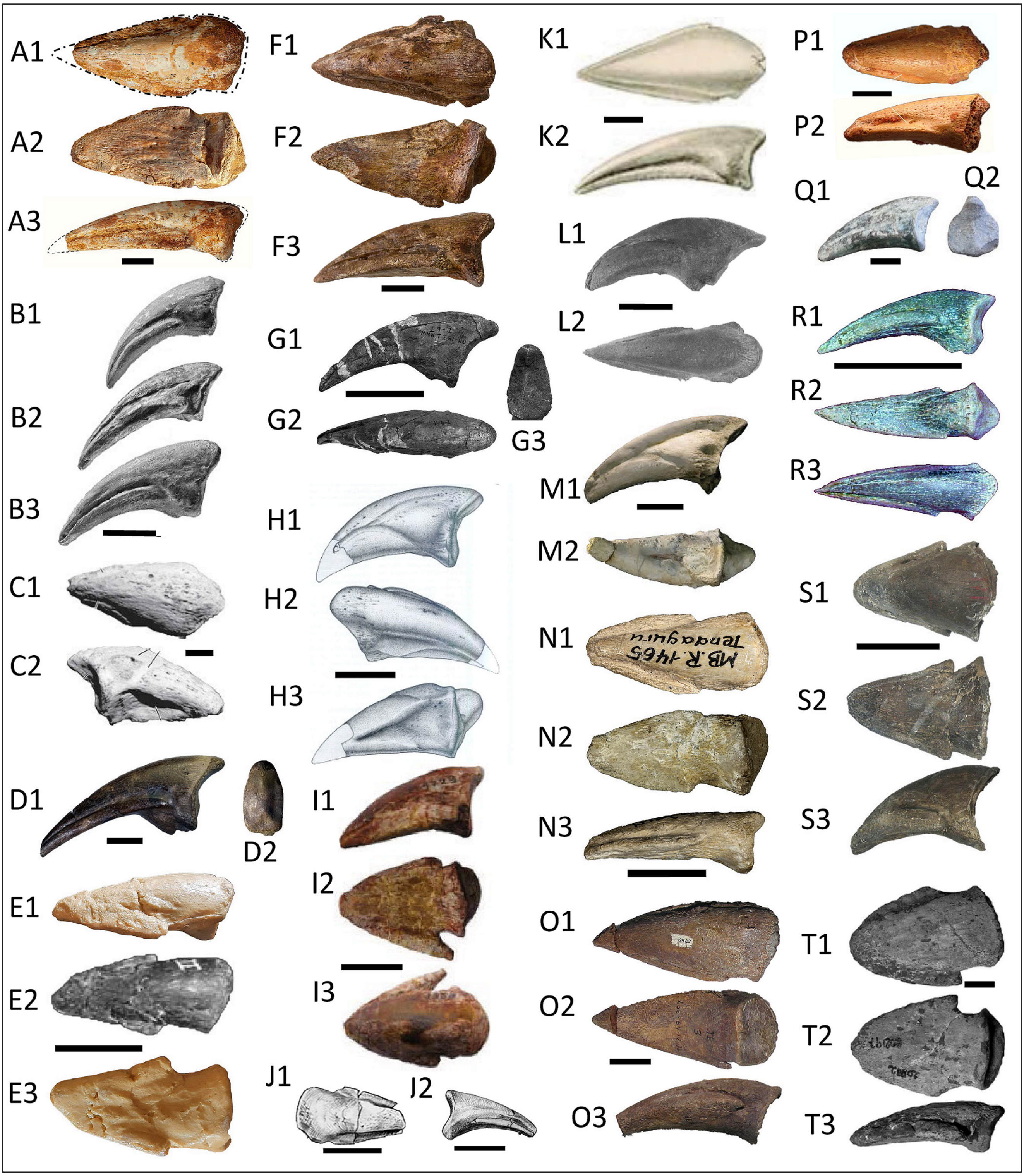

Figure 3

In abelisaurids, the pedal unguals are described as robust, tall, and gently curved with a flat ventral surface having a narrow and deep groove (Novas & Bandyopadhyay 2001; Carrano et al. 2002; Novas et al. 2005). The flexor tubercle is absent in the abelisaurids. The vascular grooves show a distinct bifurcated 'Y'-shaped pattern (Fig. 3C2, H1, M1) as observed in *Majungasaurus* (Carrano 2007), *Spectrovenator* (Zaher et al. 2020) and the Indian abelisaurid theropods from the Cretaceous for which unguals have been described (Novas & Bandyopadhyay 2001). In comparison, specimen RAJ/JAIS/CVQS002 is shallower and does not show the 'Y'-shaped pattern of vascular grooves and the excavation on the ventral surface is semi-circular and shallow, different from the deep groove of abelisaurid unguals. Abelisaurid theropods are well known from the Cretaceous of India but the specimen RAJ/JAIS/CVQS002 certainly does not belong to an abelisaurid.

Among ornithomimids, the pedal unguals are slightly recurved, higher, and transversely compressed with an almost flat ventral surface. The proximal articular surface is isosceles trapezoid-shaped, and a flexor tubercle is absent, being replaced with a deep circular flexor fossa (Brownstein 2017; McFeeters et al. 2018). Pedal unguals are narrower than RAJ/JAIS/CVQS002, and with a triangular-shaped contour in cross-section due to the presence of a sharp ridge on the dorsal surface (Fig. 3Q1, Q2). The proximodorsal lip is more prominent and triangular-shaped, in both dorsal and proximal. In the Indian specimen, the base of proximodorsal lip is robust and overhangs the proximal articular surface, but the rest of the lip is eroded to allow any comment.

The megaraptoran *Australovenator* (Hocknull et al. 2009), has narrow, slender and more recurved pedal unguals than RAJ/JAIS/CVQS002. The flexor tubercle, albeit reduced, is much developed in *Australovenator* (Fig. 3R1, R2, R3).

Notably dorsoventrally compressed, flat pedal unguals with almost straight side profile as seen in RAJ/JAIS/CVQS002 are observed in the derived Cretaceous spinosaurid *Spinosaurus aegyptiacus* (Stromer 1934: taf. I, figs. 17a–b; De Lapparent 1960: Pl VI, Fig. 10-12; Novas et al. 2005: Fig. 2; Ibrahim et al. 2014: Fig. 2, S1; Maganuco & Dal Sasso 2018: Fig 2).

RAJ/JAIS/CVQS002 is broader than deep and notably depressed with a flat ventral surface and a convex dorsal surface, just like the pedal ungual bones of *Spinosaurus* 'B' (Stromer 1934: taf. I, figs. 17a–b); MPCM 13574 (Novas et al. 2005: Fig. 2) and FSAC-KK11888 (Ibrahim et al. 2014: Fig. 2, S1), but shallower than the juvenile ungual specimen MSNM V6894 (Maganuco & Dal Sasso 2018: Fig 2), specimen CPHNAMA VT-1446-A (De França et al. 2021) and *Iberospinus* specimen ML1190-34 (Mateus & Estraviz-López 2022). The specimen RAJ/JAIS/CVQS002 is claw-shaped and elongated with the maximum proximodistal length (≈ 64 mm) exceeding four times the dorsoventral depth measured at mid-length, characteristic of the spinosaur pedal unguals noticed in FSAC-KK11888, MSNM V6894, CPHNAMA VT-1446-A (Ibrahim et al. 2014; Maganuco & Dal Sasso 2018; De França et al. 2021). The proximal articular surface is divided into two subequal articular surfaces as in MPCM 13574, FSAC-KK11888, and MSNM V6894. A shallow semi-circular depression (fossa) observed in the proximal half of the ventral surface of specimen RAJ/JAIS/CVQS002 reaching the borders, is also seen in FSAC-KK11888, MPCM 13574, MSNM V6894, CPHNAMA VT-1446-A and ML1190-34. The semi-circular depression on ventral surface is traversed by low-lying ridges in specimen RAJ/AIS/CVQS002, like the specimen MPCM 13574 and FSAC-KK11888 (digit IV), in contrast, a medial low ridge is noticed in MSNM V6894 and CPHNAMA VT-1446-A. On the ventral surface of the specimen RAJ/AIS/CVQS002, unevenly distributed large foramina are present similar to digit IV of FSAC-KK11888 (Fig. 3A, F). The vascular groove on medial surface is deeper than on the lateral surface just like digit IV of FSAC-KK11888 (Fig. 3A, F). The collateral shelves of specimen CPHNAMA VT-1446-A and FSAC-KK11888 (digit IV), are rugose with striated ornamentation and a similar condition is noticed in RAJ/AIS/CVQS002 too, though the collateral shelves of the specimen RAJ/JAIS/CVQS002 are more flared. All the above mentioned spinosaurids belong to Spinosauridae. Spinosauridae is sister clade of Megalosauridae under Megalosauroidea. The flat pedal unguals are not present in Megalosauridae, such as *Poekilopleuron* (Fig. 3B1, B2, B3) and *Afrovenator* (Fig. 3G1, G2, G3). Traditionally, Spinosauridae has been divided into Spinosaurinae (Stromer 1915) and Baryonychinae (Charig & Milner 1986). Pedal unguals are not known in Baryonychinae except for a partial pedal ungual of *Baryonyx*, but not figured in the description by Charig & Milner (1997). However, Novas et al. (2005) described this pedal ungual of *Baryonyx* as dorsoventrally higher and more recurved unlike the Indian specimen and other known spinosaurid unguals described above.

The Indian ungual RAJ/JAIS/CVQS002, possesses all the diagnostic morphological features of the Spinosaurinae clade of Spinosauridae, including elongated, slightly curved profile, flat ventral surface, semi-circular flexor fossa, traversed by 3-4 oblique ridges, medio-lateral axis larger than dorsoventral axis, total proximodistal length exceeding four times the dorsoventral depth.

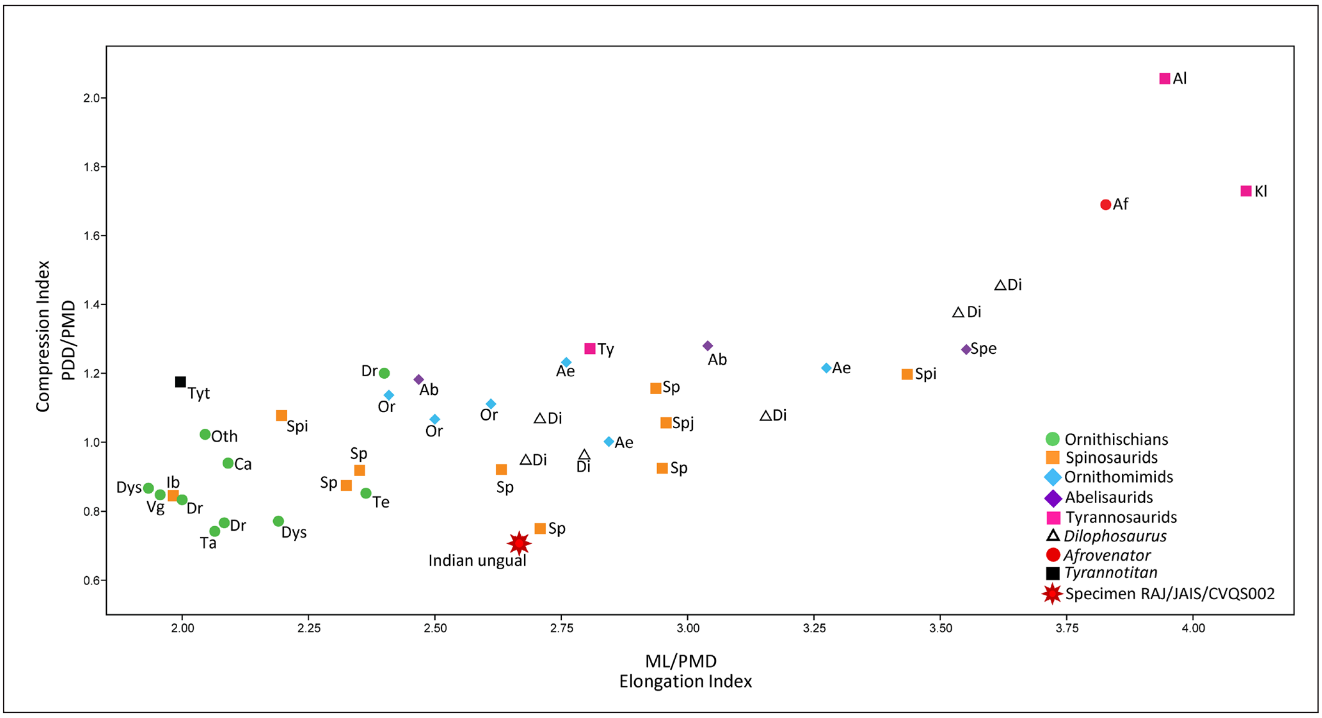

Fig. 4 - Bivariate plot of Elongation Index (ML/PMD) vs Compression Index (PDD/PMD) provides information about the shape of the unguals of different dinosaurs. Specimen RAJ/JAIS/CVQS002 is plotted near *Spinosaurus* pedal ungual digit III. Indian ungual is proximo-distally elongated and dorso-ventrally compressed like *Spinosaurus* pedal unguals. Abbreviations: Ab, Abelisaurid; Ae, *Aepyornithomimus*; Af, *Afrovenator*; Al, *Alioramus*; Ca, *Camptosaurus*; Di, *Dilophosaurus*; Dys, *Dysalotosaurus*; Ib, *Iberospinus*; Kil, *Kileskus*; Or, Ornithomimid; Oth, *Othnielosaurus*; Spe, *Spectrovenator*; Sp, *Spinosaurus*; Spi, spinosaurid; Spj, juvenile *Spinosaurus*; Ta, *Talenkauen*; Te, *Tenontosaurus*; Ty, *Tyrannosaurus*; Tyt, *Tyrannotitan*; Vg, Vegagete rhabdodontid; ML, Maximum Length; PMD, Proximal Mediolateral Diameter; PDD, Proximal Dorsoventral Diameter.

RESULTS OF MORPHOMETRIC ANALYSES

In the morphometric analyses, specimen RAJ/JAIS/CVQS002 is clearly differentiated from other theropods and ornithischians in the resulting plots, showing a spinosaurid affinity.

Bivariate Analysis (Elongation Index vs Compression Index)

In a database consisting of different-sized populations including both adult and juvenile subjects, ratios may give more accuracy than the absolute values as per the hypothesis of isometric growth of unguals suggested by Maganuco & Dal Sasso (2018). A simple bivariate plot of Elongation Index (Maximum Length/proximal mediolateral diameter) vs Compression Index (proximal dorsoventral diameter/proximal mediolateral diameter) provides information about the shape and proportions of the unguals of different dinosaurs. Interestingly, the specimen RAJ/JAIS/CVQS002 plots near *Spinosaurus aegyptiacus* (FSAC-KK11888) with a low compression index and similarly high elongation index (Fig. 4). Among dinosaur unguals with comparable high elongation index, such low compression index is noticed only in the spinosaurids. Spinosaurid pedal unguals are elongated and flattened and are characterised by having a high elongation index and somewhat lower compression index, though some positional variation is seen in the unguals of different digits. Low values of the compression index are observed in some of the ornithischians too, but most of them have very low Elongation Index (Fig. 4).

Discriminant Functional Analysis (LDA)

The complex statistics have been proved to provide more meaningful results than simple bivariate plots. The measurements of our specimen were included in the dataset of 43 ungual specimens modified after Mateus & Estraviz-López (2022) originally modified from Maganuco & Dal Sasso (2018). Correct value of the Compression Index of specimen MSNM V 6894 is included in the database as also pointed by De França et al. (2021). We subjected this quantitative dataset of six morphometric variables (ML, PMD, PDD, PDD/PMD, ML/PMD, and the angle of curvature of the ventral surface) of forty-three ungual specimens, to Discriminant Function-

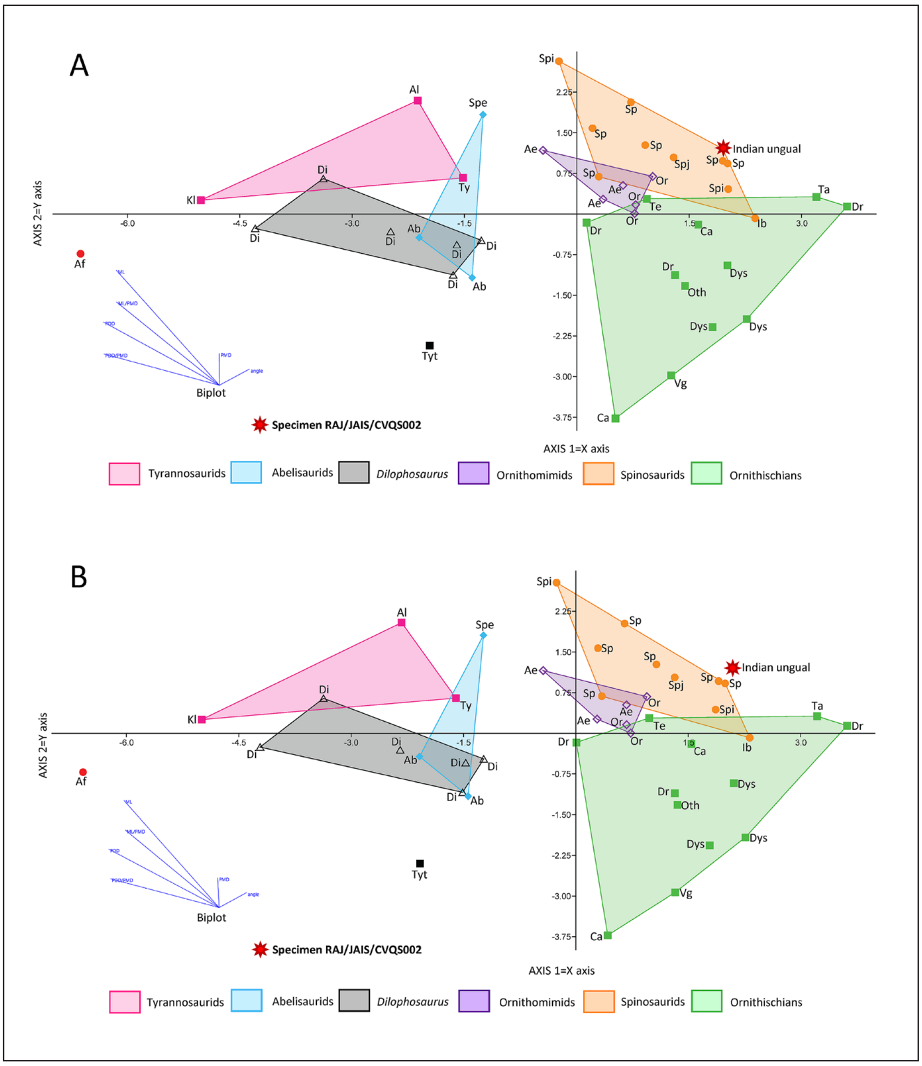

Fig. 5 - Results of the Discriminant Function Analysis showing the morphospace occupied by different theropod clades. DFA using LDA function performed on the dataset of six morphometric measurements of unguals used in the paper. Dataset modified from Maganuco & Dal Sasso (2018), Hone & Holtz (2021) and Mateus & Estraviz-López (2022) is used. A) DFA performed on all the six variables assigning the Indian ungual to spinosaurids; B) DFA performed on all the six variables without assigning the Indian ungual to any known theropod group. The specimen RAJ/JAIS/CVQS002 is retrieved as a spinosaurid in each analysis and plotted near the morphospace occupied by the spinosaurids. DFA supports the referral of the Indian specimen to Spinosauridae. Abbreviations: Ab, Abelisaurid; Ae, *Aepyornithomimus*; Af, *Afrovenator*; Al, *Alioramus*; Ca, *Camptosaurus*; Di, *Dilophosaurus*; Dys, *Dysalotosaurus*; Ib, *Iberospinus*; Kil, *Kileskus*; Or, Ornithomimid; Oth, *Othnielosaurus*; Spe, *Spectrovenator*; Sp, *Spinosaurus*; Spi, spinosaurid; Spj, juvenile *Spinosaurus*; Ta, *Talenkauen*; Te, *Tenontosaurus*; Ty, *Tyrannosaurus*; Tyt, *Tyrannotitan*; Vg, Vegagete rhabdodontid.

al Analysis (DFA) with LDA function to illustrate the morphometric distinctions. Log-transformed measurements were used to make data more homoscedastic. The 'X' axis is Axis-1, and the 'Y' axis is Axis-2. The specimen RAJ/JAIS/CVQS002 was taken as an 'unassigned taxon' as its own group as well as 'assigned to spinosaurid group' in two different analyses. These analyses brought out the differences among individuals based on their measured morphological characters of ungual phalanx. The resulting scatter plots illustrate the morphospace occupied by different clades of dinosaurs.

Analysis A includes all the six variables considering the specimen RAJ/JAIS/CVQS002 as 'assigned' to the group spinosaurid (Supp_File_3). Analysis B includes all the six variables considering the specimen RAJ/JAIS/CVQS002 as 'unassigned' or assigned to its own group (Supp_File_4). LDA outcomes confirmed the distinct separation between the spinosaurids and other clades (Fig. 5A, B). The first two canonical axes account for more than 85% of the variance. 79.07% specimens were identified correctly in analysis 'A' and 76.74% specimens were identified correctly in analysis 'B' (Table 1). Among spinosaurids, in analysis 'A' 90.9 % of spinosaurid unguals were identified correctly and in analysis 'B' 80% of the spinosaurid unguals were identified correctly. The curvature of unguals (angle of the ventral surface) and proximal width are the key variables. The results of the DFA are summarized in Table 1.

In the resulting DFA plots (Fig. 5), the abelisaurids, *Dilophosaurus*, tyrannosaurids and *Tyrannotitan* plot along the negative 'X'. Spinosaurids, ornithomimids and ornithischians plot along the positive 'X' axis. Curvature of the ventral surface separated the spinosaurids, ornithomimids and ornithischians from all the other theropods. Ornithischians plot along the positive 'X' and negative 'Y' axis. The specimen RAJ/JAIS/CVQS002 plots

Analysis	Dataset and Variables used in DFA	Assigned or Unassigned	Eigen Value Axis 1	Axis 1 (%)	Eigen Value Axis 2	Axis 2 (%)	Reclassification Rate (RR) (%)	Specimen RAJ/JAIS/CVQS002 classified as
A	All six Variables: ML, PMD, ML/PMD, PDD, PDD/PMD, Angle	Assigned Fig. 5A	4.8056	69.93	1.2216	17.78	79.07	Spinosaurid
B		Unassigned Fig. 5B	4.9243	68.12	1.2216	16.9	76.74	Spinosaurid

Tab. 1 - Discriminant Function Analyses (DFA by LDA) conducted on a dataset of six morphometric variables, with reclassification rate and percentage of variance for the two principal axes for each analysis. The specimen RAJ/JAIS/CVQS002 is analysed as 'assigned' to the group spinosaurid as well as 'unassigned' to an unknown group (group of its own) in analysis A and B respectively. In both analyses the specimen RAJ/JAIS/CVQS002 is classified as a spinosaurid.

along the positive 'X' and positive 'Y' axis in the morphospace occupied by spinosaurids in analysis A and outside the morphospace of all groups in analysis B but near to spinosaurids in the same quadrant. The specimen RAJ/JAIS/CVQS002 is retrieved as a spinosaurid in every analysis. Spinosaurids show a slight overlap with the morphospace occupied by ornithomimids and ornithischians, but the typical morphology of the spinosaurid unguals clearly differentiate them from ornithomimids and ornithischians. The morphometric analyses strongly support referral of the Indian ungual to Spinosauridae.

Taphonomy and Paleoecology

The ungual phalanx RAJ/JAIS/CVQS002, has been found in the same building stone quarry, which produced the turiasaur tooth described by Sharma et al. (2022). It is worth noting that an isolated theropod tooth crown of a non-coelurosaurian averostran with a possible megalosaurid affinity, was found in the marine Bathonian rocks of the Jaisalmer Basin, 4.5 km WSW of the study area (Sharma et al. 2023). This tooth and the here reported pedal ungual demonstrates that large theropods were present during Middle Jurassic times in NW India.

This ungual must have loosened from a floating carcass and finally deposited as a clast (intraformational) in the bioclastic rudstone. This bone does not show any roundness as would be expected from a long alluvial transportation. It did not travel much and deposited close to the source, as also suggested by the presence of angular to sub-angular quartz grains in vascular grooves. The bioclastic rudstone bed has been described as a tidal channel lag deposit by Sharma et al. (2022), where the hard skeletal remains got concentrated with wave action in a near-shore, shallow marine depositional setting. The ungual phalanx do have rough, slightly abraded edges and fine fractures, which may be due to wave action in stormy, near-shore settings.

A piscivorous diet was envisioned for the Spinodauridae (Charig & Milner 1997; Ibrahim et al. 2014; Hone & Holtz 2021). Interestingly, the pedal ungual here reported with spinosaurid affinity comes from the same beds which yielded abundant hybodont sharks and bony fish remains. This ungual most definitely belongs to an animal living near the Jurassic coast of the Jaisalmer Basin with similar locomotor adaptations and dietary habits inferred for the more derived Cretaceous spinosaurids.

Paleogeographical Implications

Middle Jurassic theropod record is scanty and mostly dominated by the Laurasian megalosaurids, remains of which are mostly found in marine sediments (Sharma et al. 2023: Fig. 6), but this record is highly skewed because of poor representation from Gondwana. Basal megalosauroids (i.e., *Piatnitzkysaurus* and *Condorraptor*) were reported from the Lower Jurassic beds of Argentina and the recent discovery of a non-coelurosaur averostran theropod tooth with a possible megalosauroid affinity from the Bathonian of the Jaisalmer Basin suggests their presence in the Middle Jurassic of India (Sharma et al. 2023). Megalosauroids had a Pangaean distribution by the Middle Jurassic. Spinosauridae is the sister clade of Megalosauridae grouped under Megalosauroidea (Benson 2010; Allain et al. 2012; Carrano et al. 2012). Spinosauridae is considered a Cretaceous clade with unambiguous fossil records from Barremian through Cenomanian (Carrano et al. 2012; Hone & Holtz 2017; Barker et al. 2021). Spinosaurids have a global presence by the Early Cretaceous with fossils found in Africa, Europe, South America, Asia and Australia

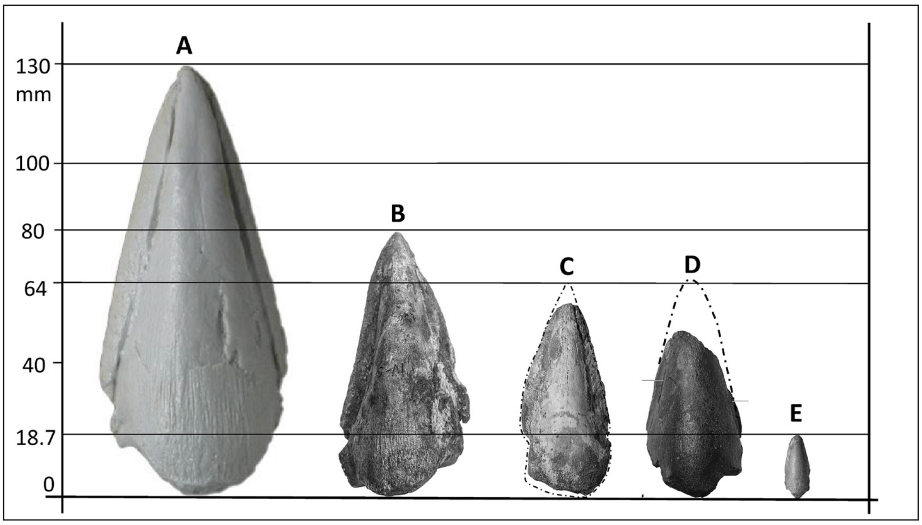

Fig. 6 - Size and shape comparison of pedal unguals of different spinosaurid specimens in dorsal view: A) *Spinosaurus* specimen FSAC-KK11888, Digit III, right pes; B) *Spinosaurus* specimen FSAC-KK11888 Digit IV, right pes; C) Indian specimen RAJ/JAIS/CVQS002 (identified as digit IV, left pes); D) Brazillian spinosaurid specimen CPHNAMA VT-1446-A Digit I, right pes; E) Juvenile *Spinosaurus* specimen MSNM V6894 Digit III.

(Allain et al. 2012; Hone & Holtz 2017; Mateus & Estraviz-López 2022). The presence of spinosaurids in the Early Cretaceous of China (Buffetaut et al. 2008) and Australia (Barrett et al. 2010) clearly indicates towards an ancestral Pangaean distribution of the Spinosauridae before Pangaea breakup, as suggested by different workers such as Sereno et al. (1998); Brusatte et al. (2010) and Allain et al. (2012). The phylogenetic analysis also supports a Middle Jurassic origin for the clade Spinosauridae (Benson 2010; Allain et al. 2012). Spinosauridae and Megalosauridae must have split at least by early Middle Jurassic to have sister group relations (Hone & Holtz 2017).

Spinosaurids were bizarre animals with conical teeth, long dorsal spines and flat pedal unguals, unlike the typical theropods. Not much is known about the early evolutionary history of the spinosaurid clade, and their record is still fragmentary. The significant gap (170 Ma through 130 Ma) in the spinosaurid lineage, may not imply a genuine absence, but points towards some preservation bias along with inadequate sampling, particularly from the Gondwanan continents. Recent discoveries indicated the presence of this clade in the Jurassic, including dental remains from the Upper Jurassic of Tanzania (Buffetaut 2008) and the Middle Jurassic of Niger (Serrano-Martinez et al. 2016). The unique pedal ungual morphology of the spinosaurids is not seen in other theropod clades and can help tracing the distribution pattern and early radiation of members of the family Spinosauridae into the Jurassic.

Discussion and conclusion

Pedal unguals of spinosaurids are described as elongated, dorsoventrally compressed, broader than deep, flat with almost straight side profile, having flat ventral surface with shallow semi-circular fossa traversed by three to four low ridges, with proximodistal length approximately four times the dorsoventral depth (Novas et al. 2005; Ibrahim et al. 2014). A similar morphology is observed in the isolated ungual specimen RAJ/JAIS/CVQS002 found in the Middle Jurassic rocks of Jaisalmer Basin, India. The comparative and morphometric analyses strongly support referral of the Indian ungual to Spinosauridae. The Indian ungual, identified as penultimate digit IV phalanx, closely resembles the ungual of digit IV of the Cretaceous *Spinosaurus aegyptiacus* (FSAC-KK11888), but shows some minute differences such as mediolateral diameter is more than the dorsoventral diameter in Indian ungual and it has more flared collateral shelves (Fig. 3A, F and Fig. 6). Therefore, the possibility that this ungual belongs to a previously unknown taxon of a basally branching Jurassic spinosaurid under Megalosauroidea seems plausible.

As per the evidence in hand, we are tentatively identifying this isolated ungual (specimen RAJ/JAIS/CVQS002) belonging to a basally branching spinosaurid (Spinosauridae) under Megalosauroidea with a slight doubt until the discovery of more complete material. This identification is supported by bivariate and multivariate analyses too. The phylogenetic analysis also suggests a Middle Jurassic origin for the clade Spinosauridae. The unique spinosaurid pedal ungual morphology can help tracing this clade through time and space. If true, this Indian specimen represents the oldest spinosaurid, thus extending the stratigraphical as well as expanding the geographical distribution of spinosaurids as a whole. More and complete specimens are obviously required for any conclusive identification, but it agrees with other probable fragmentary materials referred as to Spinosauridae from Tanzania and Portugal.

Recently, fossilized teeth of one of the oldest turiasaurian (Sharma et al. 2022) and a possible megalosauroid (Sharma et al. 2023) have been described from the Bathonian of Jaisalmer Basin. The Jaisalmer Basin representing the Tethys coast of NW India, is emerging as one of the few Jurassic vertebrate sites of eastern Gondwana, especially for dinosaurian remains. Extensive sampling is necessary for a better understanding of the evolution of Jurassic fauna, hence further exploration of the Middle Jurassic sediments of the Jaisalmer basin will be continued.

Data Availability:

The data generated and analysed in the contribution is available in Supplementary File 1.

Author Contributions:

AS performed field work, discovered the specimen, measured the section, conceived and designed the study, performed literature study, collected the data, compared and curated the data, updated and analysed the data, performed the experiments, prepared figures, authored the original draft, reviewed the drafts of the paper, finalized the draft, approved the final draft.

FEN contributed the literature, compared the data, authored the draft, approved the final draft.

SS performed field work, collected the data, photographed the specimens, reviewed the drafts, proofread the drafts, approved the final draft.

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REFERENCES

Agassiz L.J.R. (1838) - Recherches sur les poissons fossiles, Vol. 3. Imprimerie de Petitpierre, Neuchâtel.

Allain R. & Chure D. (2002) - *Poekilopleuron bucklandii*, the theropod dinosaur from the Middle Jurassic (Bathonian) of Normandy. *Palaeontology*, 45(6): 1107-1121.

Allain R., Xaisanavong T., Richir P. & Khentavong B. (2012) - The first definitive Asian spinosaurid (Dinosauria: Theropoda) from the Early Cretaceous of Laos. *Naturwissenschaften*, 99: 369-377.

Ahmad F., Quasim M.A., Ghaznavi M.A., Khan Z. & Ahmad A.H.M. (2017) - Depositional Environment of the Fort Member of the Jurassic Jaisalmer Formation, (Western Rajasthan, India) as revealed from Litho Facies and Grain Size Analysis. *Geological Acta*, 15(3): 153-167.

Averianov A.O., Krasnolutskii S.A. & Ivantsov S.V. (2010) - A new basal coelurosaur (Dinosauria: Theropoda) from the Middle Jurassic of Siberia. *Proceedings of the Zoological Institute*, 314(1): 42-57.

Barker C.T., Hone D.W.E., Naish D., Cau A., Lockwood J.A.F., Foster B., Clarkin C.E., Schneider P. & Gostling N.J. (2021) - New spinosaurids from the Wessex Formation (Early Cretaceous, UK) and the European origins of Spinosauridae. *Scientific Reports,* 11(1):19340.

Becerra M., Pol D., Rauhut O. & Cerda I. (2016) - New Heterodontosaurid remains from the Cañadón Asfalto Formation: cursoriality and the functional importance of the pes in small Heterodontosaurids. *Journal of Paleontology*, 1: 1-23.

Benson R.B.J. (2010) - A description of *Megalosaurus bucklandii* (Dinosauria, Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society*, 158: 882-935.

Bertozzo F., Dalla Vecchia F.M. & Fabbri M. (2017) - The Venice specimen of *Ouranosaurus nigeriensis* (Dinosauria, Ornithopoda). *PeerJ*, 5: e3403.

Blanford W.T. (1877) - Geological notes on the Great Indian Desert between Sind and Rajputana. *Record Geological Survey of India,* 10(Pt. 1): 10-21.

Brochu C.A. (2003) - Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology.* 22: 1-138.

Brown C.M., Boyd C.A. & Russell A.P. (2011) - A new basal ornithopod dinosaur (Frenchman Formation, Saskatchewan, Canada), and implications for late Maastrichtian ornithischian diversity in North America. *Zoological Journal of the Linnean Society,* 163(4): 1157-1198.

Brownstein C.D. (2017) - Description of Arundel Clay ornithomimosaur material and a reinterpretation of *Nedcolbertia justinhofmanni* as an "Ostrich Dinosaur": Biogeographic Implications. *Peerj,* 5: E3110, 1-20.

Brusatte S., Benson B.J. & Xing X. (2010) - The evolution of large-bodied theropod dinosaurs during the Mesozoic in Asia. *Journal of Iberian Geology*. 36(2): 275-296.

Buffetaut E. (2008) - Spinosaurid teeth from the Late Jurassic of Tengaduru, Tanzania, with remarks on the evolutionary and biogeographical history of the Spinosauridae. In: Mazin J.M., Pouch J., Hantzpergue P. & Lacombe V. (Eds.) - Mid–Mesozoic Life and Environments. Lyon:

Documents Des Laboratoires De Géologie Lyon: 26-28.

Carpenter K. & Galton P.M. (2018) - A photo documentation of bipedal ornithischian dinosaurs from the Upper Jurassic Morrison Formation, USA. *Geology of the Intermountain West,* 5: 167-207.

Carrano M.T. (2007) - The appendicular skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. In: Sampson S.D. & Krause D.W. (Eds.) - *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology. Society of Vertebrate Paleontology Memoir,* 8(27): 163-179.

Carrano M.T., Benson R.B. & Sampson S.D. (2012) - The Phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, 10: 211-300.

Carrano M.T., Sampson S.D. & Forster C.A. (2002) - The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, 22: 510-534.

Carter H.J. (1861) - On the Contribution to the Geology of Western India Including Sind and Baluchistan. *Journal Royal Asiatic Society,* 6(21): 161-206.

Chanthasit P. (2010) - The ornithopod dinosaur *Rhabdodon* from the Late Cretaceous of France: anatomy, systematics and paleobiology. Université Claude Bernard, Lyon I. English. NNT: 2010LYO10098.

Charig A.J. & Milner A.C. (1986) - *Baryonyx*, a remarkable new theropod dinosaur. *Nature*, 324(6095): 359-361.

Charig A.J. & Milner A.C. (1997) - *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum of London*, 53: 11-70.

Colbert E.H. (1962). Dinosaurs: their discovery and their World. 288 pp., London.

Cruzado-Caballero P., Díaz-Martínez I., Rothschild B., Bedell M. & Pereda-Suberbiola X. (2021) - A limping dinosaur in the Late Jurassic: Pathologies in the pes of the neornithischian *Othnielosaurus consors* from the Morrison Formation (Upper Jurassic, USA), *Historical Biology,* 33 (9): 1753-1759.

Currie P.J. & Zhao X. (1993) - A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, 30(10): 2037-2081.

Das Gupta S.K. (1975) - A Revision of the Mesozoic-Tertiary Stratigraphy of the Jaisalmer Basin, Rajasthan. *Indian Journal of Earth Sciences* 2(1): 77-94.

De França T., Santos B.N., De Oliveira M.N.Y, Alfredo M.M., Matos L.R. & Rodrigues C.F. (2021) - The first record of a spinosaurid pedal ungual from Brazil (Boca Do Forno Ravine, Itapecuru Formation, Parnaı´Ba Basin). *Historical Biology*, 34(9): 1817-1826.

De Lapparent A.F. (1960) - Les dinosauriens du "continental intercalaire" du Sahara central. *Mémoires de la Société géologique de France*, 88(A): 1-57.

Dieudonné P., Tortosa T., Torcida Fernández-Baldor F., Canudo J.I. & Díaz-Martínez I. (2016) - An unexpected early rhabdodontid from Europe (Lower Cretaceous of Salas de los Infantes, Burgos Province, Spain) and a re-examination of basal iguanodontian relationships. *PLoS ONE*, 11(6): e0156251.

Fitzinger L. (1843) - Systema Reptilium. Fasciculus Primus. Amblyglossae. Apud Braumüller and Seidel Bibliopolas, Vienna.

Forster C.A. (1990) - The postcranial skeleton of the ornithopod dinosaur *Tenontosaurus tilletti*. *Journal of Vertebrate Paleontology*, 10(3): 273-294.

Galton P.M. (1981) - *Dryosaurus*, a hypsilophodontid dinosaur from the Upper Jurassic of North America and Africa Postcranial skeleton. *Paläontologische Zeitschrift*, 55: 271-312.

Galton P. (2009) - Notes on Neocomian (Lower Cretaceous) Ornithopod dinosaurs from England - *Hypsilophodon*, *Valdosaurus*, "*Camptosaurus*", "*Iguanodon*" - and referred specimens from Romania and elsewhere. *Revue De Paleobiologie*, 28: 211-273.

Galton P. & Powell H.P. (1980) - The ornithischian dinosaur *Camptosaurus prestwichii* from the Upper Jurassic of England. *Palaeontology,* 23: 411-443.

Gauthier J. (1986) - Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences*, 8: 1-55.

Gilmore C.W. (1909). Osteology of the Jurassic reptile *Camptosaurus*, with a revision of the species of the genus, and descriptions of two new species. *Proceedings of the United States National Museum*, 36: 197-332.

Gilmore C.W. (1915) - Osteology of *Thescelosaurus*, an ornithopodous dinosaur from the Lance Formation of Wyoming. *Proceedings of the United States National Museum*, 49(2127): 591-616.

Hammer Ø., Harper D.A.T. & Paul D.R. (2001) - Past: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, 4(1), 4: 9 pp.

He X. & Cai K. (1984) - The Middle Jurassic dinosaurian fauna from Dashanpu, Zigong, Sichuan Vol. I - The ornithopod dinosaurs. Sichuan Scientific and Technological Publishing House Chengdu, 71 pp. [In Chinese with English Summary].

Hitchcock E. (1836) - Ornithichnology. Description of the footmarks of birds, (*Ornithichnites*) on New Red Sandstone in Massachusetts. *American Journal of Science*, 29(ser. 1): 307-340.

Hitchcock E. (1858) - Ichnology 01 New England. A report on the sandstone of the Connecticut valley, especially its fossil footmarks. William White, Boston.

Hocknull S.A., White M.A., Tischler T.R., Cook A.G., Calleja N.D., Sloan T., Elliott D.A. & Sereno P. (2009) - New Mid-Cretaceous (Latest Albian) Dinosaurs from Winton, Queensland, Australia. *PLoS ONE*, 4(7): e6190.

Hone D. & Holtz T.R. Jr. (2017) - A century of spinosaurs - a review and revision of the Spinosauridae with comments on their ecology. *Acta Geologica Sinica* - English Edition. 91(3): 1120-32.

Hone D. & Holtz T.R. Jr. (2021) - Evaluating the ecology of *Spinosaurus*: shoreline generalist or aquatic pursuit specialist? *Palaeontologia Electronica*, 24(1): 1-28.

Ibrahim N., Sereno P.C., Dal Sasso C., Maganuco S., Fabbri M., Martill D.M., Zouhri S., Myhrvold N. & Iurino D.A. (2014) - Semiaquatic adaptations in a giant predatory dinosaur. *Science*, 345(6204): 1613-6.

Janensch W. (1955) - Der Ornithopode *Dysalotosaurus* der Tendaguru-Schichten. *Palaeontographica*, Supplement VII, 1(3): 105-176.

Janensch W. (1961) - Skelettrekonstruktion Von *Dysalotosaurus* Lettow-Vorbecki. *Palaeontographica*, Supplement VII, 3 (4): 237-240.

Kachhara R.P. & Jodhawat R.L. (1981) - On the age of Jaisalmer Formation, Rajasthan, India. *Proceedings of IX*

Indian Colloquium on Micropalaeontology and Stratigraphy, Udaipur: 235-247.

Krishna J. (1979) - Callovian-Tithonian Ammonite Stratigraphy and Biogeography of Jaisalmer, India. Ammonoidea. Systematics Association Symposium, Abstracts: 33, York.

Madsen J. R. Jr. (1976) - *Allosaurus fragilis*: a revised osteology. *Utah Geological Survey Bulletin*, 109: 1-163.

Maganuco S., Cau A. & G. Pasini G. (2005) - First description of theropod remains from the Middle Jurassic (Bathonian) of Madagascar. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano*, 146(II): 165-202.

Maganuco S., Cau A., Dal Sasso C. & Pasini G. (2007) - Evidence of large theropods from the Middle Jurassic of the Mahajanga Basin, NW Madagascar, with implications for ceratosaurian pedal ungual evolution. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano*, 148: 261-271.

Maganuco S. & Dal Sasso C. (2018) - The smallest biggest theropod dinosaur: a tiny pedal ungual of a juvenile *Spinosaurus* from the Cretaceous of Morocco. *PeerJ*, 6: e4785.

Marsh O.C. (1879) - Notice of new Jurassic reptiles. *American Journal of Science and Arts*, 18(108): 501-505.

Marsh O.C. (1881) - Principal Characters of American Jurassic Dinosaurs, Part V. *American Journal of Science*, S3- 21(125): 417-23.

Mateus O. & Estraviz-López D. (2022) - A new theropod dinosaur from the Early Cretaceous (Barremian) of Cabo Espichel, Portugal: implications for spinosaurid evolution. *PLoS ONE*, 17: E0262614.

Mathur U.B., Pant S.C., Mehra S. & Mathur A.K. (1985) - Discovery of dinosaurian remains in Middle Jurassic of Jaisalmer, Rajasthan, Western India. *Bulletin of the Indian Geologists' Association,* 18(2): 59-65.

Mcfeeters B., Ryan M.J. & Cullen T.M. (2018) - Positional variation in pedal unguals of North American ornithomimids (Dinosauria, Theropoda): a response to Brownstein (2017). *Vertebrate Anatomy Morphology Palaeontology,* 6: 60-67.

Moreno K., Carrano M. T. & Snyder R. (2007) - Morphological changes in pedal phalanges through ornithopod dinosaur evolution: a biomechanical approach. *Journal of morphology*, 268(1): 50-63.

Norman D. (1986) - On the anatomy of *Iguanodon atherfieldensis* (Omithischia: Omithopoda). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, 56: 281-372.

Norman D.B., Witmer L.M. & Weishampel D.B. (2004) - Basal Thyreophora. In: Weishampel D.B., Dodson P., & Osmólska H. (Ed.) - The Dinosauria, 2nd Edition. University Of Californian Press: 335-342.

Novas F.E. & Bandyopadhyay S. (2001) - Abelisaurid pedal unguals from the Late Cretaceous of India. VII International Symposium on Mesozoic Terrestrial Ecosystems, Buenos Aires: 145-149.

Novas F.E., Cambiaso A.V. & Ambrioso A. (2004) - A new basal iguanodontian (Dinosauria, Ornithischia) from the Upper Cretaceous of Patagonia. *Ameghiniana*, 41(1): 75-82.

Novas F.E., Dalla Vecchia F.M. & Pais D. (2005) - Theropod pedal unguals from the Late Cretaceous (Cenomanian) of Morocco, Africa. *MACN*, F 7:167-75.

Oldham R.D. (1886) - Preliminary notes on the geology of Northern Jaisalmer. *Records of the Geological Survey of India*, 19(3): 157-160.

Ostrom J.H. (1970) - Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana. *Peabody Museum Bulletin,* 35: 1-234.

Owen R. (1842) - Report on British fossil reptiles, part II. *Report of the British Association for the Advancement of Science*, 11: 60-294.

Owen R. (1869) - Description of a great part of a jaw with the teeth of *Strophodus medius*, from the Oolite of Caen in Normandy. *Geological Magazine*, 6: 193-196.

Pal T.K., Ray S.K., Talukder B. & Naik M.K. (2007) - On the mega-invertebrate fauna (Mollusca and Brachiopoda) of Cenozoic and Mesozoic of Jaisalmer, Rajasthan and their stratigraphic implications. *Records of the Zoological Survey of India, Occasional Paper*, 280: 1-40.

Pandey D.K., Fürsich F.T. & Alberti M. (2014) - Stratigraphy and Palaeoenvironments of the Jurassic Rocks of the Jaisalmer Basin - Field Guide. *Beringeria*, *Special Issue* 9: 1-111.

Pandey D.K., Fürsich F.T. & Baron-Szabo R. (2009) - Jurassic Corals from the Jaisalmer Basin, West Rajasthan, India. *Zitteliana,* A48/49: 13-37.

Parks W.A. (1926) - *Thescelosaurus warreni*, a new species of orthopodous dinosaur from the Edmonton Formation of Alberta. *University of Toronto Studies, Geology Series*, 21: 1-42.

Pieńkowski G., Brański P., Pandey D.K., Schlög J., Alberti M. & Fürsich F.T. (2015) - Dinosaur footprints from the Thaiat Ridge and their palaeoenvironmental background, Jaisalmer Basin, Rajasthan, India. *Volumina Jurassica,* 13(1): 17-26.

Posmoşanu E. (2003) - Iguanodontian dinosaurs from the lower Cretaceous bauxite site from Romania. *Acta Palaeontologica Romaniae*, 4: 431-439.

Prasad G.V.R. & Parmar. V. (2020) - First Ornithischian and theropod dinosaur teeth from the Middle Jurassic Kota Formation of India: paleobiogeographic relationships. In: Prasad G.V.R. & Patnaik R. (Eds.) - Biological consequences of plate tectonics: new perspectives on Post-Gondwana break-up - A tribute to Ashok Sahni. *Vertebrate Paleobiology and Paleoanthropology Series*: 1-30.

Rotatori F.M., Moreno-Azanza M. & Mateus O. (2022) - Reappraisal and new material of the holotype of *Draconyx loureiroi* (Ornithischia: Iguanodontia) provide insights on the tempo and modo of evolution of thumb-spiked dinosaurs. *Zoological Journal of the Linnean Society*, 195(1): 125-156.

Rozadilla S., Agnolín F.L. & Novas F.E. (2019) - Osteology of the Patagonian ornithopod *Talenkauen santacrucensis* (Dinosauria, Ornithischia). *Journal of Systematic Palaeontology*, 17(24): 2043-2089.

Sahni M.R. (1955) - Recent research in Palaeontologic Division, Geological Survey of India. *Current Science,* 24: 187.

Sahni M.R. & Bhatnagar N.C. (1958) - New fossils from the Jurassic rocks of Jaisalmer, Rajasthan. *Records of the Geological Survey of India,* 87(2): 428-437.

Sereno P.C. (2012) - Taxonomy, morphology, masticatory function and phylogeny of heterodontosaurid dinosaurs. *Zookeys,* 226: 1-225.

Sereno P.C., Beck A.L., Dutheil D.B., Gado B., Larsson H.C.E., Lyon G.H., Marcot J.D., Rauhut O.W.M., Sadleir R.W., Sidor C.A., Varricchio D.D., Wilson G.P. & Wilson

J.A. (1998) - A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science,* 282: 1298-1302.

Sereno P.C., Forster C.A., Larsson H.C.E., Dutheil D.B. & Sues H.D. (1994) - Early Cretaceous dinosaurs from the Sahara. *Science*, 266: 267-271.

Sereno P., Myhrvold N., Henderson D., Fish F., Vidal D., Baumgart S., Keillor T., Formoso K. & Conroy L. (2022) - *Spinosaurus* is not an aquatic dinosaur. Published online 2022 Nov 30. doi: 10.7554/eLife.80092 10.1101/2022.05.25.493395.

Serrano-Martínez A., Daniel V., Lara S., Francisco O. & Fabien K. (2016) - Isolated theropod teeth from the Middle Jurassic of Niger and the early dental evolution of Spinosauridae. *Acta Palaeontologica Polonica,* 61: 403-15.

Sharma A., Hendrickx C. & Singh S. (2023) - First Theropod record from the Marine Bathonian of Jaisalmer Basin, Tethyan Coast of Gondwanan India. *Rivista Italiana di Paleontologia e Stratigrafia*, 129(1): 49-64.

Sharma A. & Singh S. (2021) - A small assemblage of marine hybodont sharks from the Bathonian of the Jaisalmer Basin, India. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen,* 301(3): 317-333.

Sharma A., Singh S. & Satheesh S. R. (2022) - The first Turiasaurian sauropod of India reported from the Middle Jurassic (Bathonian) sediments of Jaisalmer Basin, Rajasthan, India. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 304(2): 187-203.

Singh C.S.P., Jaitly A.K. & Pandey D.K. (1982) - First report of some Bajocian-Bathonian (Middle Jurassic) ammonoids and the age of the oldest sediments from Kachchh, Western India. *Newsletters on Stratigraphy,* 11: 37-40.

Singh C.S.P., Pandey D.K. & Jaitly A.K. (1983) - Discovery of *Clydoniceras* Blake and *Gracilisphinctes* Buckman (Bathonian-Middle Jurassic Ammonites) in Kachchh, Western India. *Journal of Palaeontology,* 57: 821-824.

Stromer (1915) - Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Bahariye-Stufe (unterstes Cenoman). 3. Das Original des Theropodes *Spinosaurus aegyptiacus* nov. Gen., nov. Spec. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-Physikalische Klasse*, *München* 28: 1-28.

Stromer E. (1934) - Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman) 13. Dinosauria *Abhandlungen der Bayerischen Akademie der Wissenschaften Mathematisch-naturwissenschaftliche Abteilung Neue Folge*, Heft 22.

Virchow H. (1919) - Atlas und Epistropheus bei den Schildkröten. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin,* 8: 303-332.

Weishampel D.B., Jianu C.M., Csiki Z. & Norman D.B. (2003) - Osteology and phylogeny of *Zalmoxes* (n. g.), an unusual euornithopod dinosaur from the Latest Cretaceous of Romania. *Journal of Systematic Palaeontology*, 1(2): 65-123.

Whitton M.P. (2015) - Were early pterosaurs inept terrestrial locomotors? *PeerJ*, 3. e1018. 10.7717/peerj.1018.

Yadagiri P. (1988) - A new sauropod *Kotasaurus yamanpalliensis* from Lower Jurassic Kota Formation of India. *Records of the Geological Survey of India,* 11: 102-127.

Yadagiri P. (2001) - The osteology of *Kotasaurus yamanpalliensis,* a sauropod dinosaur from the Early Jurassic Kota Formation of India. *Journal of Vertebrate Paleontology,* 21 (2): 242 252.

Zaher H., Pol D., Navarro B.A., Delcourt R. & Carvalho A.B. (2020) - An Early Cretaceous theropod dinosaur from Brazil sheds light on the cranial evolution of the Abelisauridae. *Comptes Rendus Palevol*, 19(6): 101-115.