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FIRST THEROPOD RECORD FROM THE MARINE BATHONIAN OF JAISALMER BASIN, TETHYAN COAST OF GONDWANAN INDIA

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Abstract. Middle Jurassic theropods have a scanty record worldwide, especially from Gondwana. In India, where Jurassic theropods are particularly rare and only represented by a few isolated teeth and some badly preserved bones, there is currently no record of theropods from the Middle Jurassic of western India. Here we report the first theropod dental material from Middle Jurassic marine carbonate rocks of the Jaisalmer Basin, north-western India. The specimen consists of an incomplete shed tooth crown recovered from bioclastic intraformational conglomerate bed of the Bathonian Fort Member of the Jaisalmer Formation. A cladistic analysis performed on a dentition-based data matrix revealed that the isolated crown likely pertained to a non-coelurosaur averostran possibly from the mesial dentition of a ceratosaurid, a non-spinosaurid megalosauroid, or an allosauroid. This shed tooth provides evidence that at least one taxon of medium to large-bodied theropod lived on the Tethyan coast of NW India during the Middle Jurassic. This contribution marks the Jaisalmer Basin as a new promising area in India for dinosaurian remains from the Jurassic Gondwana.

Introduction

India has a particularly rich record of the Cretaceous theropods (*Lametasaurus indicus* Matley, 1924; *Jubbulpuria tenuis* Huene & Matley, 1933; *Indosaurus matleyi* Huene & Matley, 1933; *Indosuchus raptorius* Huene & Matley, 1933; *Rahiolisaurus gujaratensis* Novas et al. 2010; *Rajasaurus narmadensis* Wilson et al., 2003; *Laevisuchus indicus* Huene & Matley, 1933; Troodontidae indet. Goswami et al., 2013). Conversely, Jurassic theropods are particularly poorly known and only include a handful of isolated specimens. The first report of theropod remains from the Jurassic of India only dates back to the end of the 20th century when Yadagiri (1982) described fragmentary material from the Early Jurassic Kota Formation, including an isolated tooth referred to the new taxon *Dandakosaurus indicus* Yadagiri, 1982, in an unpublished progress report of the Geological Survey of India. More than 30 years later, Pieńkowski et al. (2015) described theropod footprints from the Jaisalmer basin, referred to *Eubrontes* cf. *giganteus* Hitchcock, 1836 and *Grallator tenuis* Hitchcock, 1858, from the Lower Jurassic Thaiat Member of the Lathi Formation. Recently, Prasad & Parmar (2020) reported several small (<1 cm in height) isolated theropod teeth ascribed to

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an indeterminate taxon, a dromaeosaurid and *Richardoestesia*-like theropod from the Jurassic Kota Formation, whose age remains debated. If an Early Jurassic age has usually been favoured for the Kota Formation based on the presence of different vertebrate groups such as fish fauna (Jain 1973, 1980, 1983; Yadagiri & Prasad 1977), palynofossils (Prabhakar 1989), charophytes (Bhattacharya et al. 1994), and sphenodontian taxa (Evans et al. 2001), a Middle Jurassic age has also been proposed based on some other fossils such as freshwater ostracods (Govindan 1975), palynofossils (Vijaya & Prasad 2001) as well as ornithischian and dromaeosaurid teeth (Prasad & Parmar 2020). No marine intercalations or volcanic ash beds are present in the Kota Formation (Prasad & Parmar 2020) and with the absence of a definite bio-stratigraphic marker or a radio-metric datable horizon, the ages of the Kota Formation cannot be known with confidence.

In peninsular India, Jurassic sediments are exposed in the peri-cratonic Jaisalmer and Kutch basins of north-western and western India respectively, in addition to the intra-cratonic Pranhita-Godavari basin of south-central India (Prasad & Parmar 2020). During the Jurassic, an important transgression occurred in peninsular India, whereby shallow epicontinental seas covered the Jaisalmer and Kutch basins and deposited marine siliciclastic carbonate rocks (Pal et al. 2007; Pandey et al. 2014; Sharma & Singh 2021; Sharma et al. 2022). Jaisalmer and Kutch basins are famous for their Jurassic marine faunal assemblages that show Tethyan character with some amount of regional endemism (Pal et al. 2007). Globally, the Middle Jurassic is known for its scanty records of terrestrial vertebrates, dinosaurs in particular due to the invasion of land by shallow seas resulting from the rise in sea level (Mathur et al. 1985; Smith et al. 1994; Young et al. 2019; Khosla & Bajpayee 2021). In India, the first evidence of the Middle Jurassic dinosaurs came to light in 1985, when a few fragmentary bones, recorded from the Middle Jurassic rocks of the Jaisalmer Basin, were identified as dinosaurian on the basis of bone histology (Mathur et al. 1985). A recent discovery of a turiasaurian tooth in the Jaisalmer Formation confirmed the presence of large sauropods in the Jaisalmer basin during the Bathonian (Sharma et al. 2022).

The Middle Jurassic was a critical time in the evolution of theropod dinosaurs with megalosauroids becoming apex predators, allosauroids radiating into several clades, the first tyrannosauroids appearing in Laurasia, and maniraptorans evolving into birds (Young et al. 2019). This study aims to describe the first diagnostic record of an apex theropod during the Bathonian (Middle Jurassic) in India based on an isolated tooth recovered from marine carbonate deposits of the Fort Member of Jaisalmer Formation. We performed a cladistic analysis to broadly classify the tooth to the known theropod clades. Due to its fragmentary nature the crown can only be classified at a higher taxonomic level. Scarce record of theropods from the Jurassic of Gondwanan continents and the inadequate representation of terrestrial fauna from the Middle Jurassic, make every Middle Jurassic terrestrial vertebrate record worth reporting especially from Gondwana.

Geological Setting

The Jaisalmer Basin is a north-westerly sloping, peri-cratonic sedimentary basin that was formed as a result of rifting of the Indian plate from Gondwanaland (Pal et al. 2007; Pandey et al. 2012, 2014). The basin is part of the Rajasthan shelf situated at the north-western margin of the Indian craton (Pandey et al. 2014). Due to repeated marine transgressions-regressions during the Mesozoic and the Cenozoic, a thick sedimentary sequence of siliciclastic carbonates was deposited in the Jaisalmer basin, resting unconformably over the Precambrian basement of igneous and metamorphic rocks (Pandey et al. 2012). The low dipping, highly fossiliferous Mesozoic sediments are exposed as an arcuate outcrop. The Jurassic rocks in the basin are represented by the Lathi, Jaisalmer, Baisakhi and Bhadasar formations in chronological order (Das Gupta 1975) (Fig. 1).

The Jaisalmer Formation which represents the marine carbonate facies from the Jurassic, is the most fossiliferous unit of the basin. Covering the Lathi Formation (Das Gupta 1975; Garg & Singh 1983; Jain 2007), the maximum thickness of the Jaisalmer Formation is 1138 m in Ghotaru area (Khan & Khan 2015). Litho and biostratigraphically, the Jaisalmer Formation is classified into six members namely, the Hamira, Joyan, Fort, Badabag, Kuldhar and Jajiya members, in order of su-

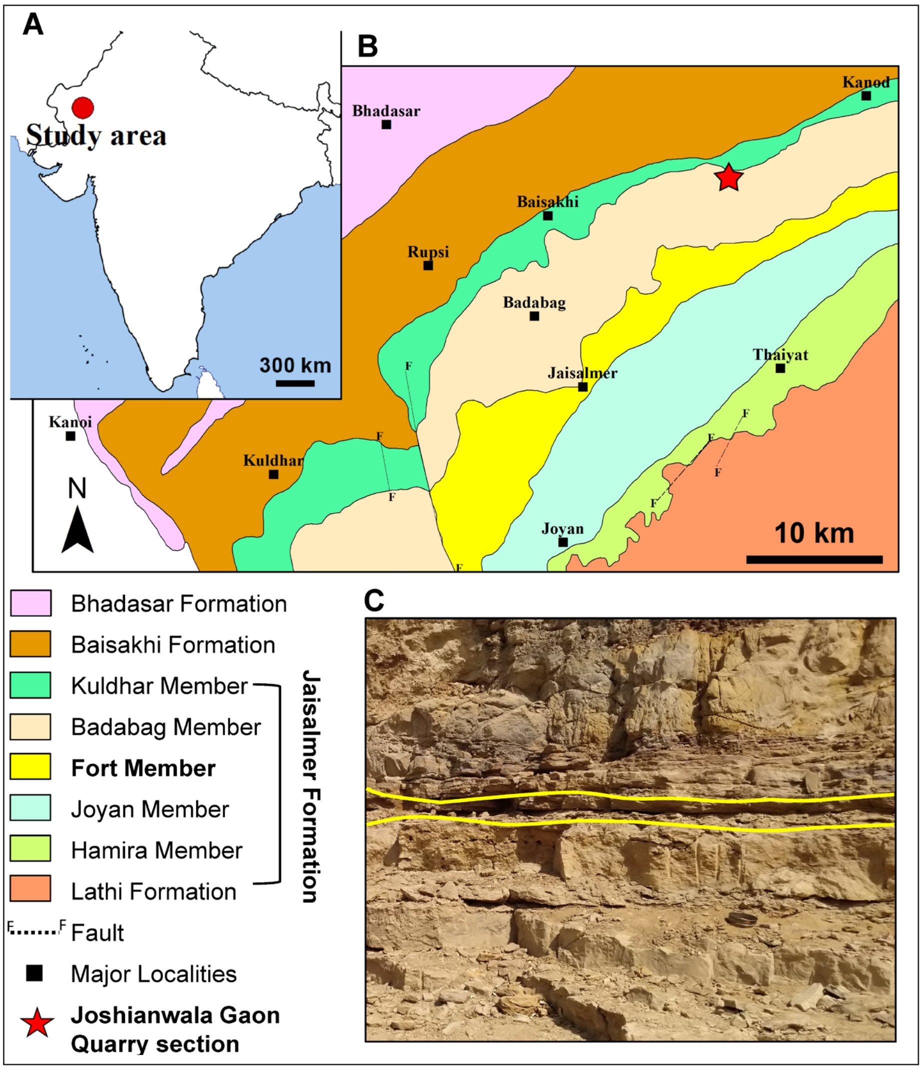


Fig. 1 - A) Map of India showing the location of the Jaisalmer Basin; B) Geological map of Jurassic deposits from the Jaisalmer Basin, Rajasthan, northwestern India (modified after Dave & Chatterjee 1996; Sharma & Singh 2021); C) Section through the Joshianwala Gaon Quarry (JWQ) with the bed that has produced the isolated theropod tooth RAJ/JAIS/JWGQ001 delimited in yellow.

perposition deposited from the pre-Bajocian to the Oxfordian (Kachhara & Jodhawat 1981; Pandey et al. 2012, 2014) (Fig. 1). The theropod crown was collected from the Fort Member of the Jaisalmer Formation, a marine carbonate facies composed of fossiliferous limestone, arenaceous limestone, calcareous sandstone, intraformational conglomerate, calcareous lime-mudstone, oolitic limestone, golden yellow coloured bioturbated fossiliferous limestone, bioclastic packstone, grainstone, and rudstone (Pandey et al. 2014; Ahmad et al. 2017; Sharma & Singh 2021). The Fort Member is highly fossiliferous, with various marine benthic faunal elements such as gastropods, bivalves, echinoids, bryozoans, crinoids, corals, and foraminifera (Pandey et al. 2014; Khan & Khan 2015; Ahmad et al. 2017). Among vertebrates, dental remains of marine hybodonts have been recovered from this unit (Sharma & Singh 2021; Kumar et al. 2022). The Fort Member overlies the Joyan Member and underlies the Badabag Member. On basis of the record of the Bajocian coral *Isastrea bernardiana* from the upper part of the Joyan Member and the late Bathonian ammonites *Macrocephalites madagascariensis, M. triangularis* and *Sivajiceras congener* from the upper part of the Badabag Member, the age of the Fort Member is considered to be early to middle Bathonian (Pandey et al. 2012).

Institutional abbreviations: **GSI**, Geological Survey of India, Jaipur, Rajasthan.

Other abbreviations: **RAJ**, Rajasthan; **JAIS**, Jaisalmer; **JWGQ**, Joshianwala Gaon Quarry; **WR**, Western Region; **SM**, Strategic Minerals; **AL**, Apical Length; **CH**, Crown Height; **CBL**, crown base length; **CBW**, Crown Base Width; **CBR**, Crown Base Ratio; **CHR**, Crown Height Ratio; **mca**: mesial carina; **dca**: distal carina; **mde**: mesial denticles; **dde**: distal denticles; **ids**, interdenticular sulci; **mud**, marginal undulations; **tud**, transverse undulations; **enl**: enamel layer; **del**: dentine layer; **toc**: tooth core; **sps**: spalled surface; **lab**: labial; **lin**: lingual.

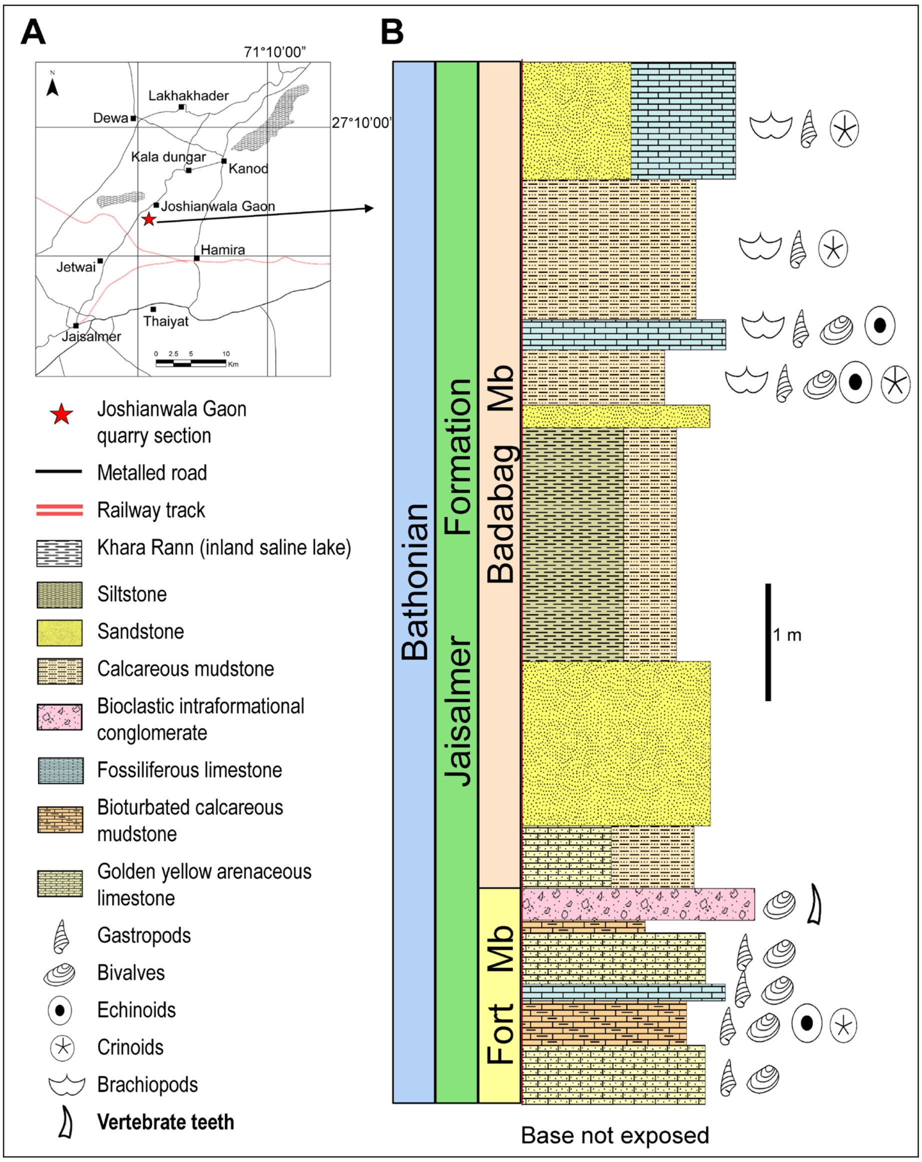


Fig. 2 - A) Location map of the study area; B) Lithologic section of the Joshianwala Gaon Quarry (modified after Sharma & Singh 2021), showing vertebrate fossils bearing intraformational conglomerate horizon (Topmost part of the Fort Member, Jaisalmer Formation). Abbreviations: Mb, Member.

Materials and methods

In 2021, some bulk sampling for exploring the hybodont dental remains had been carried out in an eight meters deep building stone quarry located 20 km NE of the Jaisalmer town on Jethwai-Kanod road, 2 km SW of Joshianwala Gaon, in Rajasthan, northwestern India (Fig 2A) (Sharma & Singh 2021). The samples were collected from a 24 cm thick matrix-supported bioclastic-mudstone-intraformational conglomerate bed (Fig 1C and 2B), which represents the topmost bed of the Fort Member overlying the echinoderm rich bioturbated limestone. Micro-vertebrate fossils were extracted by mechanical means and buffered formic acid. Several fish teeth and scales as well as teeth of marine reptiles have been extracted along with some small bone fragments. The theropod tooth was the only terrestrial faunal element found by one of us (SS) during the preparation of samples other than bone and fossil wood fragments. The tooth was found fragmented, and acetone soluble glue was used to glue the pieces back. It is registered as RAJ/JAIS/JWGQ001 in GSI, WR, Jaipur under the custody of the Director, SM-I Division and is accessible on request. The registration number contains the acronym of the locality of provenance. The specimen was comprehensively described using the modus operandi and dental terminology proposed by Hendrickx et al. (2015a) whereas, the crown was measured using the methodology proposed by Smith et al. (2005). The specimen was photographed with Canon 50D using Canon EF 100 mm f/2.8 macro lens in apical, labial, lingual, mesial, distal and basal views. Close-up shots of the enamel were taken to show details of the carina and crown ornamentation. All photographs were processed using Adobe Photoshop 23.1.0 and IrfanView version 4.60.

Cladistic analysis

To explore the phylogenetic distribution of RAJ/JAIS/JWGQ001, the specimen was scored in a dentition-based datamatrix focused on theropod dinosaurs created by Hendrickx and Mateus (2014). The latest version of the datamatrix was published by Meso et al. (2021) and includes 146 dentition-based characters scored across 107 saurischian taxa (Supplementary_File_1). A cladistic analysis using a fully constrained tree was performed on the datamatrix using TNT (Goloboff et al. 2008) following the methodology detailed by Hendrickx et al. (2020a).

Because it is uncertain whether RAJ/JAIS/JWGQ001 belongs to the mesial or the lateral dentition, we performed two separate cladistic analyses, one with the specimen scored as a mesial crown and the other as a lateral tooth. Likewise, due to the putative presence of mesial denticles on the specimen (see below), character on the mesial carina (#48 and #78 for a mesial and a lateral crown, respectively), was scored as denticulated or unknown in separate analyses. As done by Hendrickx et al. (2020a) and Meso et al. (2021), a combination of the tree-search algorithms Wagner trees, sectorial searches, TBR branch swapping, Ratchet (perturbation phase stopped after 20 substitutions) and Tree Fusing (5 rounds), until 100 hits of the same minimum tree length were reached, were used as the search strategy. The trees were additionally subjected to a final round of TBR branch swapping. The command we used in TNT is then: "xmult = hits 100 rss fuse 5 ratchet 20" followed by the "bb" command. Two additional cladistic analyses, one using the dentition-based dataset without constraints (Supplementary_File_3 & 5), and the second on a data matrix restricted to crown-based characters (Supplementary_File_2 & 4), were also conducted (see Young et al. 2019; Hendrickx et al. 2020a; Meso et al. 2021).

As the shed tooth is particularly incomplete, only two crown-based variables, the mid-crown ratio (MCR) and distocentral denticle density (DC) could be measured following the method provided by Hendrickx et al. (2015a). All the other variables such as CH, CBL, AL, CBR and CHR could only be estimated using a reconstructed version of the crown. Consequently, no morphometric analyses such as discriminant and cluster analyses were performed on RAJ/JAIS/JWGQ001.

Results of Cladistic Analysis

The cladistic analyses performed on the dentition-based datamatrix with or without considering the mesial carina as denticulated yielded relatively similar results in the placement of RAJ/JAIS/JWGQ001. Conversely, important differences in the topology of the strict consensus tree were obtained when this specimen was scored as a mesial or a lateral crown. However, RAJ/JAIS/JWGQ001 is always found among averostrans with ziphodont (blade-shape) teeth, closely related to basally branching averostrans such as ceratosaurs, megalosaurids and allosauroids (Supplementary_File_1).

The cladistic analysis conducted on the whole dentition-based datamatrix using a fully constrained tree recovered RAJ/JAIS/JWGQ001 as the sister taxon of *Eustreptospondylus* among Megalosauridae when scored as a mesial tooth and as the sister taxon of either Metriacanthosauridae among Allosauroidea or *Abelisaurus* among Abelisauridae when scored as a lateral crown (2 MPTs; L=1362; CI= 0.1909; RI= 0.4296). Similar results were obtained when scoring the character on a mesial carina as unknown or denticulated (Fig. 3).

In the cladistic analysis performed on the whole data matrix without constraining the tree, RAJ/JAIS/JWGQ001 was recovered in a polytomy comprised of *Eustreptospondylus*, *Dubreuillosaurus*, *Arcovenator*, *Dilophosaurus*, *Dracovenator* as well as various dental-based clades of ziphodont and pachydont theropods (e.g., ceratosaurs, piatnitzkysaurids, allosauroids, tyrannosauroids, and dromaeosaurids) when scored as a mesial crown and with the character on the mesial denticulated carina coded as unknown (>100 MPTs; L= 1107; CI= 0.2349; RI=0.5615). A similarly large polytomy with almost all ziphodont and conidont theropods from our dataset was obtained when the character on the mesial carina was scored as denticulated (>100 MPTs; L=1347; CI=0.193; RI=0.437). However, RAJ/JAIS/JWGQ001 was recovered as the sister taxon of *Eustreptospondylus* among this large polytomy. When RAJ/JAIS/JWGQ001 is considered from the lateral dentition, the cladistic analysis yielded a relatively well-resolved tree when the character on the mesial denticulated carina is coded as unknown (>100 MPTs; L=1083; CI=0.24; RI=0.574). In this analysis, the specimen is recovered as the sister taxon of a clade encompassing ceratosaurids,

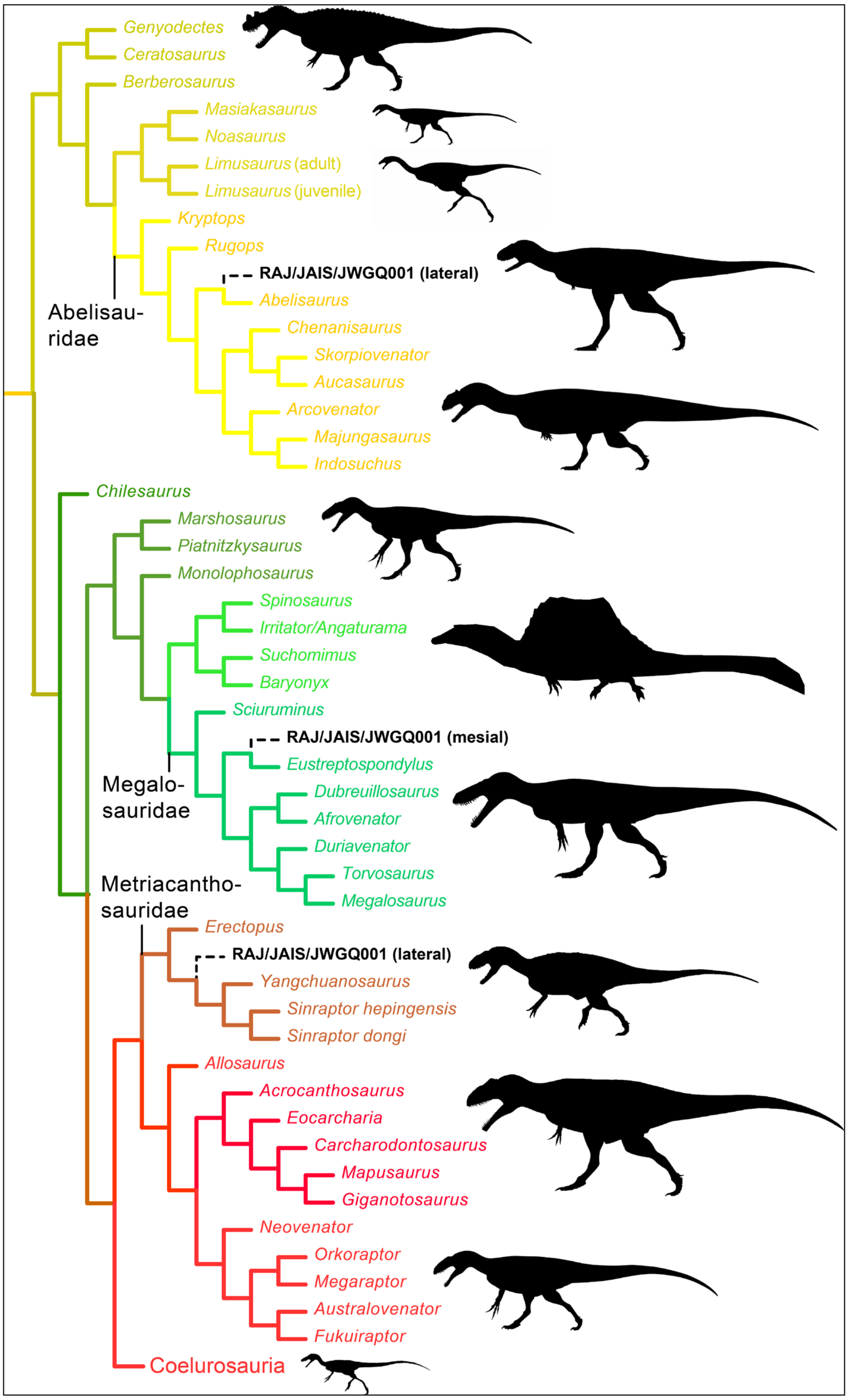


Fig. 3 - Result of the cladistic analysis performed on a dentition-based data matrix using a fully constrained topological tree of the theropod classification. The isolated theropod tooth RAJ/JAIS/JWGQ001 is recovered as a megalosaurid theropod when scored as a mesial tooth and either as an abelisaurid or a metriacanthosaurid theropod when scored as a lateral tooth. Silhouette attribution: *Limusaurus*: Ville Veikko Sinkkonen (Creative Commons Attribution-Non-Commercial-ShareAlike 3.0 Unported license; https://creativecommons.org/licenses/by-nc-sa/3.0/); *Spinosaurus* (Spinosauridae): Tasman Dixon (Public Domain Dedication 1.0); *Yangchuanosaurus* (Metriacanthosauridae): Gregory Paul (used with permission); all other silhouettes: Scott Hartman (Creative Commons Attribution-Non-Commercial-ShareAlike 3.0 Unported license; https://creativecommons.org/licenses/by-nc-sa/3.0/).

tyrannosaurids and most allosaurians. Considering the character on a mesial carina as denticulated, however, recovered RAJ/JAIS/JWGQ001 in a large polytomy with almost all ceratosaurids, non-spinosaurid megalosauroids, allosauroids, tyrannosauroids and a few dromaeosaurids (>100 MPTs; L=1200; CI=0.2167; RI=0.5135) (Supplementary_File_3 & 5).

The cladistic analysis conducted on the dentition-based datamatrix reduced to crown-based characters also yielded slightly different results when the specimen was scored as a lateral or a mesial crown. As a mesial tooth, RAJ/JAIS/JWGQ001 is found as the sister taxon of *Eustreptospondylus* in a clade of non-megalosaurine megalosaurids when the mesial denticulated carina is coded as unknown, and in a much larger clade gathering megalosaurids, ceratosaurids, abelisaurids, spinosaurids and carcharodontosaurids when the mesial denticulated carina is coded as present (>100 MPTs; L=666; CI= 0.2387; RI= 0.608). As a lateral tooth, the specimen is found in a polytomy with *Piatnitzkysaurus*, *Dromaeosaurus*, tyrannosauroids, metriacanthosaurids, neovenatorids, and megaraptorans when the mesial denticulated carina is coded as unknown and in a well-revolved clade gathering *Dromaeosaurus*, *Piatnitzkysaurus* and megaraptorans when this character is coded as present (Supplementary_File_2 & 4). The tooth is incomplete so the results of cladistic analysis should be dealt with caution.

Systematic Palaeontology

DINOSAURIA Owen, 1842
Saurischia Seeley, 1887
Theropoda Marsh, 1881
Averostra Paul, 2002

Gen. and sp. indet.

Referred Material: RAJ/JAIS/JWGQ001 is an isolated theropod tooth preserving the ziphodont crown but missing the root.

Locality: Building stone quarry located 20 km NE of Jaisalmer City on Jethwai-Kanod road, 4 km SW of Joshianwala Gaon village (Fig. 2A)

Stratigraphic Horizon and age: Fort Member, Jaisalmer Formation, Bathonian, Middle Jurassic.

Description

Condition. RAJ/JAIS/JWGQ001 is an isolated shed tooth only preserving the crown. The specimen is relatively incomplete, missing the enamel and dentin layers on most of the lingual, mesial, apical and basal most parts of the tooth. A part of the apex and basodistal portions of the crown are also missing. The enamel is only preserved on most of the labial and mesiolingual sides of the crown while the distal margin is strongly worn out (Fig. 4). Due to this, the cervical line, mesial carina, and most of the distal denticles are unpreserved. The crown also shows several mesiodistally oriented fractures on the labial surface. Nevertheless, the tooth is undeformed (i.e., there is no sign of torsion, twisting or bending) and its preservation is good enough to show several crown ornamentations on the enamel layer (see below).

Morphology. Although it is unknown whether a mesiodistal constriction was present between crown and root due to the incompleteness of RAJ/JAIS/JWGQ001, the crown shows the typical ziphodont morphology, i.e., it is labiolingually compressed, distally recurved, and finally denticulated at least on its distal carina (Fig. 4). Based on the preserved tooth core, the crown base ratio (CBR) and mid-crown base ratio (MCR) can be estimated to be around 0.72 and 0.7, respectively, indicating that the crown was weakly labiolingually compressed. In the same way, the crown height is estimated to be around 30 mm and almost certainly did not exceed 40 mm. Using a rough estimation for the crown width and height based on a reconstructed tooth, the crown most likely had a moderate elongation, with a crown height ratio (CHR) between 2.1 and 2.5. In labial/lingual views, the crown is curved distally and shows a strongly convex mesial margin and a slightly concave and almost straight distal margin (Fig. 4A and 4D). Even though the whole distal margin is worn out, a denticulated distal carina is nonetheless visible on the apical third of the crown (Fig. 4C) The ziphodont morphology of the tooth also suggests that the distal carina was probably denticulated all along the distal margin, from the base to the apex of the crown. In distal view, the distal carina is straight and strongly labially deflected (Fig. 4C). The mesial carina is unpreserved, but a faint ridge is present on the mesial surface of the tooth core and extends on almost the whole crown height (Fig. 4B). This ridge almost certainly represents the track of the mesial carina and based on its position and orientation, the mesial carina probably extended on most of the crown height, was straight and centrally positioned on the mesial surface, and did not twist basally towards the lingual side of the tooth (Fig. 4B and 4D). It is, however, unknown whether the mesial carina (denticulated or not) reached the root basally. The lingual surface of the crown is strongly convex whereas the labial surface is weakly convex and practically flat adjacent to the distal carina, giving a strongly asymmetrical profile of the crown in apical/basal views (Fig. 4E and 4F). A flat surface is also present adjacent to the distal carina on the lingual side of the crown but is mesiodistally shorter than that on the labial surface (Fig. 4E). In basal view, the outline of the preserved tooth core suggests that the cross-sectional outline of the ba-

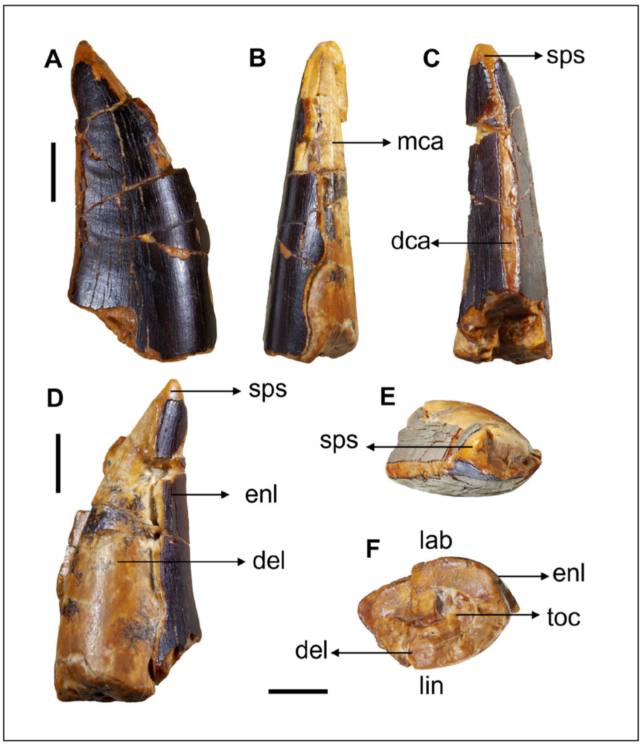


Fig. 4 - Isolated theropod crown (RAJ/JAIS/JWGQ001) from the Bathonian Jaisalmer Formation of northwestern India in A) labial; B) mesial; C) distal; D) lingual; E) apical; and F) basal views. Abbreviations: dca, distal carina; del, dentine layer; enl, enamel layer; lab, labial side; lin, lingual side; mca, mesial carina; sps, spalled surface; toc, tooth core. Scale bar equals 5 mm.

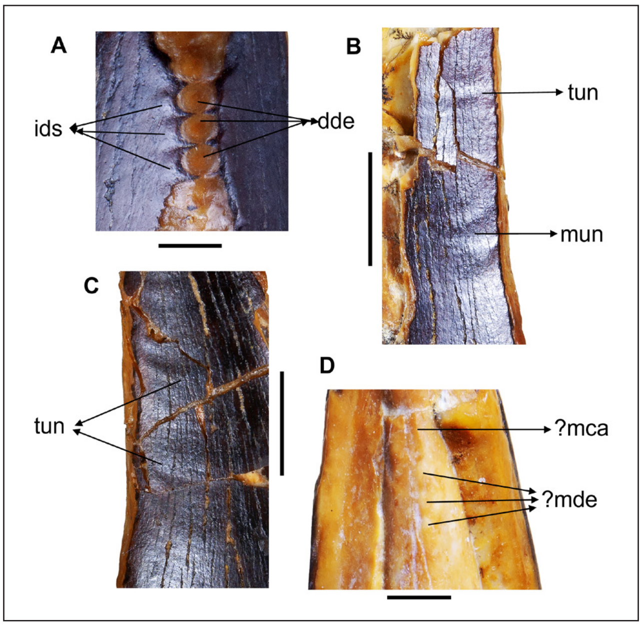


Fig. 5 - Close-up views on the denticles and crown-based ornamentations of the isolated theropod tooth (RAJ/JAIS/JWGQ001). A) distal denticles and interdenticular sulci in distal view; B) transverse and marginal undulations in lingual view; C) marginal undulations in labial view; D) mesial carina and putative mesial denticles in mesial view. Abbreviations: dde, distal denticles; ids, interdenticular sulci; mca, mesial carina; mde, mesial denticles; mun, marginal undulations; tun, transverse undulations. Scale bar equals 1 mm (A, D) and 5 mm (B–C).

se-crown was probably lenticular or lanceolate (Fig. 4F). With 0.75 mm in thickness mesially and less than 0.1 mm labially, the preserved enamel layer is significantly thinner labially than mesially in the basal most part of the crown.

Denticles. Little information can be extracted on the denticles of RAJ/JAIS/JWGQ001. The tooth core is the only portion of the crown to be preserved mesially so that no mesial denticles can be seen. However, three faint convexities are visible on the surface of the tooth core, two millimetres basal from the crown apex (Fig. 5D). These convexities are apicobasally aligned on what would be assumed to be the track of the mesial carina and the length and width of each of them are in the range of those observed for the distal denticles. It is, therefore, possible that these faint convexities represent the track of the dentine core of the mesioapical denticles. If true, this would indicate that a mesial denticulated carina was present on the crown and that there were around 11 to 12 denticles per 5 mm on the apical most part of the mesial carina.

Conversely, both the dentine core and cross-sections through the basal part of the distal denticles are clearly visible along the apical third of the crown, at around two-thirds and four-fifths of the crown height (Fig. 5A). Four denticles per two millimetres can be counted in this part of the distal carina, giving a denticle density of ten denticles per five millimetres. The cross-sectional outlines of the distal denticles reveals that their base was subcircular, that the denticles were not sporadically changing in size along the carina, and that the interdenticular space from the base of the distal denticles was narrow. Poorly developed interdenticular sulci are seen on the lingual side of the crown between the distal-most preserved denticles (Fig. 5A). They extend diagonally towards the base of the crown for less than a millimetre. Undulations resulting from the cross-sections through the enamel and dentine layers indicate that interdenticular sulci were also present lingually between the distal denticles at two-thirds of the crown.

Crown ornamentations

The enamel is blackish brown in colour and strongly polished so that the type of enamel surface texture cannot be known. Two marginal undulations adjacent to the distal carina are present on the lingual surface of the crown, at approximately one-third of the crown height (Fig. 5B). The marginal undulations are clearly visible in both distal and lingual views with the right orientation of light. They are apicobasally convex, and form elongated, mesiodistally oriented concavities in the lingual view, with the apex of the concavity pointing basally. The distance separating the two marginal undulations is equivalent to their apicobasal height. Faint transverse undulations are also present on both lingual and labial surfaces of the crown. They are particularly well-visible on both lingual and labial sides at two-thirds of the crown (Fig. 5B and 5C). Similar to the marginal undulations, they form mesiodistally elongated concavities extending along the distal half of the crown. Their distal extremities curve apically towards the distal carina. We counted two transverse undulations on the lingual surface at two-third of the crown-height, four undulations on the apical third part of the crown on the labial surface, and several extremely faint undulations along the preserved one-third of the crown. Although particularly faint, the transverse undulations seem to be more densely packed basally whereas they are more widely distributed on the apical third of the crown. The absence of an enamel layer on the apex of the crown is here interpreted as worn surfaces resulting from tooth-to-food contact on both labial and lingual sides of the tooth (Fig 4C, 4D and 4E). We, however, cannot exclude the possibility that the lack of enamel on the tip of the crown is due to taphonomic processes. No flutes, longitudinal ridges or grooves, basal striations, concave surfaces adjacent to the carinae or labial and lingual depressions are visible on the preserved enamel surface of the crown.

Discussion

Phylogenetic affinity

Despite being particularly incomplete, the shed tooth crown RAJ/JAIS/JWGQ001 shows a combination of diagnostic dental features that can help its identification namely, a low denticle density along the distal carina, a strongly labially deflected distal carina, a poorly convex, almost flat labial surface, interdenticular sulci between distal denticles, as well as marginal and transverse undulations on the crown.

Based on the ziphodont morphology and the presence of marginal and transverse undulations, interdenticular sulci and a strongly labially displaced distal carina, this tooth can confidently be referred to as a theropod dinosaur. To our knowledge, none of the other non-dinosaur clades with ziphodont teeth shows this combination of dental features. Likewise, the teeth of ornithischians, sauropodomorphs, marine reptiles, pterosaurs and crocodylomorphs do not share such morphology. Additionally, this ziphodont crown of around 30 mm in height (CH) cannot be referred to Noasauridae, Compsognathidae, Ornithomimosauria, Therizinosauria, Alvarezsauroidea, Oviraptorosauria, Troodontidae, or Avialae, as members of these clades either bear conidont or folidont, or small ziphodont crowns of less than 20 mm (Young et al. 2019; C.H. pers. obs.). Moreover, RAJ/JAIS/JWGQ001 bears ten distal denticles per 5 mm along the central part of the carina and, to our knowledge, ziphodont crowns with fewer than 12 denticles per 5 mm along the distal cainae are restricted to Dilophosauridae, Ceratosauria, Megalosauroidea, Allosauroidea, Tyrannosauroidea and some large-sized Dromaeosauridae (C.H. pers. obs.)

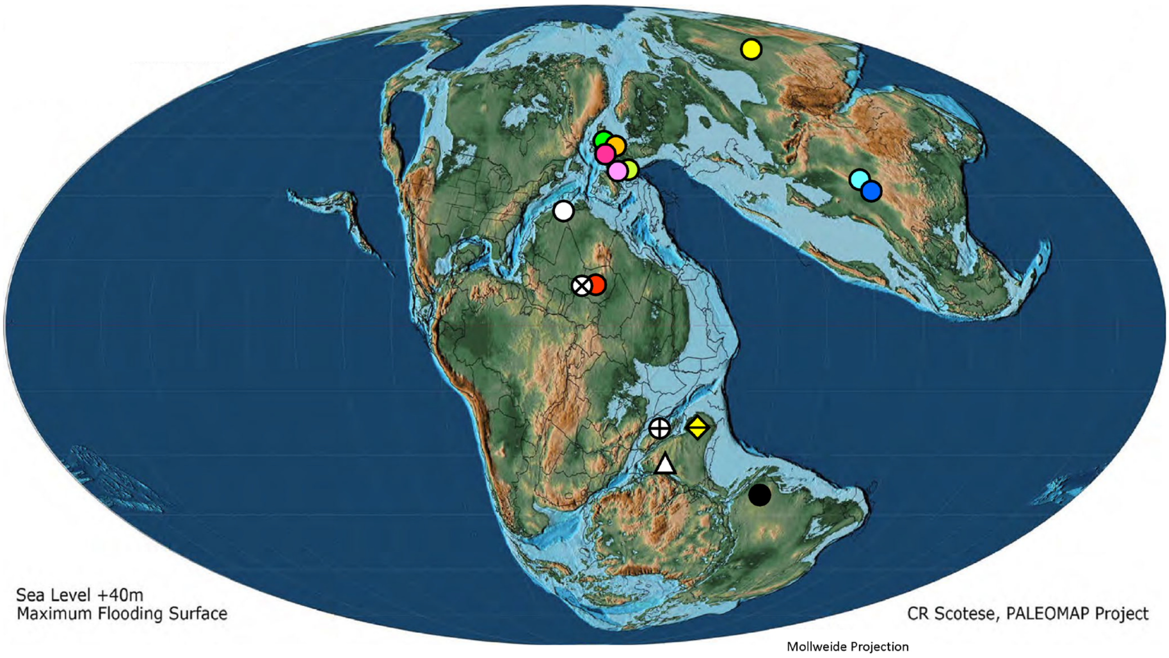
A CBR close to 0.7 associated with a strongly labially displaced distal carina suggest that the crown probably belongs to the mesial dentition i.e., the premaxilla or the anterior most portion of the dentary, (Hendrickx & Mateus 2014). Although these two dental features are also present in the lateral teeth of tyrannosaurids, this clade is restricted to the Late Cretaceous and no theropods from the Jurassic appear to show thick lateral teeth with a strongly displaced distal carina (C.H. pers. obs.). Among ziphodont theropods, a strongly labially deflected distal carina is seen in the mesial teeth of distantly related theropods such as *Dilophosaurus*, *Masiakasaurus*, ceratosaurids, *Monolophosaurus*, allosauroids (e.g., metriacanthosaurids, allosaurids, carcharodontosaurids), tyrannosauroids and a few dromaeosaurids such as *Sinornithosaurus*, *Linheraptor* and *Saurornitholestes* (Hendrickx et al. 2015b, 2019, 2020b). However, this feature is not observed in the dentition of coelophysoids, abelisaurids, megalosaurians (i.e., megalosaurids + spinosaurids) and non-dromaeosaurids neocoelurosaurs (Hendrickx et al. 2019). Among theropods with a strongly labially displaced distal carina, a mesial tooth with a straight and centrally positioned mesial carina is only present in dilophosaurids, ceratosaurids, piatnitzkysaurids and carcharodontosaurids (Hendrickx et al. 2019). It is, therefore, unlikely that this specimen belongs to a non-ceratosaurid ceratosaur, a megalosaurian, a non-carcharodontosaurid allosauroid, or a tyrannosauroid. Enamel undulations (i.e., marginal and transverse undulations) and interdenticular sulci are commonly found on the crowns of ziphodont theropods (e.g., ceratosaurs, megalosauroids, allosauroids, tyrannosauroids, dromaeosaurids; (Currie et al. 1990; Smith 2005, 2007; Hendrickx et al. 2015b, 2020a, b) but appear to be genuinely absent in the dentition of non-averostran theropods such as coelophysoids and dilophosaurids (Hendrickx et al. 2019). Current evidence points to both clades going extinct by the Early Jurassic (Hendrickx et al. 2015c) as all non-averostran theropods were replaced by more derived theropod clades by the Middle Jurassic (Rauhut et al. 2016).

RAJ/JAIS/JWGQ001 is recovered as a megalosaurid theropod when scored as mesial tooth and either as an abelisaurid or a metriacanthosaurid theropod when scored as a lateral tooth on basis of cladistic analysis performed on a dentition-based data matrix using a fully constrained topological tree (Fig. 3). Consequently, based on the result of the cladistic analysis, the stratigraphic distribution of the specimen and our current knowledge of the theropod dentition, we consider this shed crown to be from the mesial dentition of an indeterminate non-coelurosaur averostran, probably a ceratosaurid, non-megalosaurine megalosaurid, a piatnitzkysaurid, or an allosauroid. The assignment of RAJ/JAIS/JWGQ001 to a more inclusive clade of non-coelurosaur averostran is not warranted due to incompleteness of the tooth and because of considerable homoplasy in theropod dentition. It should be noted that non-coelurosaur averostrans are already known in the Early Jurassic in the Southern Hemisphere with the abelisauroid *Eoabelisaurus* (Pol & Rauhut, 2012), the piatnitzkysaurids *Piatnitzkysaurus* (Bonaparte, 1986) and *Condorraptor* (Rauhut, 2005) as well as the possible allosauroid *Asfaltovenator* (Rauhut & Pol, 2019), all from the Cañadón Asfalto Formation of southern Argentina recently dated to the late Toarcian (Fantasia et al. 2021). Other instances of Gondwanan averostrans includes *Ozraptor* from the Bajocian of Australia (Long & Molnar 1998), considered to be an abelisauroid by Rauhut et al. (2005) but referred to an indeterminate theropod by Long and Molnar (1998) and reclassified as such by Rauhut et al. (2012).

Comparison with other Gondwanan Middle Jurassic theropods

Famous Middle Jurassic vertebrate sites of Gondwana include the Isalo III Formation from the Mahajanga Basin of Madagascar, the Guelb el Ahmar site of Morocco, the Tiourarén Formation of Niger and the Kota Formation of India. All of these sites have produced fragmentary theropod material (Fig. 6) from continental, flood plain, fluvial, lacustrine, or deltaic deposits with some brackish water influence in Madagascar (Maganuco et al. 2005, 2007; Serrano-Martínez et al. 2015; Haddoumi et al. 2016; Prasad & Parmar 2020), which differs from the Jaisalmer specimen RAJ/JAIS/JWGQ001 recovered from marine carbonate rocks. Among Middle Jurassic averostrans from Gondwana, the only taxon known from dental material appears to be the megalosaurid *Afrovenator* from the probable Middle Jurassic Tiourarén Formation of Niger (Sereno et al. 1994; Rauhut & López-Arbarello 2009). *Afrovenator* only preserves a few lateral teeth which differ from RAJ/JAIS/JWGQ001 in their much stronger labiolingual compression (CBR<0.45) and the centrally positioned distal carina (Hendrickx et al. 2015b). Isolated teeth assigned to Ceratosauridae, Megalosauridae and Spinosauridae have also been reported from the same formation (Serrano-Martínez et al. 2015, 2016). The specimen RAJ/JAIS/JWGQ001 shares several dental features with some of them such as a weak labiolingual compression (CBR>0.6), a low distal denticle density (DC<13 denticles/5 mm), a labially deflected distal carina and the presence of transverse and marginal undulations, suggesting possible affinities between the Indian and North African theropod taxa. Conversely, fragmentary teeth from the Bathonian of Isalo Group of Madagascar referred to Abelisauridae, Coelurosauria and an indeterminate large-bodied theropod by Maganuco et al. (2005, 2007), clearly differ from RAJ/JAIS/JWGQ001 in the position of the distal carina, always centrally positioned in these teeth, and the salinon/parlinon cross-sectional outline at the base of the least compressed (and most likely mesial) crowns. The

Middle Jurassic Bajocian-Bathonian palaeogeography and theropod occurrences



Megalosaurus	Megalosaurid	Bathonian	Laurasia	England
Poikilopleuron	Megalosaurid	Bathonian	Laurasia	France
Dubreuillosaurus	Megalosaurid	Bathonian	Laurasia	France
Afrovenator	Megalosaurid	?Bathonian–Oxfordian	Gondwana	Niger
Proceratosaurus	Tyrannosauroid	Bathonian	Laurasia	England
Kileskus	Tyrannosauroid	Bathonian	Laurasia	Russia
Cruxicheiros	Theropoda indet.	Bathonian	Laurasia	England
Yangchuanosaurus	Metriacanthosaurid	Bathonian–Callovian	Laurasia	China
Sinraptor	Metriacanthosaurid	Bathonian–Callovian	Laurasia	China
Ozraptor	Ceratosaurid	Bajocian	Gondwana	Australia
Fragmentary theropod remains		Bathonian	Gondwana	Morocco
Fragmentary theropod remains		?Bathonian–Oxfordian	Gondwana	Niger
Fragmentary theropod remains		Bathonian	Gondwana	Madagascar
Fragmentary theropod remains		?Early to Middle Jurassic	Gondwana	India
RAJ/JAIS/JWGQ001	**Averostran**	**Bathonian**	**Gondwana**	**India**

Fig. 6 - Palaeogeographical map of the Bajocian-Bathonian showing the global distribution of Middle Jurassic theropods. Paleomap modified after Scotese (2014).

Jaisalmer theropod tooth is clearly bigger and with a much lower distal denticle density than the fragmentary theropod crowns from the Bathonian of Morocco (Haddoumi et al. 2016). Finally, the dentition of the only Middle Jurassic theropod taxon from Oceania, *Ozraptor* is not preserved, precluding any comparison with RAJ/JAIS/JWGQ001 (Rauhut et al. 2005, 2012).

Isolated teeth and some fragmentary bones from the continental Kota Formation are the only other theropod body fossils reported from the Jurassic of India (Yadagiri 1982; Prasad & Parmar 2020). Yadagiri (1982) described the single isolated crown referred to "*Dandakosaurus*" as flat, curved and with fine denticles on the interior face (= the distal carina). This crown differs from RAJ/JAIS/JWGQ001 in its much stronger labiolingual compression and subsymmetrical labial and distal profiles with centrally positioned mesial and distal carinae (Yadagiri 1982: Fig 1). Likewise, the isolated teeth reported by Prasad & Parmar (2020) all seem to belong to small-bodied theropods, and their diminutive size (CH<10 mm) is not at all comparable to the large theropod crown from the Jaisalmer Basin. The specimen RAJ/JAIS/JWGQ001 was found in marine carbonate rocks of Bathonian stage and is different from most other Gondwanan Jurassic theropod teeth with the exception of non-spinosaurid teeth described from the Tiourarén Formation of Niger

Taphonomy

Dinosaurs were terrestrial animals, though their remains have been found in marine sediments too (Buffetaut 1994; Delsate & Ezcurra 2014; Rauhut et al. 2016; Young et al. 2019). The specimen RAJ/JAIS/JWGQ001 was recovered from marine carbonate rocks of the Fort Member of the Jaisalmer Formation. The coarse-grained nature of the sediments that have yielded the theropod crown, associated with molluscs, brachiopods, echinoderms and corals, bone fragments, reptile teeth and wood fossils, supports their deposition in shallow nearshore environment under high energy conditions (Sharma & Singh 2021). The bed producing this theropod tooth is a bioclastic-intraformational-mudstone conglomerate, described by Sharma & Singh (2021) as a micro-vertebrate site, where hard skeletal remains (teeth, bone fragments, scales, scutes, etc.) got concentrated by wave action as a lag deposit, possibly in stormy conditions. Marine hybodont assemblage on basis of dental remains has been described from the same bed by Sharma & Singh (2021) and marine reptile remains will be described in a separate study. The specimen RAJ/JAIS/JWGQ001 is the only diagnostic terrestrial faunal element found from the bed. This theropod crown is broken, abraded and polished but no diagenetic alteration in colour appears to be visible. Although allochthonous, the crown indeed retains the shiny enamel suggesting it to be parautochthonous which is also supported by the presence of sub-angular to angular quartz grains in the strata (A.S. pers. obs). The theropod tooth described in this study might have been washed into the marine deposits from more upstream sources. The inland river system may have transported the floating carcasses to the coastal areas, or a transgressional phase sea-level rise caused the flooding of the inland areas and swept away the terrestrial animals or carcasses (Delsate & Ezcurra 2014; Sharma et al. 2022). The Middle Jurassic age and derived characters displayed by this tooth indicate that it could not have been reworked from significantly older strata.

Palaeobiogeography

The Jaisalmer theropod is approximately contemporaneous with the megalosaurids *Megalosaurus*, *Poekilopleuron* and *Dubreuillosaurus* (Bathonian) from Europe, the indeterminate averostran *Cruxicheiros* (Bathonian) also from Europe, the megalosaurid *Afrovenator* (?Bathonian-Oxfordian) from Northern Africa, the basally branching tyrannosauroid *Proceratosaurus* and *Kileskus* (Bathonian) from Europe and central Russia, respectively as well as the metriacanthosaurid *Yangchuanosaurus* and *Sinraptor* (Bathonian-Callovian) from China as well (Fig. 6) (Rauhut et al. 2016: Table 3). Interestingly, RAJ/JAIS/JWGQ001, was recovered as a megalosaurid theropod when scored as a mesial tooth in the cladistic analysis performed on the dentition-based data matrix using a fully constrained topological tree (Fig. 3). Results of the cladistic analysis combined with the marine deposits in which RAJ/JAIS/JWGQ001 was found, would support a megalosaurid affinity for this isolated tooth. If true, this specimen would then be the first non-avian tetanuran as well as the first megalosaurid to be found in India. Both Europe and western India were covered with shallow seas characterised by humid biomes during the Jurassic (Smith et al. 1994; Sharma & Singh 2021). The presence of the

Bathonian European marine hybodonts: *Strophodus magnus* Agassiz, 1838, *Strophodus medius* Owen, 1869 and *Planohybodus* sp. in the same bed that has yielded the theropod tooth RAJ/JAIS/JWGQ001 (Sharma & Singh 2021), also suggests a Laurasian affinity for this theropod. Surprisingly, Prasad & Parmar (2021) also reported a similarity between the Jurassic Kota fauna of India (Gondwana) and the Bathonian fauna from England (Laurasia).

During the Middle Jurassic, megalosaurids were the main theropod elements of Laurasia, the remains of which were typically found in marine sediments. Conversely, allosauroids, which became the dominant predators of the Late Jurassic, are found in inland sediments (Rauhut et al. 2016). Ceratosaurids were minor component of both Middle and Upper Jurassic theropod fauna while coelurosaurs were rapidly radiating from Middle to Late Jurassic times (Rauhut et al. 2016: fig. 27 and 28). There was a rapid radiation of averostran theropods from the Toarcian to the Bathonian, which might have been triggered by a Pliensbachian-Toarcian extinction event (Rauhut et al. 2016). Many derived clades of theropods had already reached a global distribution by the Late Jurassic. There is a possibility that some of the above mentioned theropod clades might have originated and radiated first in southern Gondwana from Early to Middle Jurassic times, but their fossil record is poorly represented (Rauhut et al. 2016). Basal megalosauroid (i.e., *Piatnitzkysaurus* and *Condorraptor*) were already present in the Early Jurassic of Argentina before the breakup of Pangaea, so a Pangaean distribution of megalosauroids cannot be ruled out. India was still a part of the Gondwana landmass at the southern Tethyan margin in Middle Jurassic times, so there was a possibility of faunal exchange between the western and eastern Gondwanan continents. Inadequate sampling from Gondwanan continents hinders our knowledge about the early evolution and distribution of theropod clades. Very little is known about the Middle Jurassic theropods. Although this incomplete tooth is identified at a higher taxonomic unit only, but it presents the Jaisalmer basin, India as one of the rare Gondwanan sites which preserved theropod remains from the marine Bathonian sediments. This specimen is significant for our understanding of the evolution and biogeography of theropods as well as the Middle Jurassic palaeogeography and paleoecology.

Conclusions

The unexpected discovery of the isolated crown from marine carbonate rocks, reveals that at least one taxon of a medium to large-bodied theropod dinosaur thrived near the Jurassic coast of the Indian sub-continent. The stratigraphic and geographic position of this isolated crown indicates the presence of a possibly new, previously undescribed taxon from India. The isolated theropod crown is referred to a non-coelurosaur averostran as the fragmentary nature of the crown does not allow to assign it to a more inclusive clade. RAJ/JAIS/JWGQ001 probably belongs to the mesial dentition of a basally branching averostran, possibly a megalosaurid based on the result of the cladistic analysis and the stratigraphy and provenance of the dental material. A Laurasian affinity of this specimen is also plausible given the presence of hybodont sharks in the theropod yielding bed, similarly to those found in coeval Bathonian sites of Europe. This finding represents the only unambiguous Middle Jurassic (Bathonian) theropod record in India and marks Jaisalmer Basin as one of the important Bathonian sites in Gondwana, that preserve dinosaur fossils. The rarity of the terrestrial vertebrates in the Jaisalmer Formation may be attributed to taphonomy bias against preservation of large specimens in shallow marine sediments and in part to sampling bias. Recent findings of dinosaur fossils from the Bathonian marine sediments provides information on the diversity of terrestrial fauna in the Jaisalmer Basin during the Middle Jurassic. Further exploration of the Middle Jurassic successions will be continued to explore the vertebrate potential of the basin, both marine and terrestrial. The discovery of more complete material in future may bring forth a better understanding of evolutionary traits and biogeography of Middle Jurassic theropods of Gondwana for a better understanding of the Middle Jurassic ecosystems.

Data Availability: The modified data originally created by Hendrickx and Mateus (2014) is used in cladistic analysis (Fig. 3). The latest version of the datamatrix was published by Meso et al. (2021) and includes 146 dentition-based characters scored across 107 saurischian taxa. The data generated and analysed in the contribution is available in the Supplementary_File_1 to 5.

Author Contributions: AS: fieldwork, section measurement, sampling, conceived and designed the study, collected the data, updated and analysed the data, performed the experiments, prepared figures, authored and reviewed the drafts of the paper, approved the final draft. CH: contributed to the data, performed the experiments,

updated and analysed the data, authored and reviewed the drafts of the paper, approved the final draft. SS: fieldwork, sampling, preparation of the specimen, photographing the specimens, reviewed the drafts of the paper, approved the final draft.

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