

# The First Record of Chigutisaurid Amphibian from the Late Triassic Tiki Formation and the probable Carnian Pluvial Episode in Central India

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A new, partially preserved skull of chigutisaurid amphibian (*Temnospondyli*) has been reported for the first time from the Late Triassic Tiki Formation of India. The specimen belongs to the genus *Compsoceroops* prevalent in the Late Triassic Maleri Formation occurring 700 km south. However, the chigutisaurid specimen recovered from the Tiki Formation is a new species when compared to that of the Maleri Formation.

Biostratigraphically, it proves that the Tiki Formation, is not only coeval with the Lower Maleri Formation but also a part of Upper Maleri too. Chigutisaurids are now known to occur in the Early and Late Triassic of Australia, Late Triassic in India, Argentina and Brazil, in Jurassic of South Africa and Australia and Cretaceous of Australia. In India the first appearance of chigutisaurids marks the Carnian – Norian Boundary. This work also attempts to correlate, again for the first time, the advent of chigutisaurids and the occurrence of Carnian Pluvial Events in Late Triassic Maleri and Tiki Formation of Central India.

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## Abstract

A new, partially preserved skull of chigutisaurid amphibian (Temnospondyli) has been reported for the first time from the Late Triassic Tiki Formation of India. The specimen belongs to the genus *Compsoceros* prevalent in the Late Triassic Maleri Formation occurring 700 km south. However, the chigutisaurid specimen recovered from the Tiki Formation is a new species when compared to that of the Maleri Formation. Biostratigraphically, it proves that the Tiki Formation, is not only coeval with the Lower Maleri Formation but also a part of Upper Maleri too. Chigutisaurids are now known to occur in the Early and Late Triassic of Australia, Late Triassic in India, Argentina and Brazil, in Jurassic of South Africa and Australia and Cretaceous of Australia. In India the first appearance of chigutisaurids marks the Carnian – Norian Boundary. This work also attempts to correlate, again for the first time, the advent of chigutisaurids and the occurrence of Carnian Pluvial Events in Late Triassic Maleri and Tiki Formation of Central India.

# Introduction

The Gondwana Successions of India are exposed in four discrete basins coinciding with some of the major river valleys throughout the Indian Subcontinent (Pascoe 1973; Robinson 1970; Veevers & Tewari 1995). Of these, the Late Triassic Maleri and the Tiki Formations of the Pranhita-Godavari Valley Basin and the Son Valley Basin respectively are long known to be coeval (Chatterjee & Roy-Chowdhury 1974; Kutty & Sengupta 1989; Mukherjee & Ray 2014; Robinson 1970). Both the Formations are known for the metoposaurids *Panthesaurus* *maleriensis* (Chakravorti & Sengupta 2019; Sengupta 2002). While *P. maleriensis* is thought to be restricted within the Carnian, the chigutisaurids appear in the Early Norian in the Late Triassic Maleri Formation (Chakravorti & Sengupta 2019; Sengupta 1995). Though considerable amount of work has been done on the microvertebrates, rhynchosaur and phytosaurs of the Tiki Formation, no recent comprehensive works have been done in the last decade on its temnospondyl faunal contents. Chakravorti & Sengupta (2019) in their taxonomic revision of the Indian metoposaurids, included the metoposaurids of the Tiki formation as well and grouped them together into a new genus *Panthesaurus maleriensis* based on morphometric and phylogenetic approaches. However, the biostratigraphic implications of the Tiki Formation based on its temnospondyl contents has not been attempted so far. Taphonomic aspects of *Panthesaurus* has recently been studied by Rakshit & Ray (2020). Also, till date no chigutisaurid remains were reported from the Late Triassic Tiki Formation though the same is widely prevalent in the Late Triassic Maleri Formation (Sengupta 1995). Therefore, the finding of a chigutisaurid amphibian from the Late Triassic Tiki Formation is very important. Weathered skull of a chigutisaurid and one of its clavicles have been excavated by the authors from the Tiki Formation. The detail description of the newly collected specimens is provided below. Recently Kumar & Sharma (2019) reported a metoposaurid skull from the Tiki Formation (Fig: 1a).

Careful study of the photograph (RH01/Pal/CHQ/Tiki/15) (Fig: 1a) reveals the skull is actually that of a chigutisaurid. The new material collected by the authors and the one figured by Kumar & Sharma (2019) as a metoposaurid are now the two chigutisaur individuals that are being reported from the Tiki Formation for the first time. Appearance of chigutisaurids in India is noted with the demise of the metoposaurids, rhynchosaurs and primitive phytosaurs. Large prosauropods also appeared during that time (Novas et al. 2010). Those events demarcate the Carnian – Norian boundary (Datta et al. 2021) in India. The Maleri Formation starts with a 250 meter thick mudstone (Dasgupta et al. 2017; Kutty & Sengupta 1989). At the top of the mudstone a sandy zone initiates the sand – mud alternations of Upper Maleri (Kutty & Sengupta 1989). This sandy zone contains maximum number of rhynchosaur fossils, abundant metoposaurids and unionids. The chigutisaurids in Maleri appear just above this sandy zone (Sengupta 1995) and no rhynchosaurs or metoposaurids are known from that level (or above that). The occurrence of chigutisaurids in Tiki is also restricted within a sandy zone which do not contain metoposaurids or rhynchosaurs. Unionids are also present there but in lesser abundance than Maleri. Phytosaur teeth are also present. This sandy horizon noticed in Maleri and Tiki, has been stratigraphically placed below the Carnian – Norian boundary and may indicate the Carnian Pluvial Events in India.

## Materials used and their preservation and methods

The skull, ISI A 202, is poorly preserved (Fig: 2a,2b,3a,3b,4,5). Only left half of the skull is preserved and the specimen is heavily eroded. Thus, the ornaments are not well observed in all the areas. The upper part of the parietal and postfrontal has coarse ridges and grooves preserved in them. Palate of two individual specimens viz: ISI A 202/1, ISI A 202/3-5 (Fig: 3a,3b) and the palate published in Kumar & Sharma (2019) (Fig:1a,b) have been studied here. The new

specimens with ISI numbers and the published specimen of Kumar & Sharma (2019) were recovered from red mudrocks at a distance of about 100 meters from the same village of Tenduadh in the Late Triassic Tiki Formation. As written earlier, photograph of a temnospondyl palate has been reported by Kumar & Sharma (2019) (Fig. 1a,b) who identified it as a metoposaurid. However, the parabolic skull outline, vaulted pterygoid, shape and proportion of the interpterygoid vacuities, wide and folded palatine ramus of the pterygoid and comparatively narrow cultriform process of the parasphenoid clearly indicate that it is not a metoposaurid. The cultriform process is wider than *Compsocerops cosgriffi* but narrower than any of the metoposaurids. This palate is comparatively well preserved and bears definite characters of a chigutisaur as it appears from the field photograph (Fig: 1a,b). Only the photograph of the palate is available for study. The palate is dorsoventrally elongated and slightly sheared. The edges of the palate are not well preserved.

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# Previous works and Literature

Tiki Formation named after a small village of Tiki in the district of Shahdol, Madhya Pradesh has been an interest to scientists for decades. Reports on the geology and palaeontology of the Tiki Formation dates back to as early as 1877 when Hughes (1877) noticed reptilian fossils near this village. Cotter (1917) noticed several other such fossils and finally Fox (1931) formally designated the area as the “Tiki stage”. Aiyengar (1937) first divided the “Tiki stage” into lithostratigraphic units viz. the lower unit being fossiliferous and composed dominantly of red and green mudstones, proportionately lesser amount of sandstones and mud-galls while the upper unit being composed of ferruginous sandstones and shales. Robinson (1970) in her memoir kept the Tiki Formation to be coeval with the Late Triassic Maleri formation. However, Dutta & Ghosh (1993) did not recognize the separate entity of the Tiki Formation and placed Tiki rocks at the upper part of the Pali Formation forming the “Pali-Tiki Formation”. Roychowdhury et al. (1975) on the basis of megaf flora assemblage noted the age of the Nidhipur beds to be Anisian and separated the upper part of the Tiki Formation to be Carnian – Rhaetian in age. Maheshwari et al. (1976) separated the Tiki Formation to be a separate entity (including the Nidhipur beds) and based on the mega flora and faunal assemblages suggested the age of the Tiki (including Nidhipur beds) Formation to be ranging from Anisian to Norian with a possible extension to Rhaetian as well. Mukherjee et al. (2012) revised the stratigraphy of the Rewa Basin and put the Tiki Formation with the coeval Carnian Lower Maleri Formation. Ray et al. (2016) in the study of vertebrate faunal assemblage of the Tiki formation also suggested Tiki Formation to be of Carnian in age but they narrowed the range to the Otischalkian to early Adamanian. The common conclusions of all these literatures are that the Late Triassic Tiki Formation is dominantly Carnian and its fauna can be correlated with the Lower Maleri fauna. So far no evidence of a Norian age was assigned to any part of the Tiki Formation. As stated earlier, based

on the faunal evidences and correlating it with the Late Triassic Maleri Formation of the Pranhita – Godavari valley a Carnian age was assigned to the Tiki Formation (Dutta & Ghosh 1993; Kutty et al. 1987; Sengupta 1992). Henceforth, through Decades, the Tiki formation was considered to be coeval with the Carnian Maleri Formation ((Mukhopadhyay et al. 2010; Sengupta 1992; Veevers & Tewari 1995). Only recently, Datta et al. (2021) while describing a new phytosaur from the Tiki Formation, commented that the age of the Tiki Formation may range from Carnian to early/Middle Norian.

Till date the faunal assemblage of the Tiki Formation includes fishes belonging to family Ceratodontidae, Hybodontidae and new undescribed forms of Xenacanthidae (Ray et al. 2016), temnospondyl amphibians belonging to Metoposauridae; reptilian belonging to families Rhynchosauridae, Rauisuchidae, Rhyncocephalia, Acrodonta, basal saurischia, Dromatheridae and Traversodontidae. Mammaliaformes are also reported from the Tiki Formation (Bandyopadhyay & Ray 2020; Ray et al. 2016). An updated list of the faunal list of the vertebrate fossils so far excavated and reported from the Tiki Formation is provided in Table 1.

## Chigutisauridae from the Tiki Formation

### Systematic Palaeontology

Temnospondyli (Zittel 1888)

Stereospondyli (Zittel 1888)

Chigutisauridae (Rusconi 1951)

*Compsocerops* (Sengupta 1995)

*Compsocerops tikiensis* sp. nov. (Fig. 2.1, 2.2)

**Type material:** ISI A 202/1 which comprises of the left half of a skull roof is the holotype. The skull and other ISI numbered referred material are housed in Geological Studies Unit, Indian Statistical Institute, Kolkata, India (Fig: 2a,b).

**Referred material:** ISI A 202/2 (Fig: 5) a nearly complete clavicle. ISI A 202/3-5 comprises of weathered and broken parts of the skull (Fig: 2a,b;3a,b) and a palate, (RH01/Pal/CHQ/Tiki/15) previously assigned to a metoposaurid by Kumar & Sharma (2019) have been referred ( Fig: 1a,b)

**Locality:** Southwest of the Village of Tenduadh (23°59'41" N; 81°25'02" E), just next to the Barakachh - Beohari Road in the district of Shahdol, Madhya Pradesh, Central India.

**Etymology:** The new species of chigutisaur is named after the Late Triassic Tiki Formation from where the specimen has been excavated and studied.

**Diagnosis of genus:** A chigutisaur temnospondyl identified as *Compsocerops* by the presence of the following combination of characters: skull outline parabolic in shape, orbits anteriorly placed, raised rim of the naris, presence of a well preserved conspicuous quadratojugal projection, presence of squamosal horn (which though broken and eroded is recognizable), putative and ill preserved postparietal horn, well preserved vaulted pterygoid, long and narrow cultriform process of the parasphenoid, dentigerous area restricted to the anterior portion of the palate, short and restricted palatine dentition not reaching to the middle of the choana, wide ramus of the pterygoid with a gentle fold, wall like quadrate ramus of the pterygoid, presence of postpterygoid process, typical shape of the ramus of the pterygoid and that of the subtemporal vacuities, long dorsal process of the clavicle with a distinct groove and bean-shaped cross section.



**Diagnosis of species:** The new species of *Compsocerops* is identified by the presence of inward curved process of the quadratojugal as opposed to the straight downward trending process of the quadratojugal in *Compsocerops cosgriffi*, presence of vomerine foramen, shorter and wider interpterygoid vacuities, wider subtemporal vacuities, base of the interpterygoid vacuities at the same level with the base of the subtemporal vacuity as opposed to *Compsocerops cosgriffi* (where base of the interpterygoid vacuity is lower than the base of the subtemporal vacuity making the interpterygoid vacuities longer and slenderer in *Compsocerops cosgriffi*) and wider cultriform process of the parasphenoid.

## Description and Comparative anatomy

### *The skull roof* (Fig: 2a,b)

The dorsal part of the skull roof can only be studied in ISI A 202.

The skull roof is parabolic in shape with broad and concave posterior part of the skull table. Even though the anterior part of the skull roof is mostly broken, a major portion of the left orbit is preserved. The orbit is subcircular in shape bordered by the prefrontal, jugal, postfrontal and postorbital. The orbit is located in the anterior half of the skull and is laterally placed. The posterior and posterolateral part of the left external nares is also preserved. It can be understood from the posterior outline of the external nares that they are oval in shape. The external nares are located very close to the anterior border of the skull roof. The posterior part of the external nares is thick and raised. This character is noted in chigutisaurs and are found in *Pelorocephalus tenax* (Marsicano 1999) and *Compsocerops cosgriffi* (Sengupta 1995). The supraorbital sensory canal in the region of the naris is unusually deep around the posterolateral border of the naris which is responsible for the thick and raised posterior part of the naris in the ISI A 202. This characteristic

feature has also been noted in *Compsoceroops cosgriffi* (Sengupta 1995) where anteriorly the naris is flushed with the skull roof. The entire disposition of the sensory sulci is not well preserved in the specimen. Apart from the supraorbital sulcus, the presence of postorbital dermal sensory sulcus through the postfrontal can be recognized by the deep continuous canal like structure in these two bones. The infraorbital sulcus is visible in the maxilla but gradually becomes less prominent as it enters the jugal to form the jugal lateral dermal sensory sulcus. Just like other comparable chigutisaurids like *Keratobrachyops australis* (Warren 1981), *Siderops kehli* (Warren & Hutchinson 1983), *Pelorocephalus tenax* (Marsicano 1999; Rusconi 1949), *Compsoceroops cosgriffi* (Sengupta 1995) the lacrimal is absent in ISI A 202 and the maxilla enters the border of the external nares. However, anterior part of the skull is fragmentary and heavily eroded. The better preserved left side of the dorsal part of the skull roof consists partially preserved prefrontal, postfrontal, postorbital and supratemporal. The squamosal is broken at the posterior part, parietal, postparietal, tabular, jugal and quadratojugals are also partially preserved. The surfaces of the bones are eroded in most places and ornamentations are poorly preserved. The parietal is comparatively large, rectangular in shape and broken along the midline. Coarse ridges and grooves can be recognized from at the anterior part of the parietal. Just as in *Compsoceroops* the postparietal of ISI A 202 (Fig: 2a,b) is much shorter in length than the parietal. The pineal foramen is not preserved in the parietal. The suture of the postparietal with the tabular is obliterated. The postparietal is broken and eroded along the midline and at its posterior part in the region of the postparietal horn. The postparietal horn is broken in ISI A 202 (Fig: 2a,b). However, there are clear evidences that the horns exist. Postparietal horns are the most unambiguous synapomorphy of *Compsoceroops*. It is preserved in *C. cosgriffi* (Sengupta 1995), *C. sp.* (Dias-da-Silva et al. 2012) and *C. tikiensis*. These horns are not preserved in any

other chigutisaur (the relevant area is not preserved in *Siderops* though (Warren & Hutchinson 1983) and *Koolasuchus* (Warren et al. 1997). The tabular is most likely to be in contact with the parietal though that part is not very well preserved. The broad tabular – parietal contact is considered to be a diagnostic character of *Compsocerops* (Sengupta 1995). The tabular horn is broken. This post-quadratojugal process is robust and despite the very poor preservation of the skull in general, the posterior quadratojugal process is well preserved. The shapes and sutural patterns of the posterior left side of the skull are very similar to *Compsocerops cosgriffi*.

### *The Palate* (Fig: 3a,b)

Kumar and Sharma 2019, (Fig: 1a,b) described the palate (RH01/Pal/CHQ/Tiki/15) as a metoposaurid palate (Fig:1a,b). However, no detailed osteological description or identifying characters were described by the authors as to why the specimen was identified to be a metoposaurid. The authors only described the palate to be the ‘dorsal’ part of a metoposaurid as it has conical teeth present on the anterior part. However, this description is vague and of no taxonomical significance whatsoever as all temnospondyls have conical teeth and both chigutisaurids and metoposaurids have teeth and tusks in the anterior part of the skulls. Again, dentition restricted to the anterior margin of the skull is a characteristic of all temnospondyls with parabolic skulls. Additionally, Kumar & Sharma (2019) grouped the palate collected from the village of Tenduadh with the specimens of metoposaurid clavicle collected from the village of Jora. This grouping is not viable as the two villages are approximately 12 kilometers apart from each other and there is a probability that these two villages might be parts of Upper and Lower parts of the Tiki Formation and may even be of different ages as discussed later. The specimen, as said in Kumar and Sharma (2019), was too friable and could not be excavated by them. Thus, there is no option to study the specimen first hand. Henceforth, the image of Kumar

and Sharma (2019), has been replicated into high resolution photograph with the required permission from the editor of the Journal of the Palaeontological Society of India to study the detail of the described specimen (RH01/Pal/CHQ/Tiki/15) (Fig: 1a,b).

Clearly, the studied specimen is the palate of a temnospondyl and definitely not the dorsal view of the skull as erroneously stated by Kumar and Sharma (2019). The palate shown in the picture (RH01/Pal/CHQ/Tiki/15) (Fig: 1a,b) has a distinct vaulted pterygoid, parabolic skull outline, comparatively narrow cultriform process than metoposaurids. The specimen (RH01/Pal/CHQ/Tiki/15), (Kumar and Sharma 2019) (Fig: 1a,b) has a parabolic skull, thickening of the pterygoid, presence of vaulted pterygoid, presence of post-pterygoid process and concave vertical wall of pterygoid that are characteristic of chigutisaurids as written repeatedly above. The specimen is indeed friable with dense networks of fractures that obscured the clear identification of the sutures. The specimen (RH01/Pal/CHQ/Tiki/15) is partly eroded along the lateral margins as well as anteriorly and posteriorly. The right half of the palate is slightly compressed, deformed and curved (Fig: 1).

The anterior portion of the palate is considerably broken both anteriorly and anterolaterally. Though the sutures cannot be delineated but the presence of vomer is very apparent. The vomer is broken anteriorly and the anterior palatal vacuity is not preserved (RH01/Pal/CHQ/Tiki/15) (Fig: 1). The posterior part of the preserved vomer includes the anterior tongue of the cultriform process of the parasphenoid. Left half of a possible vomerine cavity is preserved. The vomerine cavity is present only in Jurassic chigutisaur *Siderops kehli* (Warren and Hutchison 1983) and it is absent in *Compsocerops* (Sengupta 1995) or *Pelorocephalus* (Marsicano 1999). The left lateral margin of the right choana is aligned to the left lateral margin of the right interpterygoid vacuity. The ectopterygoids are exposed on the anterolateral margins of the interpterygoid vacuities and

are preserved on both sides. The ectopterygoid borders the anterior portion of the subtemporal vacuity inwards. The subtemporal vacuity is wide and broad bordered by the ectopterygoid and the parasphenoid on the inward margin and the quadratojugal, the alar process of the jugal on the outward lateral margin. The dentigerous area is restricted to the anterior region of the palate. The anterior and the anterolateral margins of the palate being broken, all teeth are not preserved. However, two broken ectopterygoid teeth can be seen preserved at the anterolateral corner of the ectopterygoid in contact with the palatine in the left part of the palate. The palatine teeth row in the left half of the skull are also preserved partially. Like other chigutisaur, the dentigerous area of the palate is remarkably short. The palatine row of teeth is not continuous up to the middle of the choana. This character has been considered to be a synapomorphy of *Compsocerops cosgriffi* (Sengupta 1995). Conical, inward curved four complete palatine teeth are preserved in the margin of the left palatine bone of the palate. Since, the dentigerous area is restricted to the anterior part of the skull the posterior part is longer in proportion and covered by large and wide subtemporal vacuity (Fig: 3a,b).

In (RH01/Pal/CHQ/Tiki/15) (Fig: 1a,b) (Kumar and Sharma 2019) both the interpterygoid vacuities are well preserved. The interpterygoid vacuities are quadrangular in shape, shorter and wider compared to *Compsocerops cosgriffi* (Sengupta 1995). The borders of the interpterygoid vacuities are approximately parallel sided. The interpterygoid vacuities are bordered dominantly by the cultriform process along the inward margin as well as the vomer. Anteriorly, it is bordered by the vomer and the palatine. The pterygoid forms the dominant margin of the interpterygoid vacuities laterally with a small area being occupied by the ectopterygoid. Posteriorly, these are formed by the parasphenoid. In ISI A 202/1, the interpterygoid vacuities are not completely preserved. In both the specimens ISI A 202 and (RH01/Pal/CHQ/Tiki/15)

(Kumar and Sharma 2019), the interpterygoid vacuities are shorter and broader than *Compsocerops cosgriffi* where the base levels of the interpterygoid vacuities are lower than that of the subtemporal vacuities. The subtemporal vacuity extends anteriorly to the level higher than the center of the interpterygoid vacuities.

In (RH01/Pal/CHQ/Tiki/15) (Kumar and Sharma 2019) (Fig:1a,b) both the pterygoids are preserved. They are deep and vaulted. The vertical lateral wall of the pterygoid projects posteriorly possibly up to the posterior level of the occipital condyles which are broken. The palatal ramus of the pterygoid is visible on both sides in (RH01/Pal/CHQ/Tiki/15). The palatal ramus of the pterygoid is longitudinally concave with a gentle fold which is again a character of some chigutisaurs specially *Compsocerops*. The quadrate ramus of the pterygoid is better preserved on the right side of the palate in (RH01/Pal/CHQ/Tiki/15). The quadrate ramus of the pterygoid looks like a wall as they are deeply vaulted. The ascending ramus of the pterygoid is not visible in (RH01/Pal/CHQ/Tiki/15). A broken post pterygoid process that is a projection from the posterior border of the pterygoid corpus is visible on the right side of the palate (RH01/Pal/CHQ/Tiki/15). This area on the left side of the palate of (RH01/Pal/CHQ/Tiki/15) is broken. The postpterygoid process is considered to be a apomorphic character for *Compsocerops cosgriffi* (Marsicano 1999). The suture of the quadrate and pterygoid is present on the outer side of the downturned part of the quadrate ramus of the pterygoid. In ISI A 202, (Fig: 3a,b) only the right pterygoid is ill-preserved but the bone surface is crushed. However, a distinct post pterygoid process characteristic of *Compsocerops* is present. Though the bone is crushed and compressed, yet the vaulted nature of the pterygoid can be made out because of the concavity of the vertical wall of the pterygoid. In both the specimens (RH01/Pal/CHQ/Tiki/15) (Kumar and

300 Sharma 2019) and ISI A 202, the palatine ramus of the pterygoid is much broader and wider than  
301 that in *Compsocerops cosgriffi*.

302 Just like other chigutisaurids, the base of the parasphenoid is almost hexagonal in shape with a  
303 long extension in the form of the cultriform process placed between two interpterygoid vacuities  
304 in (RH01/Pal/CHQ/Tiki/15) (Kumar and Sharma 2019). The parasphenoid has a long suture with  
305 the pterygoid laterally and the exoccipitals posteriorly. A distinct raised longitudinal keel is  
306 present on the ventral surface of the cultriform process in this specimen. The presence of this  
307 keel in the cultriform process has been noted by Marsicano (1999) as a distinguishing character  
308 present only in *Pelorocephalus mendozensis*. However, first hand studies reveal that this  
309 longitudinal keel of the cultriform process is also present in *Compsocerops cosgriffi* from Maleri  
310 Formation of Pranhita - Godavari Valley Basin. The cultriform process of parasphenoid of this  
311 specimen is comparatively narrower than all other specimens of *Compsocerops cosgriffi*. The  
312 cultriform process of the *Compsocerops* species from Tiki is wider than *C. cosgriffi*, the  
313 cultriform process is also comparatively broader than *Siderops kehli*, more comparable to the  
314 width of the cultriform process in the specimen previously denoted as *Kuttycephalus triangularis*  
315 (Sengupta 1995). The cultriform process preserved in (RH01/Pal/CHQ/Tiki/15) (Kumar and  
316 Sharma 2019) is thin and constricted in the middle part of the interpterygoid vacuities and gets  
317 broader as it progresses to the anterior part of the process. This type of cultriform process is  
318 unique among the chigutisaurids. In the specimen photographed by Kumar and Sharma (2019), the  
319 anterior tongue of the cultriform process is in contact with the vomer and lies posterior to the  
320 level of the anterior margin of the interpterygoid vacuities. The cultriform process is not  
321 preserved in ISI A 202. The occipital condyles are broken as well. In the earliest known

chigutisaur *Keratobrachyops*, the cultriform process of the parasphenoid is also narrower than  
ISI A 202.

### *The Occiput* (Fig: 4)

The occiput is very ill preserved only in ISI A 202 (Fig: 4). The occiput could not be prepared  
due to the extremely fragile nature of the skull. Removing the matrix load from the occiput  
would result in sagging of the entire specimen. However, from the little that could be studied, it  
can be said that in occipital view, the quadrate ramus of the pterygoid is deeply downturned. The  
vagus nerve foramen is preserved on the left exoccipital lateral to the broken occipital condyle.  
The ascending process of the exoccipital is wide and inclined and meets the descending process  
of the postparietal. A sub-circular, matrix filled, paraquadrate foramen is present in the  
quadratojugal. The quadrate is partially preserved in the occipital view. It is bounded by the  
squamosal, quadratojugal and the downturned pterygoid. Absence of occiput makes the  
comparison of ISI A 202 difficult with the different species of *Pelorocephalus* as different  
species of the genus are differentiated, with a great extent, by their occipital characters  
(Marsicano 1999).

### *Clavicle* (Fig: 5)

An almost complete left clavicle (ISI A 202/2) (Fig: 5) was found associated with the skull (ISI  
A 202/1) during excavation. The clavicle has flat eye-drop shaped blade and a long straight  
dorsal process that ascends almost straight, nearly at ninety degrees with the plate. The cross  
section of the process at the dorsal end is bean shaped as a feeble furrow runs along the process.



This is very similar to the clavicle of *Compsocerops cosgriffi* (Sengupta 1995), *Siderops kehli* (Warren and Hutchinson 1983) and *Koolasuchus cleelandi* (Warren et al. 1997).

[Significance of \*Compsocerops tikiensis\*. in demarcating the Carnian Pluvial Event in India](#)

The Carnian Pluvial Event (CPE) can be defined as a geologically short lived (234-232 Million years ago) monsoonal period of extreme rainfall that brought about significant changes in several depositional environments from continental to deep-water setting (Arche & Lopez-Gomez 2014; Dal Corso et al. 2015; Furin et al. 2006; Schlager & Schöllnberger 1974; Simms & Ruffell 1990). The Carnian Pluvial Event was a global phenomenon. Geochemical data suggests that global warming involved environmental and biotic changes. Radioisotopic ages coupled with biostratigraphic correlation suggest a possible link to the eruption of the Wrangellia Large Igneous Province (LIP) (Dal Corso et al. 2020). CPE was a significant (but previously neglected) time of extinction linked to the Carnian explosive diversification of many key modern groups of plants and animals (Dal Corso et al. 2020). The CPE marks a distinct change in the hydrological cycle during which the climate shifted from arid to humid conditions and back again to arid conditions (Bernardi et al. 2018). It is represented by remarkable enhancement of hydrological cycle demarcated by four episodes of increased rainfall indicated by diverse sedimentary and paleontological data, repeated Carbon Cycle perturbations, evidenced by sharp negative C-isotope excursions, coincided with global environmental changes and climate warming all of which suggests a cause and effect relationship (Dal Corso et al. 2015). The Carnian is the earliest part of the Late Triassic and its base or lower boundary is dated at approximately 237 million years based on U-Pb radiometric dating of a single crystal zircon from a tuff layer within a section having strong biostratigraphic constraints (Dal Corso et al. 2015; Dal Corso et al. 2012; Maron et al. 2019). The upper boundary of the Carnian is constrained at approximately 227

million years based on magnetostratigraphic correlations between the marine successions of Tethys and the astrochronological time scale of the continental Newark Basin (Kent et al. 2017). The Carnian is subdivided into Julian (Early Carnian) and Tuvanian (Late Carnian) substages. The Julian – Tuvanian boundary occurs at approximately 233 million years (Dal Corso et al. 2015; Kent et al. 2017). The beginning or the onset of CPE is well defined from ammonoid, conodont, and sporomorph biostratigraphic dating and synchronous in several geological settings. It coincides with the first appearance of the ammonoid genus *Austrotrachyceras* in the Julian (Dal Corso et al. 2020; Dal Corso et al. 2015; Dal Corso et al. 2012; Roghi et al. 2010; Simms & Ruffell 1990; Sun et al. 2016). However, the upper boundary or the end of CPE is poorly defined in most locations. It is usually placed at the base or within the Tuvanian 2 on the basis of sedimentological (e.g., end of terrigenous sediment supply) and chemostratigraphic (last C-isotope excursion) evidence (Dal Corso et al. 2020; Dal Corso et al. 2015; Dal Corso et al. 2018). The total duration of this pluvial event is variable. Cyclostratigraphy of marine successions of the South China Block and of continental successions of the Wessex Basin (United Kingdom) gives a duration of the CPE of approximately 1.2 ma but this is variable and longer to 1.6-1.7 million years as indicated by integrated stratigraphy (biostratigraphy and magnetostratigraphy). The CPE facilitated the Dinosaur Diversification Event (DDE) (Bernardi et al. 2018). But the role of CPE on the temnospondyls have not much been discussed barring a few papers (Buffa et al. 2019; Fortuny et al. 2019; Gee & Jasinski 2021; Lucas 2020). Two dominant groups of temnospondyls, in this context, were the metoposaurids and the chigutisaurids. According to Fortuny et al. (2019) the gigantism of the metoposaurids might have been linked to the Carnian Pluvial Event. Buffa et al. (2019) also stated that the diversification of the metoposaurids might have been linked to the CPE and the post CPE aridification led to the

extinction of the metoposaurids during the Rhaetian. Gee and Jasinski (2019) have also commented on the fact that the physiological variation of the metoposauridae and their palaeoclimatic range also corroborates to a palaeo-environmental barrier. Finally, Lucas (2020) concluded that climate change that occurred during CPE played important part in the metoposaurid evolution. According to Lucas (2020), Metoposaurids appeared during the CPE, attained their highest diversity and cosmopolitan distribution during this time and had reduced diversity and showed endemism in the post CPE climate.

The presence of *Compsocerops* in both Maleri and Tiki Formation enhances the scope to discuss the palaeoenvironment of these two Late Triassic basins in India and to compare on the possible reason of faunal turnover from Carnian to Norian (Sengupta 1995) with respect to the amphibious temnospondyls.

In the light of the newly excavated chigutisaurid *C. tikiensis*, the faunal changeover in the Tiki Formation is now more apparent and as follows:

### Tiki Formation

No detail sedimentological or geochemical studies has been carried out in the Late Triassic Tiki Formation in India to analyse the associated changes from Carnian to Norian through the humid phase of the Carnian Pluvial Episode. Though Ahmed and Ray (2010) presented geochemical analysis of 42 nodular carbonate confirming their pedogenic origin, but no details of the localities of collection in terms of lower and upper Tiki have been provided. The map of the temnospondyl bearing localities of Tiki Formation has been modified here with faunal boundaries (hypothetical faunal boundary demarcated in red dotted line) after Mukherjee et al. (2012) (Fig: 6). Till date no temnospondyl fauna has been recorded from the upper part Tiki Formation. Excavation taken up in 2018 revealed the first chigutisaurid from the Tiki Formation

in the Tenduadh locality (Fig: 7) in the Upper part of Tiki Formation. Several vertebrae and post cranial bones of metoposaurid have been excavated from the Jora and Tiki Nala sections which has been assigned to lower Tiki Formation

Based on the changes in the faunal assemblage in the lower and the upper Tiki Formation and considering the lithostratigraphy, a boundary between the basal and upper Tiki Formation has been assigned and the zone demarcating the Carnian to Norian faunal turnover in the Tiki Formation has been approximated and marked in red dotted line in the map (Fig: 6).

The lithological logs modified after Kumar and Sharma (2019) and Mukherjee et al. (2012) reveal that just like the Maleri Formation, the basal Tiki Formation is dominated by a large band of red mudrock intercalated with peloidal calcirudite-calcarenite (Sarkar 1988) (Fig: 8). The Jora Nala section in the Carnian basal Tiki has been logged in detail in this work (Fig:8a). This shows the dominance of greenish to reddish siltstones and mudstones in the Jora Nala section with sparse deposition of trough cross bedded sandstones in between. Terrestrial influx of sediments is significantly low at that time period as denoted by the sparse occurrence of sandstones in the basal Tiki Formation (Fig: 8a,b,c). The presence of *Unio* beds in between the basal thick layers of mud reflect to a stagnant quiet and well-watered environment. This basal mud encompasses areas like the Jora and Tiki river sections. Abundant post cranial fragments of metoposaurid and rhynchosaurs have been collected from these sections. Moving upwards in the direction of the dip of the beds, there is a sudden in influx of siliciclastic sediments marked by thick sandstone units with little intermittent mudstone. This could be a demarcation of the rapid influx of siliciclastic sediments that took place during CPE in the Tiki Formation. Only two dominant sand bodies are observed in Tiki before the recurrence of a thick horizon of mud and subsequently sand-mud alternations indicating the onset of seasonality and aridity in the Norian.

The Norian of Tiki Formation is demarcated by red mudstones, whitish sandstones and sparse calcirudites. The Norian Upper Tiki Formation is exposed in sections near Tenduadh as shown in the map (Fig: 6) and an estimated approximate faunal boundary between the Carnian and the Norian in the Tiki Formation is also furnished as in Fig: 6.

Tiki has a long history of yielding fossil vertebrates (Bandyopadhyay & Ray 2020; Chatterjee & Roy-Chowdhury 1974) (Table 1). It has a rich Late Triassic faunal association marked by different taxa of Chondrichthyes and Osteichthyes fishes, a metoposaur *Panthesaurus*, a phytosaur *Volcanosuchus* belonging to the subfamily Mystriosuchinae and leptosuchomorphs, a rhynchosaur *Hyperodapedon tikiensis*, a rauisuchid named *Tikisuchus*, cynodonts and mammaliaformes taxa among others (Bandyopadhyay & Ray 2020; Chatterjee & Majumdar 1987; Mukherjee & Ray 2014). The Tiki faunal assemblage was thought to be coeval to the Lower Maleri faunal assemblage (Datta 2005; Kutty & Sengupta 1989). However, Datta et al. (2019) stated that the Tiki fauna ranges from Middle Carnian to Early Norian and is younger than Lower Maleri Fauna. The Norian Upper Maleri fauna has chigutisaurids. Discovery of a chigutisaurid from upper part of Tiki Formation confirms to Datta et al. (2019) regarding the presence of Norian fauna in Tiki. Presence of *Compsocerops* in Tiki, for the first time, confirms the presence of Upper Maleri faunal element in Tiki. Lucas (2020) thought that the demise of metoposaurids at most part of the world was at the end of Carnian and that tallies with the last appearance datum of the metoposaurids of Maleri. The chigutisaurids, both in Maleri and Tiki have their first appearance datum at the onset of the Norian.

## Maleri Formation

The overall palaeoenvironment and sedimentology of the Maleri formation has been worked upon by several workers (Dasgupta & Ghosh 2018; Sarkar 1988). Most of these studies were

done on the Maleri Formation as a whole without distinguishing its basal and upper parts. However, no detail analyses about the changes in sedimentology or geology or geochemistry has been done to study the changes in pattern of sedimentation from the Carnian basal Maleri to the Norian Upper Maleri.

The temnospondyl bearing (metoposaurid and chigutisaurid) localities of the Maleri Formation has been extensively mapped and modified after (Dasgupta et al. 2017; Kutty & Sengupta 1989) (Fig: 10) and a boundary between the Carnian basal Maleri and Norian Upper Maleri has been established from both lithological and faunal contents (Fig: 10 – faunal boundary indicated by green broken line). From the field studies and maps it is evident that though sandstone - mudstone alternation is present throughout the Maleri Formation, the Carnian basal Maleri is abundant in red mudrocks and calcirudites (Fig: 10,11) and moving towards Upper Maleri there is a sudden increase in the deposition on siliciclastic sediments leading to more frequent occurrence of sandstone bands alternating with red mudstone (Fig: 11). The abundance of red mudstone in basal Maleri Formation (Fig: 12) with sudden increase in the frequency of sandstone bands in the upper part can be correlated with the advent of the Carnian Pluvial Event (CPE) in India. The CPE had significant impact on the terrestrial environment and ecosystem globally. The evidence of CPE has never been worked upon or mentioned in India because of the lack of proper age constraints present in the Late Triassic Formations in India, both in the Maleri and Tiki Formations. However, evidence from detail geological mapping, logs and associated faunal turnover in the Late Triassic Maleri Formation all point towards the distinctive effect of CPE in India. The overall thickness of the Maleri Formation is about 350-600 m which is variable in different places. From the map of the Maleri Formation and from log of the same near Achlapur and Nalapur (Fig: 11) it is evident that the basal part of the Maleri Formation has a large stretch

or band of red mudrock dominated unit. This unit of red mudrock stretches from about 100m-200m in thickness in basal Maleri and is the thickest band of red mudrock encountered in the entire Maleri Formation. It encompasses villages namely Aigerrapalli (19°15'22.4"N; 79°27'23.4"E), Achlapur (19°09'34"N; 79°31'51"E) and Nambala (19°13'47"N; 79°26'07"E), areas slightly north of village Gampalpalli (19°10'11"N; 79°30'53"E) and is rich in vertebrate fossils, the most significant among them being rhynchosaurs and metoposaurids. This significantly thick basal Maleri mudstone has sporadic carbonate grainstones (*sensu* (Dunham 1962); calcarenites–calcirudites of Sarkar 1988) and presence of palaeosols with no significant siliciclastic deposition of sandstone present within this mud. The upper part of the Formation is approximately 200–350 m thick and has three to four multistoreyed sheet sandstone bodies (each 10–35 m thick) vertically separated by mudrock dominated intervals (15–55 m thick). The mudrock intervals in the upper part are lithologically similar to those occurring in the lower part of the Formation. The mudrock units comprises of both stratified and massive mudstones (Dasgupta et al. 2017) with sporadic carbonate grainstones (calcirudite of Sarkar 1988). Moving upwards from the thick stretch of mudrock, the influx of siliciclastic sedimentation increases as evident from the increase in the deposition of frequent sandstone units. The beginning of these sandstone units is marked by the presence of metoposaurids and rhynchosaurs and unionid fossils in a sandy zone. In the upper part, apart from the chigutisaurids, there are basal sauropods like *Jaklapallisaurus*, sauropodomorphs like *Nambalia*, probable Guaibasaurids and *Herrerasaurus* like forms (Novas et al. 2010). The authors in the same work, also mentioned that early theropods are known from the Norian-Rhaetian time from North and South America, India, South Africa, Europe and the demise of members of Lower Maleri fauna like rhynchosaurs together with global extinction of *Chiniquodon* (cynodont) and Proterocampsidae

(archosauriform) mark the Carnian – Norian boundary and also the North Tethyan Pluvial Event of end Carnian (CPE). Benton et al. (2018) have argued that CPE triggered the diversification of early dinosaurs. It has been discussed earlier that indications of CPE are present in Maleri and Tiki Formations of India. The sudden appearance of a number of basal dinosaur like *Jaklapallisaurus*, *Nambalia*, probable Guaibasauridae and *Herrerasaurus* (Novas et al. 2010) in the Norian Upper Maleri fauna also corresponds to that.

Thus, the palaeoenvironment of the Maleri Formation shifted from comparatively arid and dry climate in the Julian at the basal substage of Carnian to a high competence fluvial – lacustrine environment with presence of small, ephemeral and vegetated swamps or ponds along the flow path of the channels at the time of Carnian Pluvial Event from the end of Julian to Tuvanian and back again to fluvial deposition in the Norian (Dasgupta et al. 2017). The episodes of increased rainfall during the Carnian Pluvial Episode demarcated by increased frequency of sandstone deposition is intervened by seasonality as evident from the red mudrock alternations between sandstones. Similar climatic shifts are seen from the coeval Santa Maria to Caturrita formations of Brazil (Dal Corso et al. 2015). These shifts indicating a major variation of the hydrological regime in terrestrial depositional settings suggest an enhancement of hydrological cycle during the CPE. Recently, Lucas (2010) stated that the demise of metoposaurids in most parts of the world during the Carnian is related to the end of enhanced hydrological cycle at the dying phase of CPE. The disappearance of key herbivorous groups such as dicynodonts and rhynchosaurs of Carnian and their places taken up by giant sauropodomorphs seems to be linked to CPE which is not documented in India so far.

Also, the *Hyperodapedon* Assemblage Zone (HAZ) is characterized by the presence of rhynchosaur *Hyperodapedon* and is present in the lower part of the Ischigualasto Formation of



Argentina, the Lossiemouth Sandstone Formation of Scotland, and the Lower Maleri Formation of India (Langer et al. 2010). The HAZ is dated as late Carnian to early Norian, approx. 228–224 Ma by some authors (Benton et al. 2018; Brusatte et al. 2010; Ezcurra et al. 2017). Most metoposaurids in the Gondwana deposits are considered to be Carnian in age (Chakravorti & Sengupta 2019; Gee & Jasinski 2021; Sengupta 2002). The demise of the metoposaurids *Panthalosaurus maleriensis* (Chakravorti & Sengupta 2019) in India along with the demise of *Hyperodapedon* in both Late Triassic Maleri and Tiki Formation also points to the presence and effect of CPE in India. The demise of the metoposaurids left vacant niche to be occupied by the chigutisaurids in the Norian suggesting short lived aridity at post Carnian stage.

### The Effect of CPE on the Terrestrial Ecosystem of Maleri and Tiki Formations

The Carnian of Argentina has its age radiometrically constrained between  $231.4 \pm 0.3$  and  $225.9 \pm 0.9$  Ma (Martínez et al. 2016) and similar reports are present from Santa Maria and Caturrita Formations of Brazil ( $233.2 \pm 0.7$  and  $225.4 \pm 0.4$  Ma) (Langer et al. 2018). The onset of CPE is well constrained in stratigraphic sections like the Southern Alps of Italy, Northern Calcareous Alps of Austria, Transdanubian Range of Hungary, and the Nanpanjiang Basin of the South China block and is placed at the substages Julian 1 – Julian 2 boundary of the Carnian (Gallet et al. 1994). Due to the lack of any radiometric dating, Late Triassic Maleri and Tiki Formations are poorly constrained and pose difficulty in global correlation, their correlation based only on available fauna. The CPE has always been dated as mid Carnian (Ruffell et al. 2016) but this is not a unanimous viewpoint. Italian Dolomites occur between the Aonoides/Austriacum interval (about Julian) and the base of the Subbullatus Zone (Tuvalian), dated at 234–232 Ma (Dal Corso et al. 2015; Roghi et al. 2010). Further constraint has been documented in borehole successions of southwest UK, which indicate a maximum duration of 1.09 MYA (Miller et al. 2017). The precise

radiometric dating to constrain the Maleri and Tiki Formations and to denote the beginning of CPE in India will shed further light on pattern of faunal diversification post CPE event in the subcontinent and help in the global stratigraphic correlation. A continental carbon isotope record in southwest England shows multiple carbon cycle perturbations during CPE (Miller et al. 2017). The CPE is not only the time interval of increased humidity but also a major carbon perturbation. Unfortunately, no carbon isotope data is noted from the Maleri and the Tiki Formations of India.

## Conclusion

1. In the current work the skull of a new species of chigutisarid amphibian *Compsocerops tikiensis* from the Late Triassic Tiki Formation of the Rewa Gondwana Basin has been described in detail. The presence of chigutisaurid *Compsocerops tikiensis* in the Upper part of the Tiki Formation is the first evidence of the Norian chigutisaurid amphibian from the said Formation and is important for correlation of the Late Triassic basins worldwide.
2. Along with the extinction of the rhyncosaurs and *Parasuchus* (primitive phytosaur), chiniquodontids (cynodonts), the Carnian – Norian Extinction Event (CNEE) also caused the extinction of the metoposaurids in India. Chigutisaurids appeared in Norian and India is the only place which accommodates definite metoposaurids and chigutisaurids within the same formations (the Late Triassic Maleri and Tiki Formations) the former being replaced by the latter. Incidentally, among the phytosaurs, the *Parasuchus* of Lower Maleri fauna is replaced by the *Leptosuchus* like forms of Upper Maleri and *Volcanosuchus statisticae* in upper part of Tiki Formation.
3. The post CNEE empty niche left by the metoposaurids in the Late Triassic Gondwana deposits of India (controversially Brazil as well, see (Dias-da-Silva et al. 2011)) were

occupied by the chigutisaurids in the Norian. The availability of phytosaur teeth along with *C. tikiensis* only indicated their co-existence in the same aquatic niche but does not necessarily point towards any prey-predatory relationship between the phytosaurids and the chigutisaurids. However, detailed studies on histology and growth pattern of the chigutisaurids might shed light on the gigantism of these amphibious animals in the post CNEE and recovery of the temnospondyls.

4. The presence of both metoposaurids and chigutisaurids and the faunal turnover from the Carnian to the Norian along with the extinction of the rhynchosaurs (*Hyperodapedon*) and *Parasuchus* in the Carnian of both the Late Triassic Maleri and Tiki Formation and the presence of prosauropods in the Upper Maleri Formation and undescribed dinosauriformes including theropod-like forms (Bandyopadhyay & Ray 2020) sheds light and documents for the first time the existence and effect of the Carnian Pluvial Episode in India.

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**Table 1**(on next page)

Vertebrate fossil assemblage of the Late Triassic Tiki Formation

Vertebrate fossil assemblage of the Late Triassic Tiki Formation of the Rewa Basin, India  
(modified after Bandopadhyay and Ray 2020).



1 Table 1

Order/Family	Genus and Species	Order/Family	Genus and Species
<b>CHONDRICHTHYES</b>		<b>DIAPSIDA</b>	
Lonchididae	<i>Lonchidion estesi</i>	Phytosauria	<i>Volcanosuchus statisticae(?) leptosuchomorph</i>
	<i>Lonchiodon incumbens</i>	Rhynchosauria	<i>Hyperodapedon tikiensis</i>
	<i>Pristisodus tikiensis</i>	Rauisuchidae	<i>Tikisuchus romeri</i>
Xenacanthidae	<i>Mooreodontus indicus</i>	Rhynchocephalia	<i>Undescribed</i>
	<i>Mooreodontus jaini</i>	Archosauriformes	<i>Galtonia sp., Protecovasaurus sp., other intermediate forms</i>
	<i>Tikiodontus asymmetricus</i>	Dinosauriformes	<i>Undescribed Theropod-like (?) forms</i>
<b>OSTEICHTHYES</b>		Aetosauria	<i>Undescribed</i>
Ptychocerato-dontidae	<i>Ceratodus sp.</i>	<b>SYNAPSIDA</b>	
	<i>Ptychoceratodus oldhami</i>	Cynodontia	<i>Ruberodon roychowdhurii</i>
Gnathorhizidae	<i>Gnathorhiza sp.</i>	Mammaliaformes	<i>Tikitherium copei</i>
Actinopterygii	<i>Undescribed</i>		<i>Gondwanadon tapani</i>
<b>AMPHIBIA</b>			
Metoposauridae	<i>Panthesaurus maleriensis</i>		
Chigutisauridae	<i>Compsocerops tikiensis</i>		

2

3 Vertebrate fossil assemblage of the Late Triassic Tiki Formation of the Rewa Basin, India  
 4 (modified after Bandopadhyay and Ray 2020).

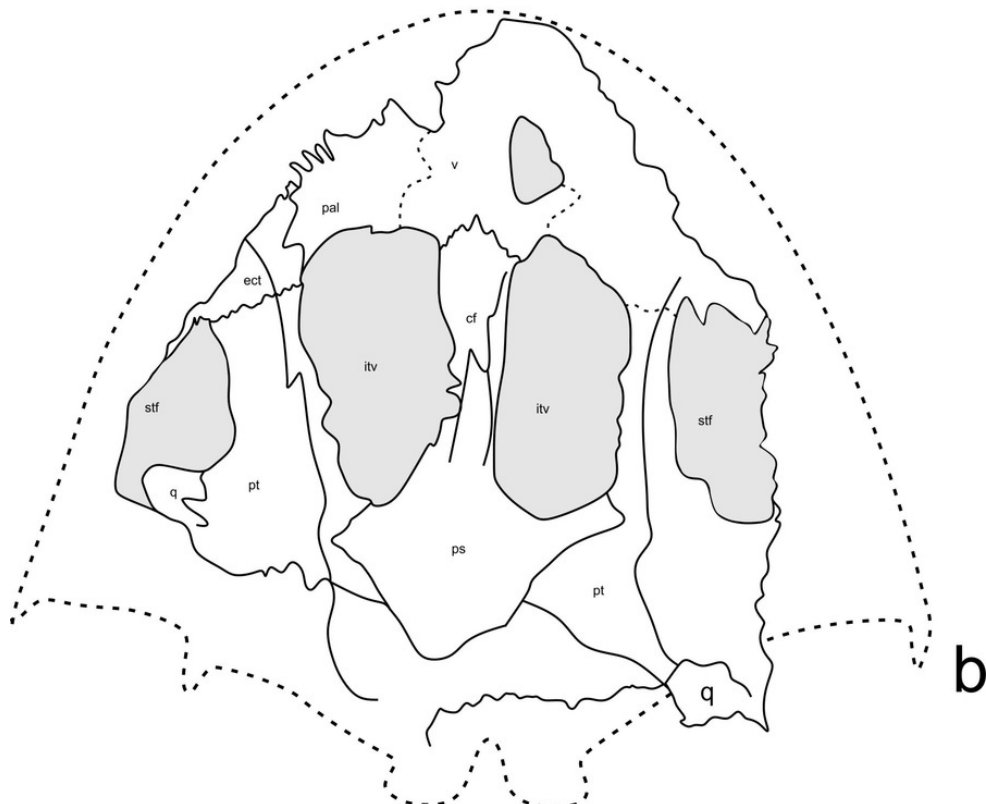
# Figure 1

Palatal surface of the skull photograph (RH01/Pal/CHQ/Tiki/15) Kumar and Sharma 2019, recreated with permission from the editor of the Palaeontological Society of India.

a. Shows the field photograph published in Kumar and Sharma (2019). b. is the line drawing showing the disposition of the bones in the palatal surface of the skull published in Kumar and Sharma (2019). The abbreviation stated in the figure are as follows: cf = cultriform process, ect= ectopterygoid, itv = interpterygoid vacuity, pal= palatine, ps = parasphenoid, q = quadrate, stf = subtemporal foramen, v = vomer.



**a**

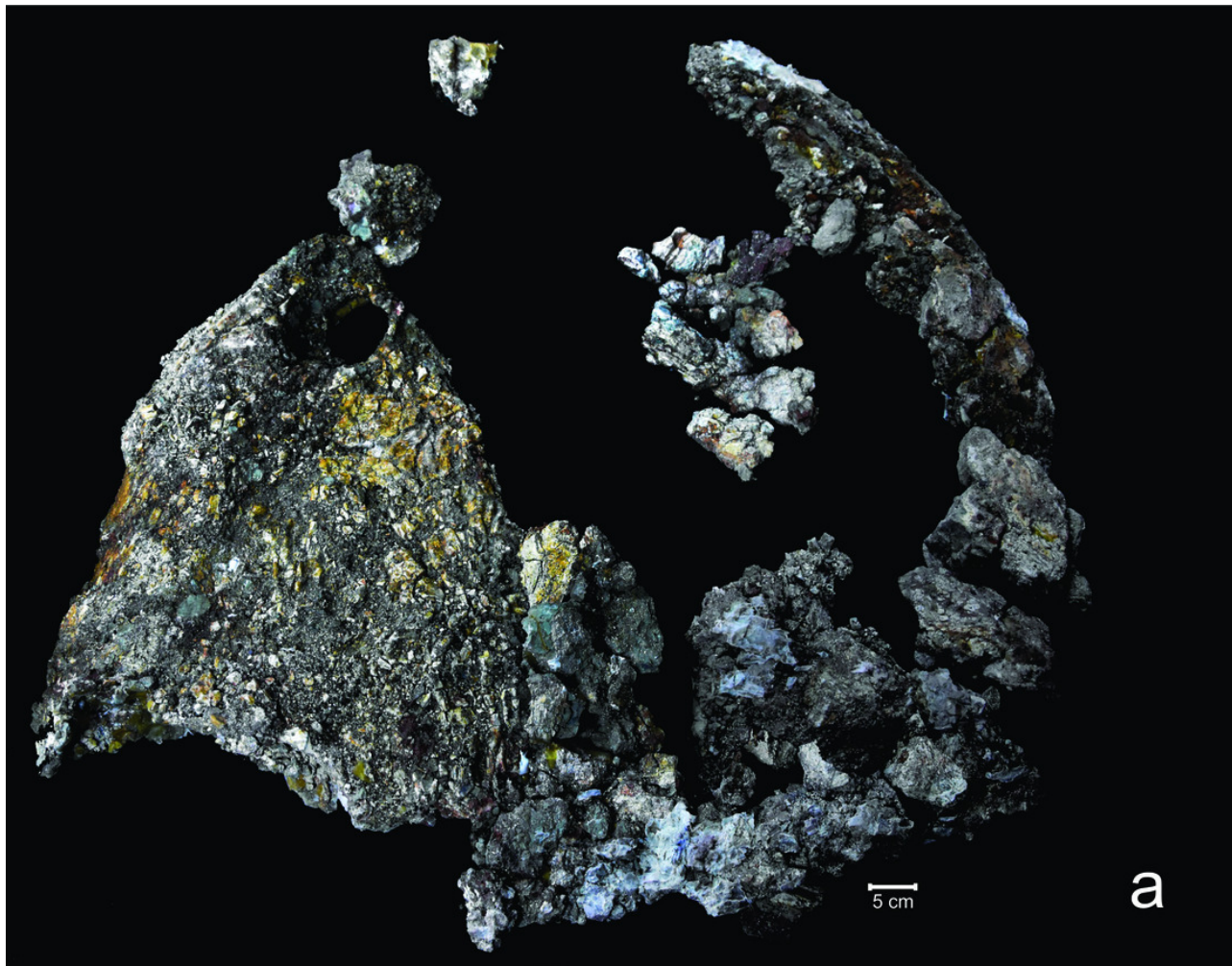


**b**

# Figure 2

Dorsal surface of the skull roof of ISI A 202 *Compsoceroops tikiensis*.

a. Reconstructed photograph of the dorsal surface of the skull roof of ISI A 202. Scale bar = 5 cm. b. Line drawing showing the disposition of the preserved bones in the dorsal part of the skull roof in ISI A 202. The abbreviation stated in the figure are as follows: j=jugal, mx=maxilla, n=nasal, p = parietal, po = postorbital, pof = postfrontal, pp = postparietal, prf = prefrontal, qj = quadratojugal, sq = squamosal, st = supratemporal, t = tabular. Scale bar = 5 cm.

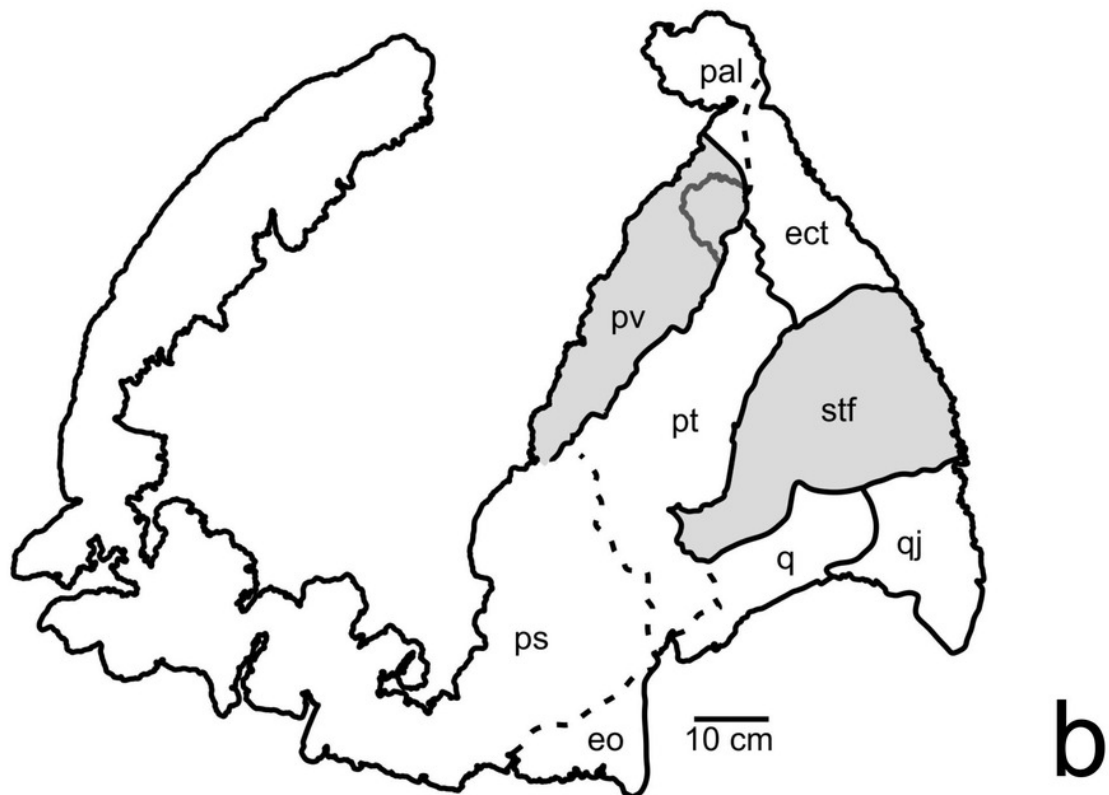
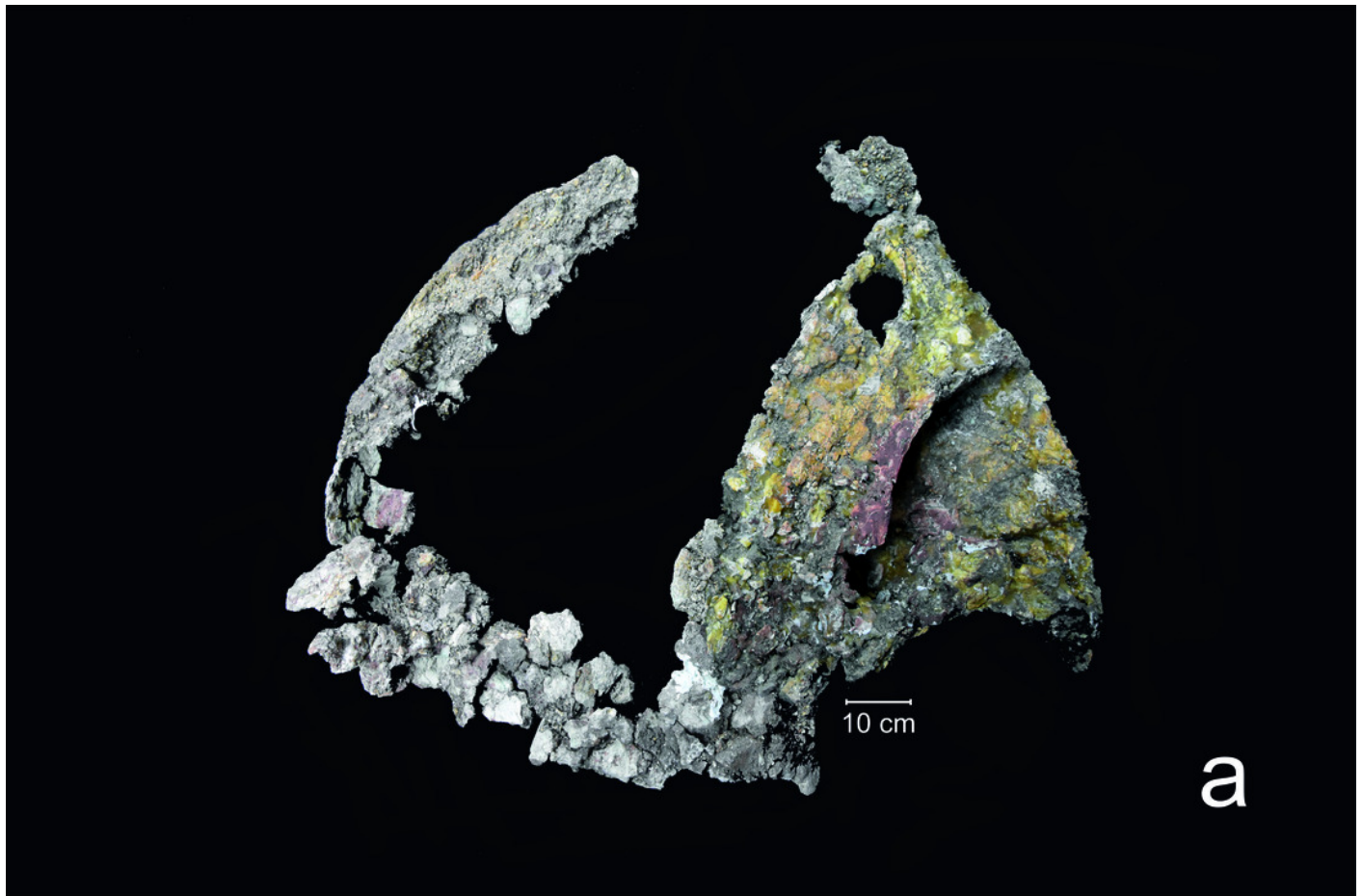


# Figure 3

Palatal surface of the skull of ISI A 202 *Compsocerops tikiensis*.

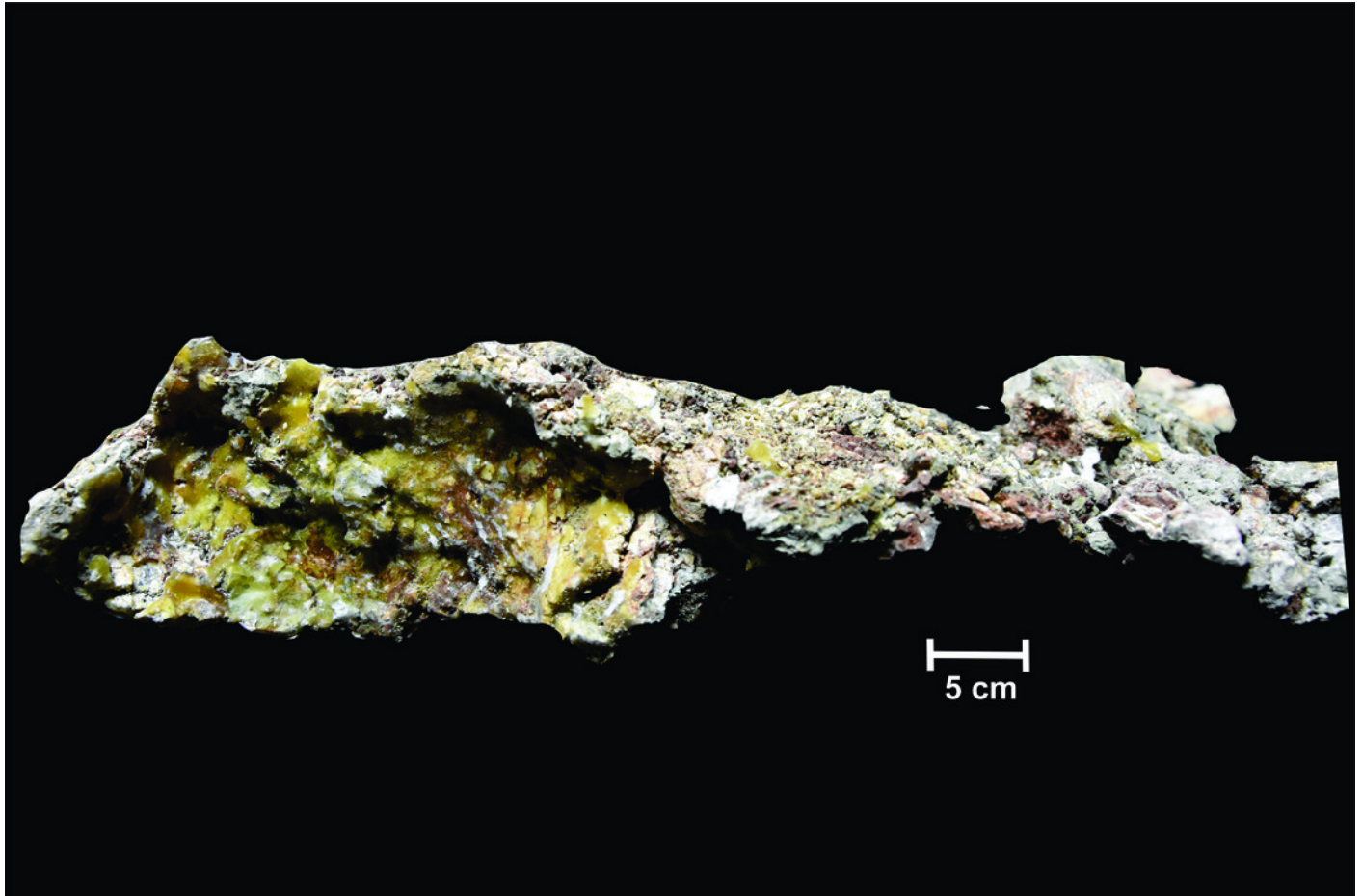
a. Reconstructed photograph of the palatal surface of the skull of ISI A 202. Scale bar = 10 cm. b. Line drawing showing the disposition of the preserved bones in the dorsal part of the skull roof in ISI A 202. The abbreviation stated in the figure are as follows: ect = ectopterygoid, eo = eoccipital, pal = palatine, ps= parasphenoid, pt= pterygoid, pv= palatine vacuity, q= quadrate, stf = subtemporal foramen.





# Figure 4

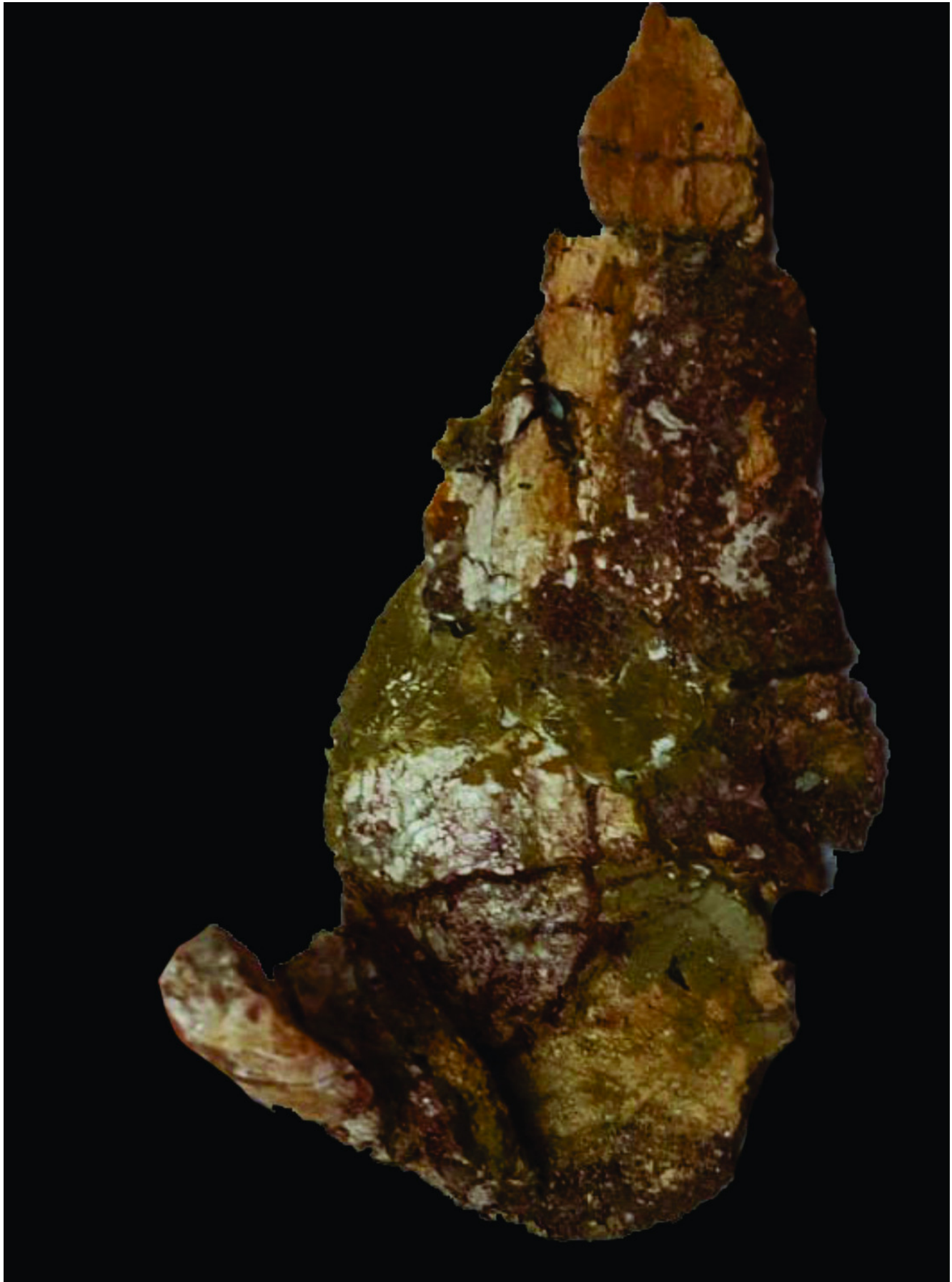
The poorly preserved occiput of ISI A 202 *Compsoceroops tikiensis*.





# Figure 5

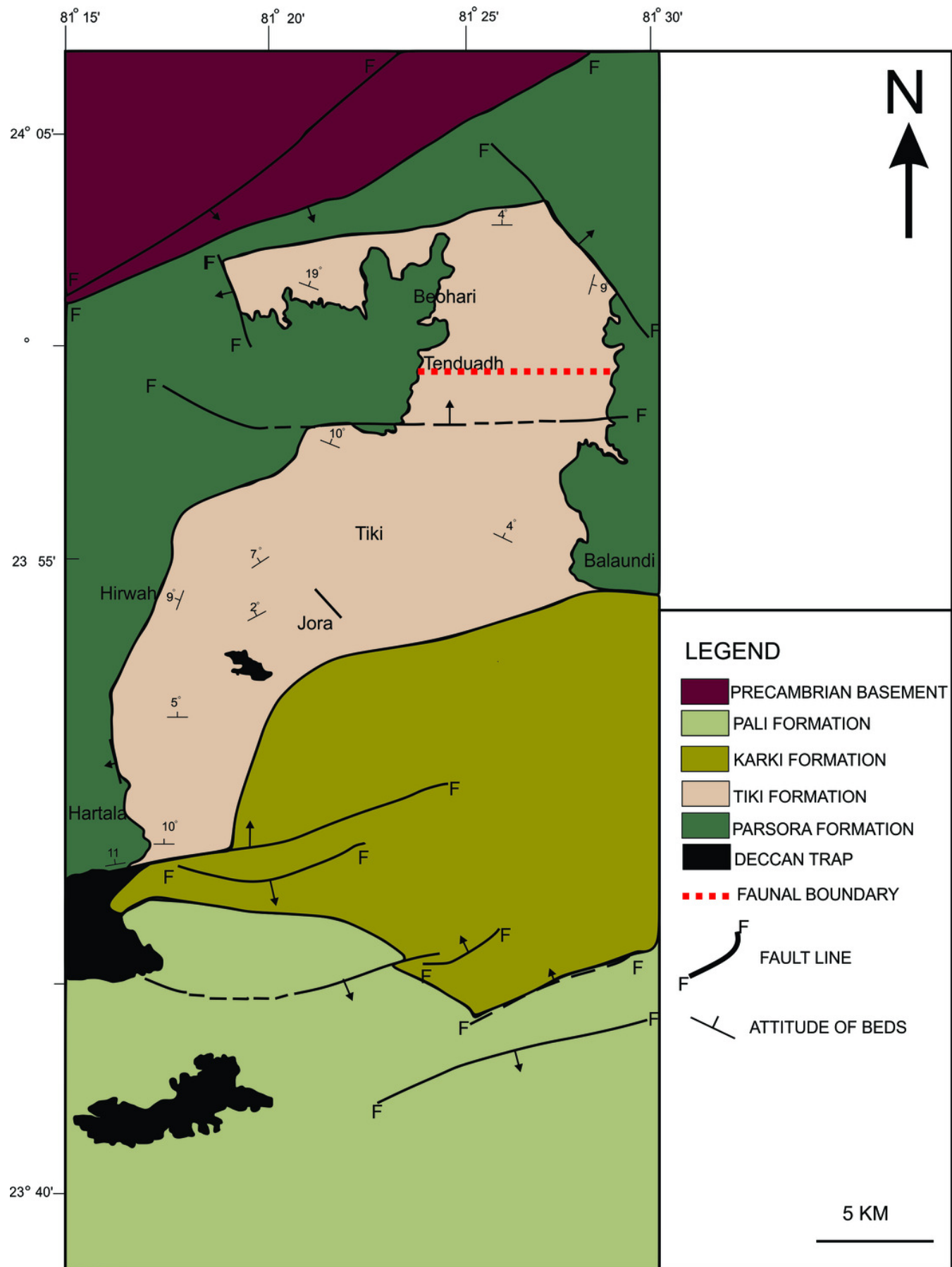
Poorly preserved clavicle of ISI A 202 *Compsoceroops tikiensis*.



# Figure 6

Geological Map showing the Tiki Formation, Rewa Basin, India.

Geological map of the Tiki Formation, Rewa Basin, India, modified after Mukherjee et al. (2012). The red dotted line shows the hypothetical faunal boundary.





# Figure 7

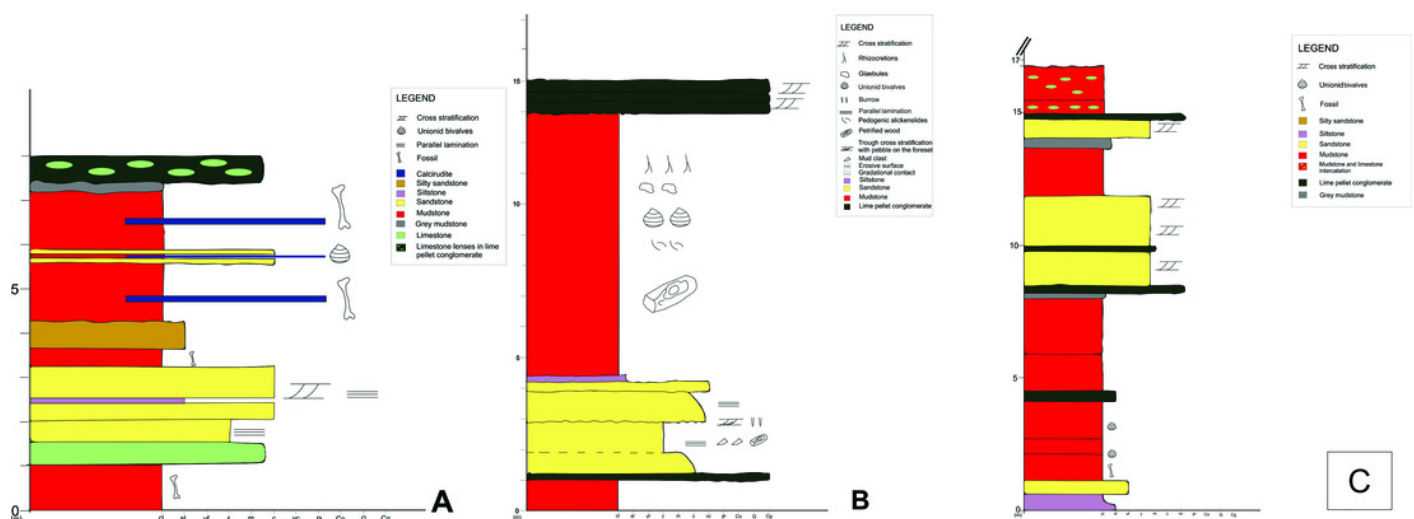
Field photograph showing the exposure of *Compsocerops tikiensis* embedded in mudstone in the Upper part of the Tiki Formation.



# Figure 8

Lithologs of the Tiki Formation.

a. Litholog in the Jora Nala Section in the Lower Tiki Formation. b. Litholog in the Lower part of Tiki Formation modified after Mukherjee et al. (2012). c. Litholog of the Tiki Formation modified after Kumar and Sharma (2019).





# Figure 9

Field photograph of the sand-mud alternation in the Tiki Formation near Tenduadh.

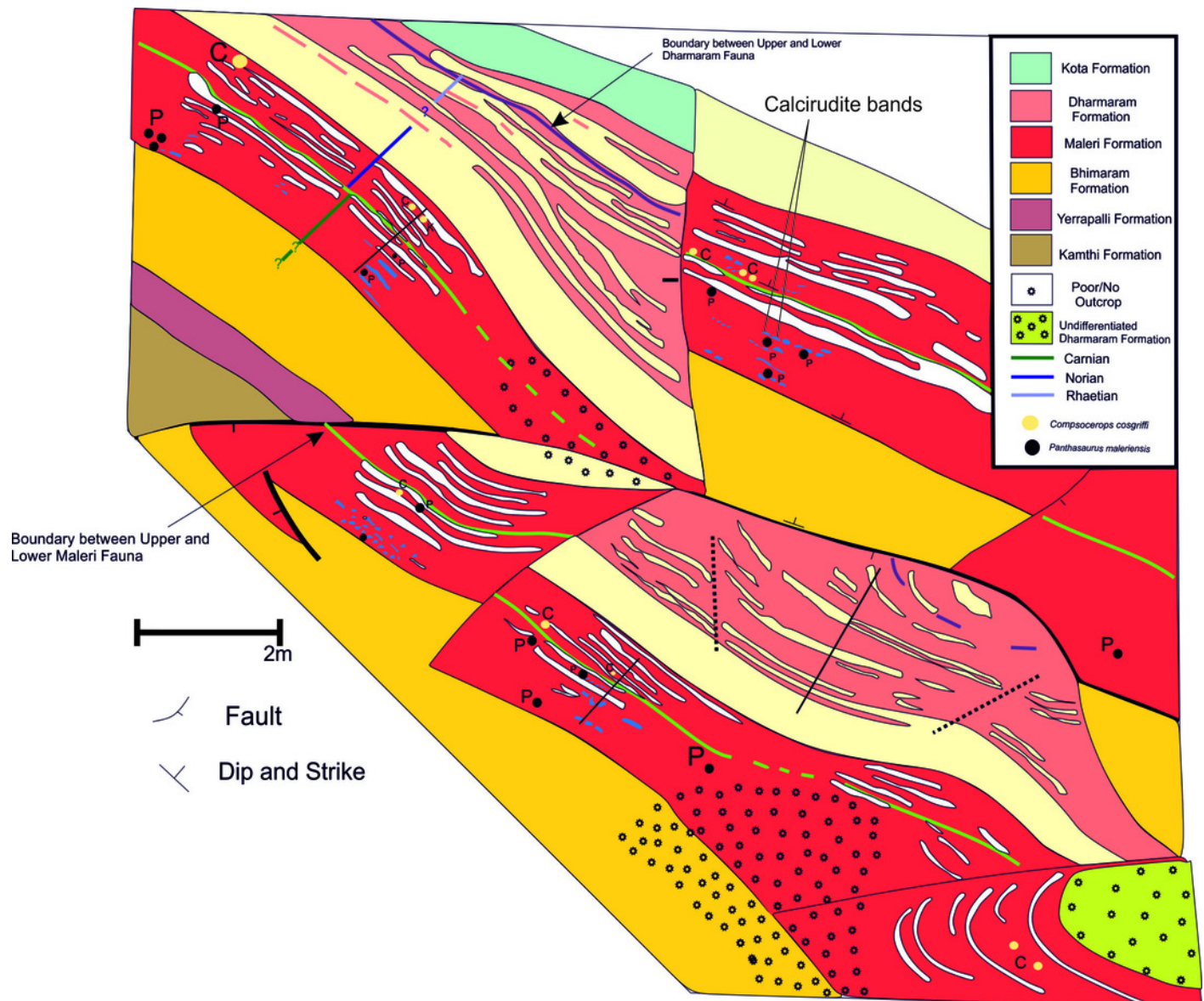
a. Trough cross- bedded sandstone in the Tiki Formation b. Extensive mudstone in the Tiki Formation.



# Figure 10

Geological map of the Maleri Formation, Pranhita-Godavari Valley Basin, India

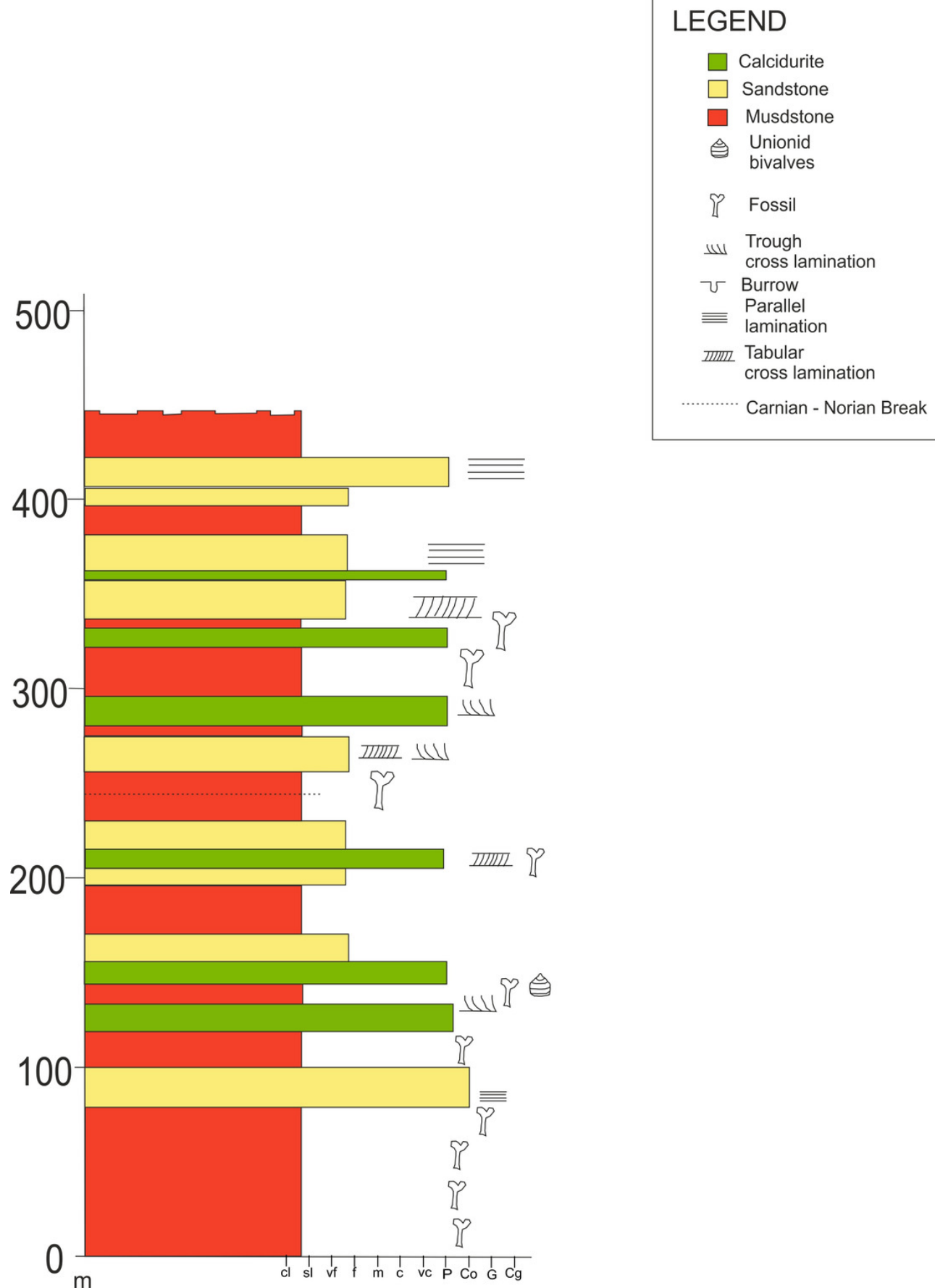
Geological map modified after Kutty and Sengupta (1989), Dasgupta et al. (2017) showing the sand- mud alternations in the Maleri Formation, Pranhita- Godavari Valley Basin, India. The green line represents the faunal boundary that occurred due to the faunal turnover from the Carnian Lower Maleri to the Norian Upper Maleri Formation.





# Figure 11

Litholog of the Maleri Formation modified after Kutty and Sengupta (1989).



# Figure 12

Field photograph showing the abundance of red mudstone in the basal part of the Maleri Formation.

