

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. Chigutisaurids are now known to occur in Australia's Early and Late Triassic, the Late Triassic in India, Argentina, and Brazil, the Jurassic of South Africa and Australia, and the Cretaceous of Australia. In India, the first appearance of chigutisaurids marks the Carnian - middle Carnian / Norian Boundary. This work also attempts to correlate, again for the first time, the advent of chigutisaurids and the occurrence of Carnian Pluvial Episodes (CPE) in the Late Triassic Maleri and Tiki Formation of Central India. The new specimen belongs to the genus *Compsocerops* 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. It has the presence of an inward curved process of the quadratojugal as opposed to the straight downward trending process of the quadratojugal, the presence of vomerine foramen, shorter and wider interpterygoid vacuities, wider subtemporal vacuities, the base of the interpterygoid vacuities at the same level with the base of the subtemporal vacuity, it proves that the Tiki Formation is coeval with the Lower Maleri Formation and a part of Upper Maleri.

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11 **Abstract**

12 A new, partially preserved skull of chigutisaurid amphibian (temnospondyli) has been reported for
13 the first time from the Late Triassic Tiki Formation of India. Chigutisaurids are now known to
14 occur in Australia's Early and Late Triassic, the Late Triassic in India, Argentina, and Brazil, the
15 Jurassic of South Africa and Australia, and the Cretaceous of Australia. In India, the first
16 appearance of chigutisaurids marks the Carnian – middle Carnian / Norian Boundary. This work
17 also attempts to correlate, again for the first time, the advent of chigutisaurids and the occurrence
18 of Carnian Pluvial Episodes (CPE) in the Late Triassic Maleri and Tiki Formation of Central India.
19 The new specimen belongs to the genus *Compsocerops* prevalent in the Late Triassic Maleri
20 Formation occurring 700 km south. However, the chigutisaurid specimen recovered from the Tiki
21 Formation is a new species when compared to that of the Maleri Formation. It has the presence of
22 an inward curved process of the quadratojugal as opposed to the straight downward trending
23 process of the quadratojugal, the presence of vomerine foramen, shorter and wider interpterygoid
24 vacuities, wider subtemporal vacuities, the base of the interpterygoid vacuities at the same level

25 with the base of the subtemporal vacuity, it proves that the Tiki Formation is coeval with the Lower
26 Maleri Formation and a part of Upper Maleri.

27 Introduction

28 Temnospondyls are a very diverse and widespread group of extinct amphibians that thrived from
29 the Carboniferous to the Cretaceous reaching their peak in the Triassic ([Konietzko-Meier et al. 2018](#);
30 [Konietzko-Meier et al. 2019](#)). Capable of flourishing in both land and water in a variety of ecological
31 niches, the fossils of these extinct amphibians are found in almost all places from Antarctica in the
32 South to Greenland in the North, India being no exception ([Schoch et al. 2014](#)). The temnospondyl
33 fossils in India are found in various Gondwana deposits throughout the country ([Chakravorti &](#)
34 [Sengupta 2019](#); [Chowdhury 1965](#); [Sengupta 1995](#); [Sengupta 2002](#); [Tripathi 1969](#)). Chigutisaurids are by
35 far one of the most important temnospondyl amphibians having the longest temporal range
36 ([Marsicano 1999](#)) ranging from the Early Triassic to the Cretaceous ([DIAS-da-SILVA et al. 2012](#)).
37 However, the majority of them originated in the Upper Carnian to Lower Norian of the Late
38 Triassic Period. The family Chigutisauridae is much less diversified than the other temnospondyl
39 families. Falling within the superfamily Brachyopoidea which comprises parabolic, brevirostrine
40 skulled temnospondyls, Chigutisauridae forms a single monophyletic family in the phylogenetic
41 position ([Warren & Marsicano 2000](#)). The spatial and temporal distribution of the chigutisauridae is
42 schematically represented in Table -1 along with their general habitat ([Bandyopadhyay & Ray 2020b](#);
43 [Bonaparte 1975](#); [Cabrera 1944](#); [DIAS-da-SILVA et al. 2012](#); [Pledge 2013](#); [Rusconi 1949](#); [Rusconi 1951](#);
44 [Sengupta 1995](#); [Warren 1981](#); [Warren & Marsicano 2000](#)). The earliest origin of the family
45 chigutisauridae is *Keratobrachyops australis* in the Early Triassic of Australia ([Warren 1981](#)) with
46 the latest being *Koolasuchus cleelandi* ([Warren et al. 1997](#)) in the Cretaceous of Australia as well.

47 So far, the origin and diversification of chigutisaurids remain restricted only to the Gondwana
48 countries.

49 The Gondwana successions of India are exposed in four discrete basins coinciding with some of
50 the major river valleys throughout the Indian subcontinent ([Pascoe 1973](#); [Robinson 1970](#); [Veevers &](#)
51 [Tewari 1995](#)). Of these, the Late Triassic Maleri and the Tiki Formations of the Pranhita-Godavari
52 Valley Basin and the Son Valley Basin respectively are long known to be coeval ([Chatterjee 1974](#);
53 [Chatterjee & Roy-Chowdhury 1974](#); [Mukherjee & Ray 2014](#); [Robinson 1970](#)). Both Formations are
54 known for the metoposaurid *Panthatasaurus maleriensis* ([Arche & Lopez-Gomez 2014](#); [Chakravorti &](#)
55 [Sengupta 2019](#); [Sengupta 2002](#)). In the Late Triassic Maleri Formation *P. maleriensis* is thought to
56 be restricted within the Carnian and the chigutisaurids appear in the mid-Carnian to early Norian
57 ([Chakravorti & Sengupta 2019](#); [Sengupta 1995](#)). Though a considerable amount of work has been
58 done on the microvertebrates ([Bhat 2017](#); [Hussain 2018](#); [Ray et al. 2016a](#)) rhynchosaurs ([Mukherjee &](#)
59 [Ray 2012](#); [Mukherjee & Ray 2014](#)) and phytosaurs ([Datta et al. 2021a](#); [Datta et al. 2019a](#); [Datta et al.](#)
60 [2021b](#)) of the Tiki Formation; no comprehensive work has been done in the last decade on its
61 temnospondyl faunal contents. ([Chakravorti & Sengupta 2019](#)) in their taxonomic revision of the
62 Indian metoposaurids, included the metoposaurids of the Tiki Formation and grouped them into a
63 new genus *Panthatasaurus maleriensis* based on morphometric and phylogenetic approaches.
64 However, the biostratigraphic implications of the Tiki Formation based on its temnospondyl
65 contents have not been attempted so far, though, the taphonomic aspects of metoposaurids from
66 the Tiki Formation have been discussed by ([Rakshit & Ray 2020](#)). Also, to date, no chigutisaurid
67 remains were reported from the Late Triassic Tiki Formation though the same is widely prevalent
68 in the Late Triassic Maleri Formation ([Sengupta 1995](#)). Therefore, the finding of a chigutisaurid
69 amphibian from the Late Triassic Tiki Formation is very important in the context of correlating

70 the Late Triassic Maleri and Tiki Formation, India, and their position concerning global
71 biostratigraphic correlation. This paper will subsequently highlight a brief geological setting of the
72 Tiki Formation followed by the taxonomic status of chigutisaurids from the Tiki Formation and
73 subsequently its role in demarcating the Carnian Pluvial Episode in India.

74 *The Carnian Pluvial Episode – A Global Climatic Consequence*

75 The Carnian Pluvial Episode (CPE) can be defined as a geologically short-lived (234-232 Million
76 Years Ago) monsoonal period of extreme rainfall that brought about significant changes in several
77 depositional environments ([Arche & Lopez-Gomez 2014](#); [Dal Corso et al. 2015](#); [Furin et al. 2006](#);
78 [Schlager & Schöllnberger 1974](#); [Simms & Ruffell 1990](#)). The Carnian Pluvial Episode was a global
79 phenomenon. Geochemical data suggest that global warming involved environmental and biotic
80 changes. Radioisotopic ages coupled with biostratigraphic correlation suggest a possible link to
81 the eruption of the Wrangellia Large Igneous Province (LIP) ([Dal Corso et al. 2020](#)). CPE was a
82 significant (but previously neglected) time of extinction linked to the Carnian explosive
83 diversification of many key modern groups of plants and animals ([Dal Corso et al. 2020](#)). The CPE
84 marks a distinct change in the hydrological cycle during which the climate shifted from arid to
85 humid conditions and back again to arid conditions ([Bernardi et al. 2018](#)). It is represented by
86 remarkable enhancement of the hydrological cycle demarcated by four episodes of increased
87 rainfall indicated by diverse sedimentary and paleontological data, repeated Carbon Cycle
88 perturbations, evidenced by sharp negative C-isotope excursions, coincided with global
89 environmental changes and climate warming all of which suggest a cause-and-effect relationship
90 ([Dal Corso et al. 2015](#)).

91 The Carnian is the earliest part of the Late Triassic and its base or lower boundary is dated at
92 approximately 237 million years based on U-Pb radiometric dating of a single crystal zircon from
93 a tuff layer within a section having strong biostratigraphic constraints ([Dal Corso et al. 2015](#); [Dal](#)
94 [Corso et al. 2012](#); [Maron et al. 2019](#)). The upper boundary of the Carnian is constrained at
95 approximately 227 million years based on magnetostratigraphic correlations between the marine
96 successions of Tethys and the astrochronological time scale of the continental Newark Basin ([Kent](#)
97 [et al. 2017](#)). The Carnian is subdivided into Julian (Early Carnian) and Tuvanian (Late Carnian)
98 substages. The Julian – Tuvanian boundary occurs at approximately 233 million years ([Dal Corso et](#)
99 [al. 2015](#); [Kent et al. 2017](#)). The beginning of the onset of CPE is well defined from ammonoid,
100 conodont, and sporomorph biostratigraphic dating and is synchronous in several geological
101 settings. It coincides with the first appearance of the ammonoid genus *Austrotrachyceras* in the
102 Julian ([Dal Corso et al. 2020](#); [Dal Corso et al. 2012](#); [Roghi et al. 2010](#); [Simms & Ruffell 1990](#); [Sun et al.](#)
103 [2016](#)). However, the upper boundary or the end of CPE is poorly defined in most locations. It is
104 usually placed at the base or within the Tuvanian 2 based on sedimentological (e.g., end of
105 terrigenous sediment supply) and chemostratigraphic (last C-isotope excursion) evidence ([Dal](#)
106 [Corso et al. 2020](#); [Dal Corso et al. 2015](#); [Dal Corso et al. 2018](#)). The total duration of this pluvial episode
107 is variable. Cyclostratigraphy of marine successions of the South China Block and continental
108 successions of the Wessex Basin (United Kingdom) gives a duration of the CPE of approximately
109 1.2 ma but this is variable and longer than 1.6-1.7 million years as indicated by integrated
110 stratigraphy (biostratigraphy and magnetostratigraphy).

111 *Temnospondyl amphibians in the Carnian Pluvial Episode*

112 The CPE facilitated the Dinosaur Diversification Event (DDE) ([Bernardi et al. 2018](#)). However, the
113 role of CPE on the temnospondyls has not much been discussed barring a few papers ([Buffa et al.](#)

114 [2019](#); [Fortuny et al. 2019](#); [Gee & Jasinski 2021a](#); [Lucas 2020a](#)). The amphibious temnospondyls living
115 both on land and water were the most sensitive to the changes in climate. Two dominant groups
116 of temnospondyls, in this context, were the metoposaurids and the chigutisaurids. According to
117 [\(Fortuny et al. 2019\)](#) the gigantism of the metoposaurids might have been linked to the Carnian
118 Pluvial Episode. [\(Buffa et al. 2019\)](#) also stated that the diversification of the metoposaurids might
119 have been linked to the CPE and the post-CPE aridification led to the extinction of the
120 metoposaurids during the Rhaetian. [\(Gee & Jasinski 2021a\)](#) have also commented on the fact that
121 the physiological variation of the metoposauridae and their palaeoclimatic range also corroborates
122 a palaeo-environmental barrier. Finally, [\(Lucas 2020b\)](#) concluded that climate change that occurred
123 during CPE played an important part in the metoposaurid evolution. According to [\(Lucas 2020b\)](#),
124 Metoposaurids appeared during the CPE, attained their highest diversity and cosmopolitan
125 distribution during this time and had reduced diversity and showed endemism in the post-CPE
126 climate.

127 Thus, the presence of *Compsocerops* in both Maleri and Tiki Formation enhances the scope to
128 discuss the palaeoenvironment of these two Late Triassic basins in India and to compare the
129 possible reason for faunal turnover from Carnian to Norian concerning the amphibious
130 temnospondyls [\(Sengupta 1995\)](#).

131 Geological setting of the Tiki Formation and its comparison to the Maleri 132 Formation

133 The Tiki Formation named after the small village of Tiki in the district of Shahdol, Madhya
134 Pradesh has been an interest to scientists for decades. Reports on the geology and palaeontology
135 of the Tiki Formation date back to as early as 1877 when [\(Hughes 1877\)](#) noticed reptilian fossils
136 near this village. [\(Cotter 1917\)](#) noticed several other such fossils and finally [\(Fox 1931\)](#) formally

137 designated the area as the “Tiki stage”. ([Aiyengar 1937](#)) first divided the “Tiki stage” into
138 lithostratigraphic units viz. the lower unit being fossiliferous and composed dominantly of red and
139 green mudstones, proportionately lesser number of sandstones and mud-galls while the upper unit
140 is composed of ferruginous sandstones and shales. ([Robinson 1970](#)) in her memoir kept the Tiki
141 Formation to be coeval with the Late Triassic Maleri Formation. However, ([Dutta & Ghosh 1993](#))
142 did not recognize the separate entity of the Tiki Formation and placed Tiki rocks in the upper part
143 of the Pali Formation forming the “Pali-Tiki Formation”. ([Roychowdhury et al. 1975](#)) based on the
144 megafloora assemblage noted the age of the Nidpur beds is Anisian and separated the upper part of
145 the Tiki Formation to be Carnian – Rhaetian in age. ([Maheshwari et al. 1976](#)) separated the Tiki
146 Formation to be a separate entity (including the Nidpur beds) and based on the mega flora and
147 faunal assemblages suggested the age of the Tiki (including Nidpur beds) Formation to be ranging
148 from Anisian to Norian with a possible extension to Rhaetian. ([Mukherjee et al. 2012](#)) revised the
149 stratigraphy of the Rewa Basin and put the Tiki Formation with the coeval Carnian Lower Maleri
150 Formation. ([Ray et al. 2016b](#)) in the study of vertebrate faunal assemblage of the Tiki formation
151 also suggested Tiki Formation be of Carnian in age but they narrowed the range to Otischalkian to
152 early Adamanian. The common conclusions of all this literature are that the Late Triassic Tiki
153 Formation is dominantly Carnian and its fauna can be correlated with the Lower Maleri fauna. So
154 far, no evidence of a Norian age was assigned to any part of the Tiki Formation. As stated earlier,
155 based on the faunal pieces of evidence and correlating it with the Late Triassic Maleri Formation
156 of the Pranhita – Godavari valley a Carnian age was assigned to the Tiki Formation ([Dutta & Ghosh](#)
157 [1993](#); [Kutty et al. 1987](#); [SENGUPTA 1992](#)). Henceforth, through the Decades, the Tiki formation was
158 considered to be coeval with the Carnian Maleri Formation ([Mukhopadhyay et al. 2010](#); [SENGUPTA](#)
159 [1992](#); [Veevers & Tewari 1995](#)). Only recently, ([Datta et al. 2021b](#)) while describing a new phytosaur

160 from the Tiki Formation, commented that the age of the Tiki Formation may range from Carnian
161 to Early/Middle Norian.

162 To date, the faunal assemblage of the Tiki Formation includes fishes belonging to the family
163 Ceratodontidae, Hybodontidae and new undescribed forms of Xenacanthidae ([Ray et al. 2016a](#)),
164 temnospondyl amphibians belonging to Metoposauridae; reptilian belonging to families
165 Rhynchosauridae, Rauisuchidae, Acrodonta, basal Saurischia, Dromatheridae, and
166 Traversodontidae. Mammaliaformes are also reported from the Tiki Formation (Tables 2a and 2b)
167 ([Bandyopadhyay & Ray 2020b](#); [Ray et al. 2016a](#)).

168 The appearance of chigutisaurids in India is noted with the demise of the metoposaurs,
169 rhynchosaur, and primitive phytosaurs. Prosauropods, large in size also appeared during that time
170 ([Novas et al. 2010](#)). These faunal turnovers were thought to demarcate India's Carnian – Norian
171 boundary ([Datta et al. 2021b](#)). However, recent signatures ([Dal Corso et al. 2015](#)) of the pluvial event
172 and its role in extinction might shift this boundary to Carnian – mid-Carnian/Norian.

173 The Maleri Formation starts with a 250-meter-thick mudstone ([Dasgupta et al. 2017](#); [Kutty &](#)
174 [Sengupta 1989](#)). At the top of the mudstone, a sandy zone initiates the sand–mud alternations of
175 Upper Maleri ([Kutty & Sengupta 1989](#)). This sandy zone contains a maximum number of
176 rhynchosaur fossils, abundant metoposaurids, and unionids. The chigutisaurids in Maleri appear
177 just above this sandy zone ([Sengupta 1995](#)) and no rhynchosaur or metoposaurids are known from
178 that level (or above that). The occurrence of chigutisaurids in upper part of Tiki Formation is also
179 restricted within a sandy zone which do not contain metoposaurids or rhynchosaur. Unionids are
180 also present there but in lesser abundance than Maleri. Phytosaur teeth are also present. This sandy
181 horizon noticed in Maleri and Tiki has been stratigraphically placed below the Carnian – mid-
182 Carnian/ Norian boundary and may indicate the Carnian Pluvial Episodes (CPE) in India.

183 **Materials used with an overview of their preservation and methods**

184 The new skull material along with the clavicle (ISI A 202) excavated by the authors and the
185 specimen RH01/Pal/CHQ/Tiki/15 previously described as metoposaurid ([Kumar & Sharma 2019](#))
186 has been studied in detail and referred to in this paper. The map of the temnospondyl-bearing
187 localities of the Tiki Formation has been modified here with faunal boundaries (hypothetical faunal
188 boundary demarcated in a red dotted line) after ([Mukherjee & Ray 2012](#)) (Fig: 1). The temnospondyl
189 bearing (metoposaurid and chigutisaurid) localities of the Maleri Formation have also been
190 extensively mapped and modified after ([Dasgupta et al. 2017](#); [Kutty & Sengupta 1989](#)) (Fig: 2). Some
191 distinct sections have been logged in the Tiki Formation and has been compared with the existing
192 and modified logs of the Late Triassic Tiki and Maleri Formation.

193 **Preservation of specimen ISI A 202** - The skull along with a fragmentary clavicle, ISI A 202, is
194 poorly preserved (Figs: 3,4,5,6). Only the left half of the skull is preserved and the specimen is
195 heavily eroded. Thus, the ornaments are not well observed in all the areas. The upper part of the
196 parietal and postfrontal have coarse ridges and grooves preserved in them. The skull, its fragments
197 and the clavicle, all have been excavated from the same point in the location and were present
198 together with the same individual as the skull.

199 **Preservation of specimen RH01/Pal/CHQ/Tiki/15-**

200 Only the picture of the palate published as *Metoposaurus* in the paper ([Kumar & Sharma 2019](#))(Fig:
201 7) could be studied. As mentioned in the paper ([Kumar & Sharma 2019](#)) the material could not be
202 excavated from the field. The photograph of the said publication was reproduced with permission
203 of the journal editor and a higher resolution image was reproduced for better clarity and study. The

204 palate is dorsoventrally elongated and slightly sheared. The edges of the palate are not well
205 preserved.

206 The new specimens with ISI numbers, ISI A 202 and the published specimen of ([Kumar & Sharma](#)
207 [2019](#)) RH01/Pal/CHQ/Tiki/15 were recovered from mudrocks at a distance of about 100 meters
208 from each other from the village of Tenduadh in the Late Triassic Tiki Formation. Thus, ISI A 202
209 and RH01/Pal/CHQ/Tiki/15 (previously published by ([Kumar & Sharma 2019](#)) as metoposaurid) are
210 now the two chigutisaurid individuals that are being reported for the first time from the Tiki
211 Formation.

212 The electronic version of this article in Portable Document Format (PDF) will represent a
213 published work according to the International Commission on Zoological Nomenclature (ICZN),
214 and hence the new names contained in the electronic version are effectively published under that
215 Code from the electronic edition alone. This published work and the nomenclatural acts it contains
216 have been registered in ZooBank, the online registration system for the ICZN. The ZooBank
217 LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through
218 any standard web browser by appending the LSID to the prefix <http://zoobank.org/>. The LSID for
219 this publication is [urn:lsid:zoobank.org:pub:1B45D1E1-9FFE-421D-8060-4174334A7EF4](http://zoobank.org/pub:1B45D1E1-9FFE-421D-8060-4174334A7EF4). The
220 online version of this work is archived and available from the following digital repositories: PeerJ,
221 PubMed Central SCIE, and CLOCKSS.

222 Chigutisauridae from the Tiki Formation

223 Systematic Palaeontology

224 Temnospondyli ([von Zittel 1887](#))

225 Stereospondyli [Zittel 1888](#)

226 Chigutisauridae ([Rusconi 1951](#))

227 *Compsocerops* ([Sengupta 1995](#))

228 *Compsocerops tikiensis* sp. nov. (ISI A 202/1, ISI A 202/2, ISI A 202/3, ISI A 202/4, and ISI A
229 202/5, RH01/Pal/CHQ/Tiki/15) (Fig: 3)

230 **Type material:** ISI A 202/1 which comprises the left half of a skull roof, ISI A 202/2 – a
231 nearly complete clavicle and ISI A 202/3, ISI A 202/4, and ISI A 202/5 – broken parts of the skull
232 are the holotype. The holotype materials are housed in Geological Studies Unit, Indian Statistical
233 Institute, Kolkata, India (Fig: 3).

234 **Paratypes:** ISI A 202/2, ISI A 202/3, ISI A 202/4 and ISI A 202/5, RH01/Pal/CHQ/Tiki/15.

235 **Referred material:** A palate (RH01/Pal/CHQ/Tiki/15) previously assigned to a
236 metoposaurid by (Kumar & Sharma 2019) has been referred (Fig: 7). The parabolic skull outline,
237 vaulted pterygoid, shape and proportion of the interpterygoid vacuities, wide and folded palatine
238 ramus of the pterygoid, and comparatively narrow cultriform process of the parasphenoid in
239 RH01/Pal/CHQ/Tiki/15 indicate that it is not a metoposaurid. The cultriform process is wider than
240 *Compsocerops cosgriffi* but narrower than any of the metoposaurids. This palate is comparatively
241 well preserved and bears definite characteristics of a chigutisaur as it appears from the field
242 photograph (Fig: 7). Only the photograph of the palate is available for study.

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

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

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

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

266 **Description and comparative anatomy**

267 *The skull roof* (Fig: 3)

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

269 The skull roof is parabolic in shape with a broad and concave posterior part of the skull table. Even
270 though the anterior part of the skull roof is mostly broken, a major portion of the left orbit is
271 preserved. The orbit is subcircular in shape and bordered by the prefrontal, jugal, postfrontal and
272 postorbital. The orbit is located in the anterior half of the skull and is laterally placed. The posterior
273 and posterolateral part of the left external nares is also preserved. It can be understood from the
274 posterior outline of the external nares that they are oval. The external nares are located very close
275 to the anterior border of the skull roof. The posterior part of the external nares is thick and raised.
276 This character is noted in chigutisaurids and is found in *Pelorocephalus tenax* ([Marsicano 1999](#))
277 and *Compsocerops cosgriffi* ([Sengupta 1995](#)). The supraorbital sensory canal in the region of the
278 naris is unusually deep around the posterolateral border of the naris which is responsible for the
279 thick and raised posterior part of the naris in the ISI A 202. This characteristic feature has also
280 been noted in *Compsocerops cosgriffi* ([Sengupta 1995](#)) where anteriorly the naris is flushed with
281 the skull roof. The entire disposition of the sensory sulci is not well preserved in the specimen.
282 Apart from the supraorbital sulcus, the presence of postorbital dermal sensory sulcus through the
283 postfrontal can be recognized by the deep continuous canal like structure in these two bones. The
284 infraorbital sulcus is visible in the maxilla but gradually becomes less prominent as it enters the
285 jugal to form the jugal lateral dermal sensory sulcus. Just like other comparable chigutisaurids
286 like *Keratobrachyops australis* ([Warren 1981](#)), *Siderops kehli* ([Warren & Hutchinson 1983](#)),
287 *Pelorocephalus tenax* ([Marsicano 1999](#); [Rusconi 1949](#)), *Compsocerops cosgriffi* ([Sengupta 1995](#)) the
288 lacrimal is absent in ISI A 202 and the maxilla enters the border of the external nares. However,
289 the anterior part of the skull is fragmentary and heavily eroded. The better-preserved left side of
290 the dorsal part of the skull roof consists of partially preserved prefrontal, postfrontal, postorbital
291 and supratemporal. The squamosal is broken at the posterior part, and parietal, postparietal,

292 tabular, jugal and quadratojugals are also partially preserved. The surfaces of the bones are eroded
293 in most places and ornamentations are poorly preserved. The parietal is comparatively large,
294 rectangular and broken along the midline. Coarse ridges and grooves can be recognized from the
295 anterior part of the parietal. Just as in *Compsocerops* the postparietal of ISI A 202 (Fig: 3) is much
296 shorter in length than the parietal. The pineal foramen is not preserved in the parietal. The suture
297 of the postparietal with the tabular is obliterated. The postparietal is broken and eroded along the
298 midline and at its posterior part in the region of the postparietal horn. The postparietal horn is
299 broken in ISI A 202 (Fig: 3). However, there is clear evidence that the horns exist. Postparietal
300 horns are the most unambiguous synapomorphy of *Compsocerops*. It is preserved in *C. cosgriffi*
301 ([Sengupta 1995](#)), *C. sp.* ([DIAS-da-SILVA et al. 2012](#)) and *C. tikiensis* sp. nov. These horns are not
302 preserved in any other chigutisaur (the relevant area is not preserved in *Siderops* ([Warren &](#)
303 [Hutchinson 1983](#)) and *Koolasuchus* ([Warren et al. 1997](#)). The tabular is most likely to be in contact
304 with the parietal though that part is not very well preserved. The broad tabular–parietal contact is
305 considered to be a diagnostic character of *Compsocerops* ([Sengupta 1995](#)). The tabular horn is
306 broken. This post-quadratojugal process is robust and despite the very poor preservation of the
307 skull in general, the posterior quadratojugal process is well preserved. The shapes and sutural
308 patterns of the posterior left side of the skull are very similar to *Compsocerops cosgriffi*.

309 *The Palate* (Fig: 4)

310 Kumar and Sharma 2019, (Fig: 7) described the palate (RH01/Pal/CHQ/Tiki/15) as a metoposaurid
311 palate (Fig:7). However, no detailed osteological description or identifying characters were
312 described by the authors as to why the specimen was identified to be a metoposaurid. The authors
313 only described the palate to be the ‘dorsal’ part of a metoposaurid as it has conical teeth present
314 on the anterior part. However, this description is vague and of no taxonomical significance

315 whatsoever as all temnospondyls have conical teeth and both chigutisaurids and metoposaurids
316 have teeth and tusks in the anterior part of the skulls. Again, dentition restricted to the anterior
317 margin of the skull is a characteristic of all temnospondyls with parabolic skulls. Additionally,
318 ([Kumar & Sharma 2019](#)) grouped the palate collected from the village of Tenduadh with the
319 specimens of metoposaurid clavicle collected from the village of Jora. This grouping is not viable
320 as the two villages are approximately 12 kilometres apart from each other and there is a probability
321 that these two villages might be parts of the Upper and Lower parts of the Tiki Formation and may
322 even be of different ages as discussed later. The specimen, as said in ([Kumar & Sharma 2019](#)), was
323 too friable and could not be excavated by them. Thus, there is no option to study the specimen
324 first-hand. Henceforth, the image of ([Kumar & Sharma 2019](#)), has been replicated into a high-
325 resolution photograph with the required permission from the editor of the Journal of the
326 Palaeontological Society of India to study the detail of the described specimen
327 (RH01/Pal/CHQ/Tiki/15) (Fig: 7).

328 The studied specimen is the palate of a temnospondyl and not the dorsal view of the skull as
329 erroneously stated by ([Kumar & Sharma 2019](#)). The palate showed in the picture
330 (RH01/Pal/CHQ/Tiki/15) (Fig:7) has a distinct vaulted pterygoid, parabolic skull outline, and
331 comparatively narrow cultriform process than metoposaurids. The specimen
332 (RH01/Pal/CHQ/Tiki/15), ([Kumar & Sharma 2019](#)) (Fig:7) has a parabolic skull, thickening of the
333 pterygoid, presence of vaulted pterygoid, presence of post-pterygoid process and concave vertical
334 wall of pterygoid that are characteristic of chigutisaurids as written repeatedly above. The
335 specimen is indeed friable with dense networks of fractures that obscured the clear identification
336 of the sutures. The specimen (RH01/Pal/CHQ/Tiki/15) is partly eroded along the lateral margins

337 as well as anteriorly and posteriorly. The right half of the palate is slightly compressed, deformed
338 and curved (Fig: 7).

339 The anterior portion of the palate is considerably broken both anteriorly and anterolaterally.
340 Though the sutures cannot be delineated, the presence of vomer is very apparent. The vomer is
341 broken anteriorly and the anterior palatal vacuity is not preserved (RH01/Pal/CHQ/Tiki/15) (Fig:
342 7). The posterior part of the preserved vomer includes the anterior tongue of the cultriform process
343 of the parasphenoid. The left half of a possible vomerine cavity is preserved. The vomerine cavity
344 is present only in Jurassic chigutisaur *Siderops kehli* ([Warren & Hutchinson 1983](#)) and it is absent in
345 *Compsocerops* ([Sengupta 1995](#)) or *Pelorocephalus* ([Marsicano 1999](#)). The left lateral margin of the
346 right choana is aligned to the left lateral margin of the right interpterygoid vacuity. The
347 ectopterygoids are exposed on the anterolateral margins of the interpterygoid vacuities and are
348 preserved on both sides. The ectopterygoid borders the anterior portion of the subtemporal vacuity
349 inwards. The subtemporal vacuity is wide and broad bordered by the ectopterygoid and the
350 parasphenoid on the inward margin and the quadratojugal, the alar process of the jugal on the
351 outward lateral margin. The dentigerous area is restricted to the anterior region of the palate. The
352 anterior and the anterolateral margins of the palate are broken, and all teeth are not preserved.
353 However, two broken ectopterygoid teeth can be seen preserved at the anterolateral corner of the
354 ectopterygoid in contact with the palatine in the left part of the palate. The palatine teeth row in
355 the left half of the skull is also preserved partially. Like other chigutisaurids, the dentigerous area
356 of the palate is remarkably short. The palatine row of teeth is not continuous up to the middle of
357 the choana. This character has been considered to be a synapomorphy of *Compsocerops cosgriffi*
358 ([Sengupta 1995](#)). Conical, inward curved four complete palatine teeth are preserved in the margin
359 of the left palatine bone of the palate. Since, the dentigerous area is restricted to the anterior part

360 of the skull the posterior part is longer in proportion and covered by large and wide subtemporal
361 vacuity (Fig: 4).

362 In (RH01/Pal/CHQ/Tiki/15) (Fig:7) ([Kumar & Sharma 2019](#)) both the interpterygoid vacuities are
363 well preserved. The interpterygoid vacuities are quadrangular in shape, shorter and wider
364 compared to *Compsocerops cosgriffi* ([Sengupta 1995](#)). The borders of the interpterygoid vacuities
365 are approximately parallel-sided. The interpterygoid vacuities are bordered dominantly by the
366 cultriform process along the inward margin as well as the vomer. Anteriorly, it is bordered by the
367 vomer and the palatine. The pterygoid forms the dominant margin of the interpterygoid vacuities
368 laterally with a small area being occupied by the ectopterygoid. Posteriorly, these are formed by
369 the parasphenoid. In ISI A 202/1, the interpterygoid vacuities are not completely preserved. In
370 both, the specimens ISI A 202 and (RH01/Pal/CHQ/Tiki/15) ([Kumar & Sharma 2019](#)), the
371 interpterygoid vacuities are shorter and broader than *Compsocerops cosgriffi* where the base levels
372 of the interpterygoid vacuities are lower than that of the subtemporal vacuities. The subtemporal
373 vacuity extends anteriorly to the level higher than the centre of the interpterygoid vacuities.

374 In (RH01/Pal/CHQ/Tiki/15) ([Kumar & Sharma 2019](#)) (Fig:7) both the pterygoids are preserved.
375 They are deep and vaulted. The vertical lateral wall of the pterygoid projects posteriorly possibly
376 up to the posterior level of the occipital condyles which are broken. The palatal ramus of the
377 pterygoid is visible on both sides in (RH01/Pal/CHQ/Tiki/15). The palatal ramus of the pterygoid
378 is longitudinally concave with a gentle fold which is again a character of some chigutisaurids
379 specially *Compsocerops*. The quadrate ramus of the pterygoid is better preserved on the right side
380 of the palate (RH01/Pal/CHQ/Tiki/15). The quadrate ramus of the pterygoid looks like a wall as
381 they are deeply vaulted. The ascending ramus of the pterygoid is not visible in
382 (RH01/Pal/CHQ/Tiki/15). A broken post pterygoid process that is a projection from the posterior

383 border of the pterygoid corpus is visible on the right side of the palate (RH01/Pal/CHQ/Tiki/15).
384 This area on the left side of the palate of (RH01/Pal/CHQ/Tiki/15) is broken. The postpterygoid
385 process is considered to be an apomorphic character for *Compsocerops cosgriffi* ([Marsicano 1999](#)).
386 The suture of the quadrate and pterygoid is present on the outer side of the downturned part of the
387 quadrate ramus of the pterygoid. In ISI A 202, (Fig: 4) only the right pterygoid is ill-preserved but
388 the bone surface is crushed. However, a distinct post pterygoid process characteristic of
389 *Compsocerops* is present. Though the bone is crushed and compressed, the vaulted nature of the
390 pterygoid can be made out because of the concavity of the vertical wall of the pterygoid. In both,
391 the specimens (RH01/Pal/CHQ/Tiki/15) ([Kumar & Sharma 2019](#)) and ISI A 202, the palatine ramus
392 of the pterygoid is much broader and wider than that in *Compsocerops cosgriffi*.

393 Just like other chigutisaurids, the base of the parasphenoid is almost hexagonal with a long
394 extension in the form of the cultriform process placed between two interpterygoid vacuities in
395 (RH01/Pal/CHQ/Tiki/15) ([Kumar & Sharma 2019](#)). The parasphenoid has a long suture with the
396 pterygoid laterally and the exoccipitals posteriorly. A distinct raised longitudinal keel is present
397 on the ventral surface of the cultriform process in this specimen. The presence of this keel in the
398 cultriform process has been noted by ([Marsicano 1999](#)) as a distinguishing character present only
399 in *Pelorocephalus mendozensis*. However, first-hand studies reveal that this longitudinal keel of
400 the cultriform process is also present in *Compsocerops cosgriffi* from the Maleri Formation of
401 Pranhita - Godavari Valley Basin. The cultriform process of parasphenoid of this specimen is
402 comparatively narrower than all other specimens of *Compsocerops cosgriffi*. The cultriform
403 process of the *Compsocerops* species from Tiki is wider than *C. cosgriffi*, the cultriform process
404 is also comparatively broader than *Siderops kehli*, more comparable to the width of the cultriform
405 process in the specimen previously denoted as *Kuttycephalus triangularis* ([Sengupta 1995](#)). The

406 cultriform process preserved in (RH01/Pal/CHQ/Tiki/15) ([Kumar & Sharma 2019](#)) is thin and
407 constricted in the middle part of the interpterygoid vacuities and gets broader as it progresses to
408 the anterior part of the process. This type of cultriform process is unique among the chigutisaurids.
409 In the specimen photographed by ([Kumar & Sharma 2019](#)), the anterior tongue of the cultriform
410 process is in contact with the vomer and lies posterior to the level of the anterior margin of the
411 interpterygoid vacuities. The cultriform process is not preserved in ISI A 202. The occipital
412 condyles are broken as well. In the earliest known chigutisaur *Keratobrachyops*, the cultriform
413 process of the parasphenoid is also narrower than ISI A 202.

414 *The Occiput* (Fig: 5)

415 The occiput is very ill preserved only in ISI A 202 (Fig: 5). The occiput could not be prepared due
416 to the extremely fragile nature of the skull. Removing the matrix load from the occiput would
417 result in the sagging of the entire specimen. However, from the little that could be studied, it can
418 be said that in occipital view, the quadrate ramus of the pterygoid is deeply downturned. The vagus
419 nerve foramen is preserved on the left exoccipital lateral to the broken occipital condyle. The
420 ascending process of the exoccipital is wide and inclined and meets the descending process of the
421 postparietal. A sub-circular, matrix filled, paraquadrate foramen is present in the quadratojugal.
422 The quadrate is partially preserved in the occipital view. It is bounded by the squamosal,
423 quadratojugal and the downturned pterygoid. The absence of occiput makes the comparison of ISI
424 A 202 difficult with the different species of *Pelorocephalus* as different species of the genus are
425 differentiated, to a great extent, by their occipital characters (Marsicano 1999).

426 *Clavicle* (Fig: 6)

427 An almost complete left clavicle (ISI A 202/2) (Fig: 6) was found associated with the skull (ISI A
428 202/1) during excavation. The clavicle has a flat eye-drop shaped blade and a long straight dorsal
429 process that ascends almost straight, nearly at ninety degrees with the plate. The cross-section of
430 the process at the dorsal end is bean shaped as a feeble furrow runs along the process. This is very
431 similar to the clavicle of *Compsocerops cosgriffi* ([Sengupta 1995](#)), *Siderops kehli* ([Warren &
432 Hutchinson 1983](#)) and *Koolasuchus cleelandi* ([Warren et al. 1997](#)).

433 Results

434 *Tiki Formation:*

435 To date, no temnospondyl fauna has been recorded from the upper part Tiki Formation. Excavation
436 taken up in 2018 by the authors revealed the first chigutisaurid from the Tiki Formation in the
437 Tenduadh locality (Fig: 8) in the upper part of the Tiki Formation. Several vertebrae and
438 postcranial bones of metoposaurid have been excavated from the Jora and Tiki Nala sections which
439 have been assigned to the lower Tiki Formation from our field studies. Based on the changes in
440 the faunal assemblage in the lower and the upper Tiki Formation (Tables 2a and 2b) and
441 considering the lithostratigraphy, a boundary between the basal and upper Tiki Formation has been
442 assigned and the zone demarcating the Carnian to Norian faunal turnover in the Tiki Formation
443 has been approximated and marked in red dotted line in the map (Fig: 1). The lithological logs
444 modified after ([Kumar & Sharma 2019](#)) and ([Mukherjee & Ray 2012](#)) reveal that just like the Maleri
445 Formation, the basal Tiki Formation is dominated by a large band of red mudrock intercalated with
446 peloidal calcirudite-calcarenite ([Sarkar 1988](#)) (Fig: 9). The Jora Nala section in the Carnian basal
447 Tiki has been logged in detail in this work (Fig:9a). This shows the dominance of greenish to

448 reddish siltstones and mudstones in the Jora Nala section with sparse deposition of trough cross-
449 bedded sandstones in between.

450 *Maleri Formation*

451 In the revised map of the Maleri Formation after ([Dasgupta et al. 2017](#); [Kutty & Sengupta 1989](#)) a
452 boundary between the Carnian basal Maleri and Middle Carnian / Norian Upper Maleri has been
453 established from both lithological and faunal contents (Fig: 2 – faunal boundary indicated by a
454 green broken line). From our field studies and maps it is evident that though sandstone - mudstone
455 alternation is present throughout the Maleri Formation, the Carnian basal Maleri is abundant in red
456 mudrocks and calcirudites (Fig: 2,10) and moving towards Upper Maleri there is a sudden increase
457 in the deposition on siliciclastic sediments leading to the more frequent occurrence of sandstone
458 bands alternating with red mudstone (Fig: 10).

459 Discussion

460 The CPE had a significant impact on the terrestrial environment and ecosystem globally. The
461 evidence of CPE has never been worked upon or mentioned in India because of the lack of proper
462 age constraints present in the Late Triassic Maleri and Tiki Formations in India.

463 *Tiki Formation*

464 No detailed sedimentological or geochemical studies have been carried out in the Late Triassic
465 Tiki Formation in India to analyse the associated changes from Carnian to Norian through the
466 humid phase of the Carnian Pluvial Episode. Though, ([Ahmed & Ray 2010](#)) presented a geochemical
467 analysis of 42 nodular carbonates confirming their pedogenic origin, no details of the localities of
468 collection in terms of lower and upper Tiki have been provided.

469 The terrestrial influx of sediments is significantly low at the period denoted by the sparse
470 occurrence of sandstones in the basal Tiki Formation (Fig: 9). The presence of *Unio* beds in
471 between the basal thick layers of mud reflects a stagnant quiet and well-watered environment. This
472 basal mud encompasses areas like the Jora and Tiki River sections. Abundant postcranial
473 fragments of metoposaurids and rhynchosaurs have been collected from these sections. Moving
474 upwards in the direction of the dip of the beds, there is a sudden influx of siliciclastic sediments
475 marked by thick sandstone units with little intermittent mudstone. This could be a demarcation of
476 the rapid influx of siliciclastic sediments that took place during CPE in the Tiki Formation. Only
477 two dominant sand bodies are observed in Tiki before the recurrence of a thick horizon of mud
478 and subsequently sand-mud alternations indicating the onset of seasonality and aridity in the
479 Norian. The Norian of Tiki Formation is demarcated by red mudstones, whitish sandstones and
480 sparse calcirudites. The Norian Upper Tiki Formation is exposed in sections near Tenduadh as
481 shown in the map (Fig: 1) and an estimated approximate faunal boundary between the Carnian and
482 the Norian in the Tiki Formation is also furnished as in Fig: 1. Tiki has a long history of yielding
483 fossil vertebrates ([Bandyopadhyay & Ray 2020b](#); [Chatterjee & Roy-Chowdhury 1974](#)) (Table 1). It has
484 a rich Late Triassic faunal association as shown in Table 2a and 2b ([Bandyopadhyay & Ray 2020a](#);
485 [Chatterjee & Majumdar 1987](#); [Mukherjee & Ray 2014](#)). The Tiki faunal assemblage was thought to be
486 coeval to the Lower Maleri faunal assemblage ([Datta 2005](#); [Kutty & Sengupta 1989](#)). However, ([Datta
487 et al. 2019b](#)) stated that the Tiki fauna ranges from Middle Carnian to Early Norian and is younger
488 than Lower Maleri Fauna. The mid Carnian / Norian Upper Maleri fauna has chigutisaurids. The
489 Discovery of a chigutisaurid from the upper part of the Tiki Formation confirms ([Datta et al. 2019b](#))
490 regarding the presence of Middle Carnian / Norian fauna in the Tiki Formation.

491

492 ***Maleri Formation***

493 The abundance of red mudstone in the basal Maleri Formation (Fig: 11) with a sudden increase in
494 the frequency of sandstone bands in the upper part can be correlated with the advent of the Carnian
495 Pluvial Episode (CPE) in India. The overall palaeoenvironment and sedimentology of the Maleri
496 formation have been worked upon by earlier workers ([Dasgupta & Ghosh 2018](#); [Sarkar 1988](#)). Most
497 of these studies were done on the Maleri Formation as a whole without distinguishing its basal and
498 upper parts. Also, no detailed analyses about the changes in sedimentology or geology or
499 geochemistry have been done to study the changes in the pattern of sedimentation from the Carnian
500 basal Maleri to the Norian Upper Maleri.

501 Evidence from detailed geological mapping, logs and associated faunal turnover in the Late
502 Triassic Maleri Formation all point toward the distinctive effect of CPE in India. The overall
503 thickness of the Maleri Formation is about 350-600m which is variable in different places. From
504 the map of the Maleri Formation and log of the same near Achlapur and Nalapur (Fig: 10), it is
505 evident that the basal part of the Maleri Formation has a large stretch or band of red mudrock-
506 dominated unit. This unit of red mudrock stretches from about 100m-200m in thickness in basal
507 Maleri and is the thickest band of red mudrock encountered in the entire Maleri Formation (Fig:
508 12). It encompasses villages namely Aigerrapalli (19°15'22.4" N; 79°27'23.4" E), Achlapur
509 (19°09'34" N; 79°31'51" E) and Nambala (19°13'47" N; 79°26'07" E), areas slightly north of
510 village Gampalpalli (19°10'11" N; 79°30'53" E) and is rich in vertebrate fossils, the most
511 significant among them being rhynchosaurs and metoposaurids. This significantly thick basal
512 Maleri mudstone has sporadic carbonate grainstones [*sensu* ([Dunham 1962](#)); calcarenites–
513 calcirudites of ([Sarkar 1988](#))] and the presence of palaeosols with no significant siliciclastic
514 deposition of sandstone present within this mud. The upper part of the Formation is approximately

515 200–350 m thick and has three to four multi-storeyed sheet sandstone bodies (each 10–35 m thick)
516 vertically separated by mudrock-dominated intervals (15–55 m thick). The mudrock intervals in
517 the upper part are lithologically similar to those occurring in the lower part of the Formation. The
518 mudrock units comprise both stratified and massive mudstones ([Dasgupta et al. 2017](#)) with sporadic
519 carbonate grainstones (calcirudite of ([Sarkar 1988](#))). Moving upwards from the thick stretch of
520 mudrock, the influx of siliciclastic sedimentation increases as evident from the increase in the
521 deposition of frequent sandstone units. The beginning of these sandstone units is marked by the
522 presence of metoposaurids and rhynchosaurs and unionid fossils in a sandy zone. In the upper part,
523 apart from the chigutisaurids, there are basal sauropods like *Jaklapallisaurus*, and
524 sauropodomorphs like *Nambalia*, probable Guaibasaurids-and-Herrerasaurus-like forms ([Novas et](#)
525 [al. 2010](#)). The authors in the same work, also mentioned that early theropods are known from the
526 Norian-Rhaetian time from North and South America, India, South Africa, and Europe and the
527 demise of members of Lower Maleri fauna like rhynchosaurs together with the global extinction
528 of *Chiniquodon* (cynodont) and Proterocampsidae (archosauriform) mark the Carnian – Norian
529 boundary and also the North Tethyan Pluvial Episode of end Carnian (CPE). ([Benton et al. 2018](#))
530 have argued that CPE triggered the diversification of early dinosaurs. It has been discussed earlier
531 those indications of CPE are present in Maleri and Tiki Formations of India. The sudden
532 appearance of several basal dinosaurs like *Jaklapallisaurus*, *Nambalia*, probable Guaibasauridae
533 and *Herrerasaurus* ([Novas et al. 2010](#)) in the Norian Upper Maleri fauna also corresponds to that.

534 Thus, the palaeoenvironment of the Maleri Formation shifted from a comparatively arid and dry
535 climate in the Julian at the basal substage of Carnian to a high competence fluvial-lacustrine
536 environment with the presence of small, ephemeral and vegetated swamps or ponds along the flow
537 path of the channels at the time of Carnian Pluvial Episode from the end of Julian to Tuvlian and

538 back again to fluvial deposition in the Norian ([Dasgupta et al. 2017](#)). The episodes of increased
539 rainfall during the Carnian Pluvial Episode demarcated by increased frequency of sandstone
540 deposition are intervened by seasonality as evident from the red mudrock alternations between
541 sandstones. Similar climatic shifts are seen from the coeval Santa Maria to Caturrita formations
542 of Brazil ([Dal Corso et al. 2015](#)). These shifts indicating a major variation of the hydrological regime
543 in terrestrial depositional settings suggest an enhancement of the hydrological cycle during the
544 CPE. Recently, ([Lucas 2010](#)) stated that the demise of metoposaurids in most parts of the world
545 during the Carnian is related to the end of the enhanced hydrological cycle at the dying phase of
546 CPE. The disappearance of key herbivorous groups such as dicynodonts and rhynchosaurs of
547 Carnian and their places taken up by giant sauropodomorphs seems to be linked to CPE which is
548 not documented in India so far.

549 Also, the *Hyperodepadon* Assemblage Zone (HAZ) is characterized by the presence of
550 rhynchosaur *Hyperodepadon* and is present in the lower part of the Ischigualasto Formation of
551 Argentina, the Lossiemouth Sandstone Formation of Scotland, and the Lower Maleri Formation
552 of India ([Langer et al. 2010](#)). The HAZ is dated as late Carnian to early Norian, approx. 228–224
553 Ma by some authors ([Benton et al. 2018](#); [Brusatte et al. 2010](#); [Ezcurra et al. 2017](#)). Most metoposaurids
554 in the Gondwana deposits are considered to be Carnian in age ([Chakravorti & Sengupta 2019](#); [Gee &](#)
555 [Jasinski 2021b](#); [Sengupta 2002](#)). The demise of the metoposaurids *Panthesaurus maleriensis*
556 ([Chakravorti & Sengupta 2019](#)) in India along with the demise of *Hyperodepadon* ([Chatterjee 1974](#);
557 [Mukherjee et al. 2012](#)) in both Late Triassic Maleri and Tiki Formation also points to the presence
558 and effect of CPE in India. The demise of the metoposaurids left a vacant niche to be occupied by
559 the chigutisaurids in the Norian suggesting short-lived aridity in post Carnian stage.

560 The Carnian of Argentina has its age radiometrically constrained between 231.4 ± 0.3 and 225.9
561 ± 0.9 Ma ([Martínez et al. 2016](#)) and similar reports are present from Santa Maria and Caturrita
562 Formations of Brazil (233.2 ± 0.7 and 225.4 ± 0.4 Ma) ([Langer et al. 2018](#)). The onset of CPE is
563 well constrained in stratigraphic sections like the Southern Alps of Italy, Northern Calcareous Alps
564 of Austria, Transdanubian Range of Hungary, and the Nanpanjiang Basin of the South China block
565 and is placed at the substages Julian 1 – Julian 2 boundary of the Carnian ([Gallet et al. 1994](#)). Due
566 to the lack of any radiometric dating, Late Triassic Maleri and Tiki Formations are poorly
567 constrained and pose difficulty in global correlation, their correlation is based only on available
568 fauna. The CPE has always been dated as mid-Carnian ([Ruffell et al. 2016](#)) but this is not a
569 unanimous viewpoint. The Italian Dolomites occur between the Aonoides/Austriacum interval
570 (about Julian) and the base of the Subbullatus Zone (Tuvalian), dated at 234–232 Ma ([Dal Corso et](#)
571 [al. 2015](#); [Roghi et al. 2010](#)). Further constraint has been documented in borehole successions in the
572 southwest UK, which indicates a maximum duration of 1.09 MYA ([Miller et al. 2017](#)). The precise
573 radiometric dating to constrain the Maleri and Tiki Formations and to denote the beginning of CPE
574 in India will shed further light on the pattern of faunal diversification post CPE event in the
575 subcontinent and help in the global stratigraphic correlation. A continental carbon isotope record
576 in southwest England shows multiple carbon cycle perturbations during CPE ([Miller et al. 2017](#)).
577 The CPE is not only the time interval of increased humidity but also a major carbon perturbation.
578 Unfortunately, no carbon isotope data is noted from the Maleri and the Tiki Formations of India.

579 Conclusion

- 580 1. In the current work a new species of chigutisarid amphibian, *Compsocerops tikiensis* sp.
581 nov. from the Late Triassic Tiki Formation of the Rewa Gondwana Basin has been
582 described in detail. The presence of chigutisaurid *Compsocerops tikiensis* sp. nov. in the

583 Upper part of the Tiki Formation is the first evidence of the Norian chigutisaurid amphibian
584 from the said Formation and is important for correlation of the Late Triassic basins
585 worldwide.

586 2. The presence of *Compsocerops* ([Sengupta 1995](#)) in Tiki, for the first time, confirms the
587 presence of the Upper Maleri faunal element in Tiki. ([Lucas 2020b](#)) thought that the demise
588 of metoposaurids in most parts of the world was at the end of Carnian and that tallies with
589 the last appearance datum of the metoposaurids of Maleri. The chigutisaurids, both in
590 Maleri and Tiki have their first appearance datum at the onset of the Middle Carnian or
591 Early Norian.

592 3. Along with the extinction of the rhynosaurs and *Parasuchus* (primitive phytosaur)
593 ([CHATTERJEE 1978](#)), chiniquodontids (cynodonts), the Carnian – Norian Extinction Event
594 (CNEE) also caused the extinction of the metoposaurids in India. Chigutisaurids appeared
595 in Middle Carnian / Norian and India is the only place which accommodates definite
596 metoposaurids and chigutisaurids within the same formations (the Late Triassic Maleri and
597 Tiki Formations) the former being replaced by the latter. Incidentally, among the
598 phytosaurs, the *Parasuchus* of Lower Maleri fauna is replaced by the *Leptosuchus* like
599 forms of Upper Maleri and *Volcanosuchus statisticae* ([Datta et al. 2021b](#)) in the upper part
600 of the Tiki Formation.

601 4. The post-CNEE empty niche left by the metoposaurids in the Late Triassic Gondwana
602 deposits of India (controversially Brazil as well, see ([Dias-da-Silva et al. 2011](#))) was occupied
603 by the chigutisaurids in the Norian. The availability of phytosaur teeth along with *C.*
604 *tikiensis* sp. nov. only indicated their co-existence in the same aquatic niche but does not
605 necessarily point towards any prey-predatory relationship between the phytosaurids and

606 the chigutisaurids. However, detailed studies on histology and growth pattern of the
607 chigutisaurids might shed light on the gigantism of these amphibious animals in the post-
608 CNEE and recovery of the temnospondyls.

609 5. The presence of both metoposaurids and chigutisaurids and the faunal turnover from the
610 Carnian to the Norian along with the extinction of the rhynchosaurs (*Hyperodapedon*)
611 ([Mukherjee et al. 2012](#)) and *Parasuchus* ([CHATTERJEE 1978](#)) in the Carnian of both the Late
612 Triassic Maleri and Tiki Formation and the presence of prosauropods in the Upper Maleri
613 Formation and undescribed dinosauriformes including theropod-like forms
614 ([Bandyopadhyay & Ray 2020b](#)) sheds light and documents for the first time the existence and
615 effect of the Carnian Pluvial Episode in India.

616 6. The finding of *Compsocerops tikiensis* sp. nov. from the Tiki Formation and assessing its
617 importance in global palaeoclimatic and palaeoclimatic correlation paves the way for future
618 scope of works in finding the effect of CPE in India and comparing its faunal diversification
619 at a global scale. Also, finding any new and better-preserved specimen of *Compsocerops*
620 *tikiensis* sp. nov. from the Tiki Formation would help to establish the phylogenetic
621 relationship of the other chigutisaurids around the world with that of the Indian
622 counterparts. As the specimens are deformed broken and have poor preservation potential,
623 phylogenetic analysis is beyond the scope of this paper as it will add more missing and
624 misinterpreted data.

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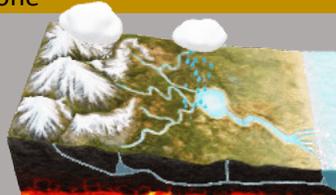
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Table 1 (on next page)

Spatial and temporal range of the family Chigutisauridae along with their paleoecology and paleoenvironment.

Abbreviations Max ma = Maximum age million years ago, Min ma = Minimum age million years ago, Fm. = Geological Formations from which the specimen had been excavated. The table has been modified after data was acquired from the Paleobiology Database on 10th May 2022, using the family name "Chigutisauridae". Data for the table was modified after Bonaparte 1957; Marsicano 1999; Dias - da- Silva and Sengupta 2012; Warren 2006; Pledge 2013; Cabrera 1944; Rusconi 1949; Rusconi 1951; Sengupta 1995; Warren and Hutchinson 1983; Warren 1981; Warren and Marsicano 2000)

1 Table 1

Name	Early_interval	Late_interval	Max_ma	Min_ma	Country	Fm.	Lithology	Palaeoenvironm
<i>Koolasuchus cleelandi</i>	Late Aptian	–	122.46	112.03	Australia	Eumeralla Fm.	Sandstone	
<i>Koolasuchus cleelandi</i>	Late Aptian	–	122.46	112.03	Australia	Eumeralla Fm.	Sandstone	
<i>Koolasuchus cleelandi</i>	Late Aptian	–	122.46	112.03	Australia	Eumeralla Fm.	Sandstone	
<i>Koolasuchus cleelandi</i>	Late Aptian	–	122.46	112.03	Australia	Eumeralla Fm.	Sandstone	
<i>Koolasuchus cleelandi</i>	Aptian	–	125	113	Australia	Eumeralla Fm.	Sandstone	
<i>Siderops kehli</i>	Pliensbachian	Toarcian	190.8	174.1	Australia	Evergreen Fm.	Ironstone/Sandstone	
<i>Chigutisauridae indet</i>	Mid Carnian	–	228	–	Australia	Leigh Creek Fm. Santa Maria	Siltstone	
<i>Compsocerops</i>	Mid Carnian	Norian	228	208.5	Brazil	Fm. Upper Maleri	Mudstone	
<i>Compsocerops cosgriffi</i>	Mid Carnian	Norian	228	208.5	India	Fm. Upper Maleri	Mudstone	
<i>Kuttycephalus triangularis</i>	Mid Carnian	Norian	228	208.5	India	Fm.	Mudstone	
<i>Compsocerops tikiensis</i>	Mid Carnian	Norian	228	208.5	India	Upper Tiki Fm	Mudstone	
<i>Pelorocephalus mendozensis</i>	Carnian	Norian	237	208.5	Argentina	Cacheuta Fm.	"Siliciclastic"	
<i>Pelorocephalus tenax</i>	Carnian	Norian	237	208.5	Argentina	Cacheuta Fm.	"Siliciclastic"	
<i>Pelorocephalus cacheutensis</i>	Carnian	Norian	237	208.5	Argentina	Cacheuta Fm.	"Siliciclastic"	
<i>Pelorocephalus ischigualastensis</i>	Carnian	Norian	237	208.5	Argentina	Ischigualasto Fm.	Siliciclastic	
<i>Keratobrachyops australis</i>	Induan	–	252.17	251.2	Australia	Arcadia Fm.	Mudstone	

2 Table -1: The table shows the spatial and temporal range of the family Chigutisauridae along with their paleoecology and paleoenvironment.

3 Abbreviations Max ma = Maximum age million years ago, Min ma = Minimum age million years ago, Fm. = Geological Formations from which the
4 specimen had been excavated. The table has been modified after data was acquired from the Paleobiology Database on 10th May 2022, using
5 the family name "Chigutisauridae". Data for the table was modified after Bonaparte 1957; Marsicano 1999; Dias – da- Silva and Sengupta 2012;
6 Warren 2006; Pledge 2013; Cabrera 1944; Rusconi 1949; Rusconi 1951; Sengupta 1995; Warren and Hutchinson 1983; Warren 1981; Warren and
7 Marsicano 2000)

Table 2 (on next page)

Fossils excavated from the Late Triassic Tiki Formation modified after Bandopadhyay and Ray 2020

2a. Fish fossils excavated from the Late Triassic Tiki Formation (modified after Bandopadhyay and Ray 2020).

2b. Vertebrate fossil assemblage (tetrapod content) of the Late Triassic Tiki Formation of the Rewa Basin, India (modified after Bandopadhyay and Ray 2020).

1 Table 2a

Order/Family	Genus and Species	Order/Family	Genus and Species
Chondrichthyes		Osteichthyes	
Lonchididae	<i>Lonchidion estesi</i>	Ptychoceratodontidae	<i>Ceratodus sp.</i>
	<i>Lonchiodon incumbens</i>		<i>Ptychoceratodus oldhami</i>
	<i>Pristrisodus tikiensis</i>	Gnathorhizidae	<i>Gnathorhiza sp.</i>
Xenacanthidae	<i>Mooreodontus indicus</i>	Actinopterygii	Undescribed
	<i>Mooreodontus jaini</i>		
	<i>Tikiodontus asymmetricus</i>		

2 **Table- 2a:** Fish fossils excavated from the Late Triassic Tiki Formation (modified after Bandopadhyay and Ray 2020).

3 Table 2b

Order/Family	Genus and Species	Order/Family	Genus and Species
Amphibia		Diapsida	
Metoposauridae	<i>Panthesaurus maleriensis</i>	Archosauriformes	<i>Galtonia sp.</i> , <i>Protecovasaurus sp.</i> , and other intermediate forms
Chigutisauridae	<i>Compsocerops tikiensis</i>	Dinosauriformes	Undescribed Theropod-like (?) forms
Diapsida		Aetosauria	Undescribed
Phytosauria	<i>Volcanosuchus statisticae(?) leptosuchomorph</i>	Synapsida	

Rhynchosauria	<i>Hyperodapedon tikiensis</i>	Cynodontia	<i>Ruberodon roychowdhurii</i>
Rauisuchidae	<i>Tikisuchus romeri</i>	Mammaliaformes	<i>Tikitherium copei</i>
Rhynchocephalia	<i>Undescribed</i>		<i>Gondwanadon tapani</i>

4

5 **Table- 2b:** Vertebrate fossil assemblage (tetrapod content) of the Late Triassic Tiki Formation of the Rewa Basin, India (modified
6 after Bandopadhyay and Ray 2020).

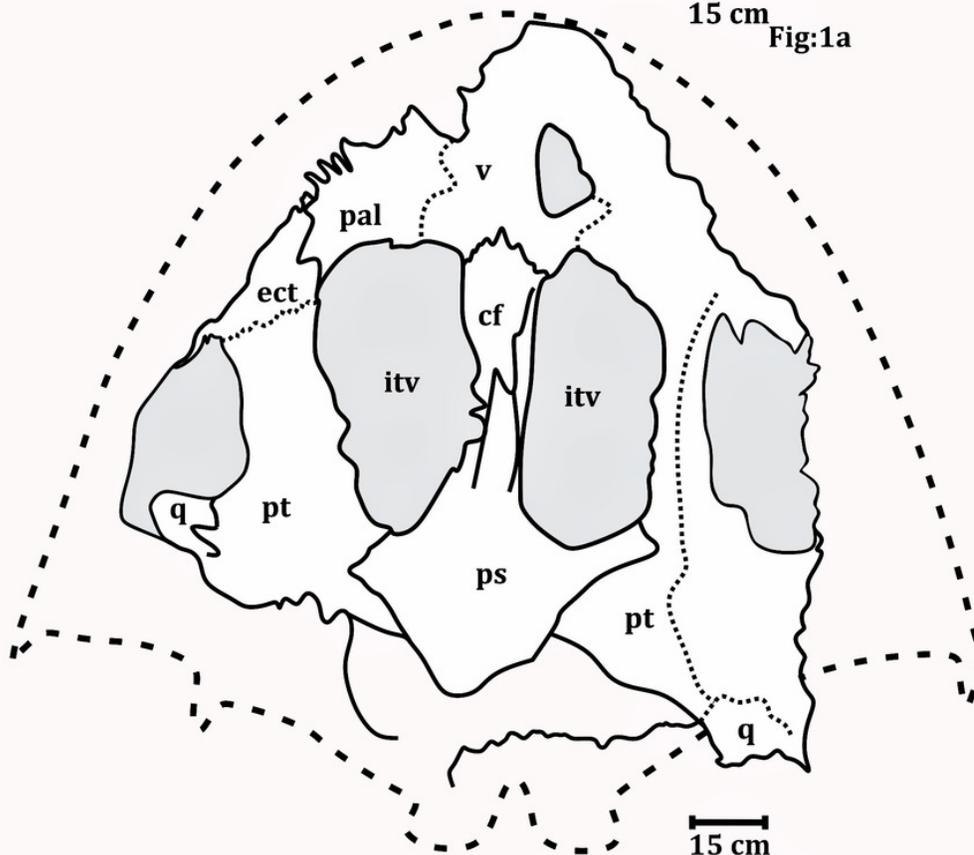
Figure 1

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.



15 cm Fig:1a

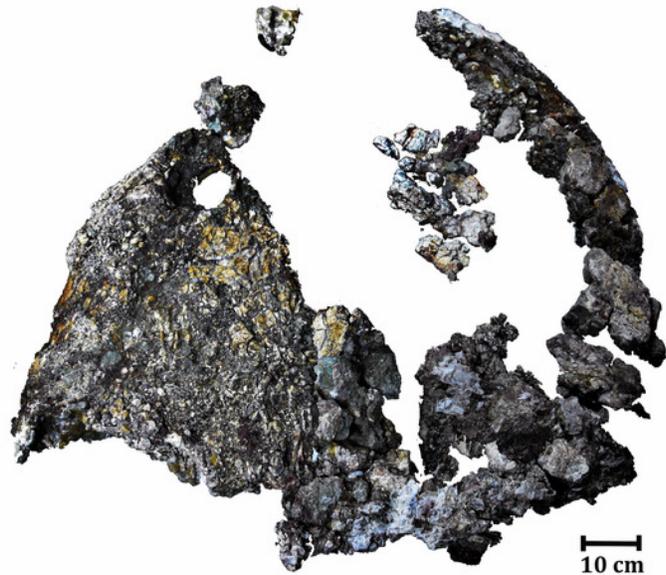


15 cm Fig:1b

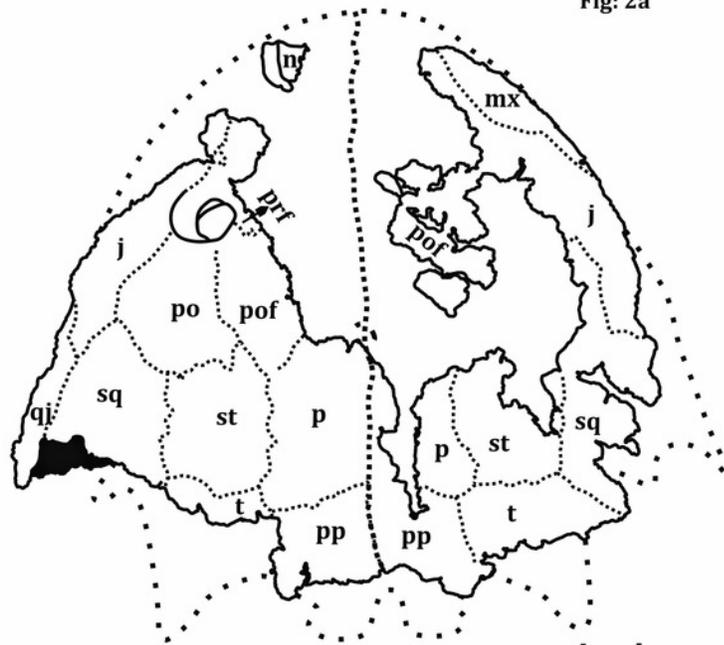
Figure 2

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.



10 cm
Fig: 2a

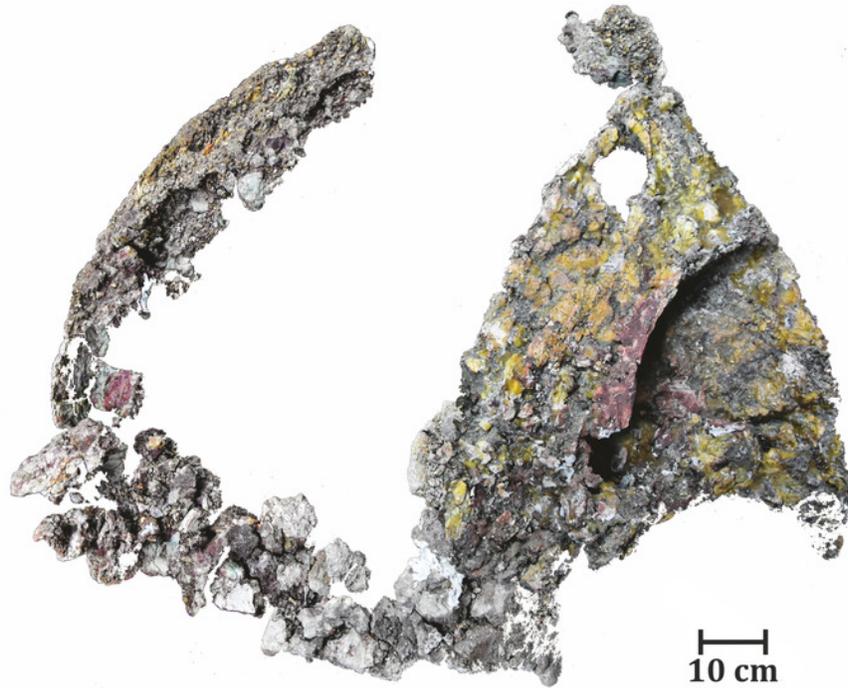


10 cm
Fig: 2b

Figure 3

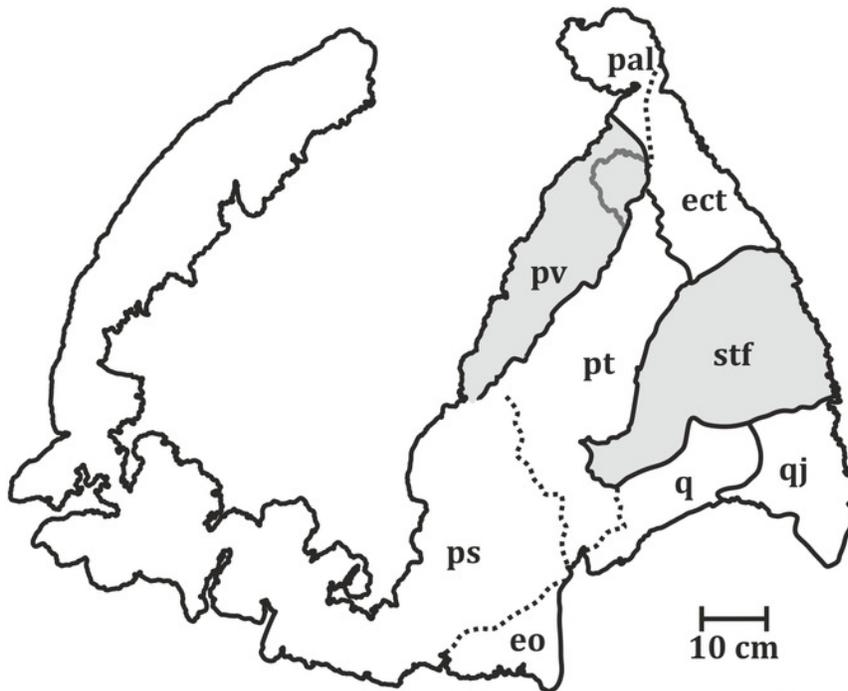
Palatal surface of the skull of ISI A 202 *Compsocerops tikiensis*.

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.



10 cm

Fig: 3a



10 cm

Fig: 3b

Figure 4

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

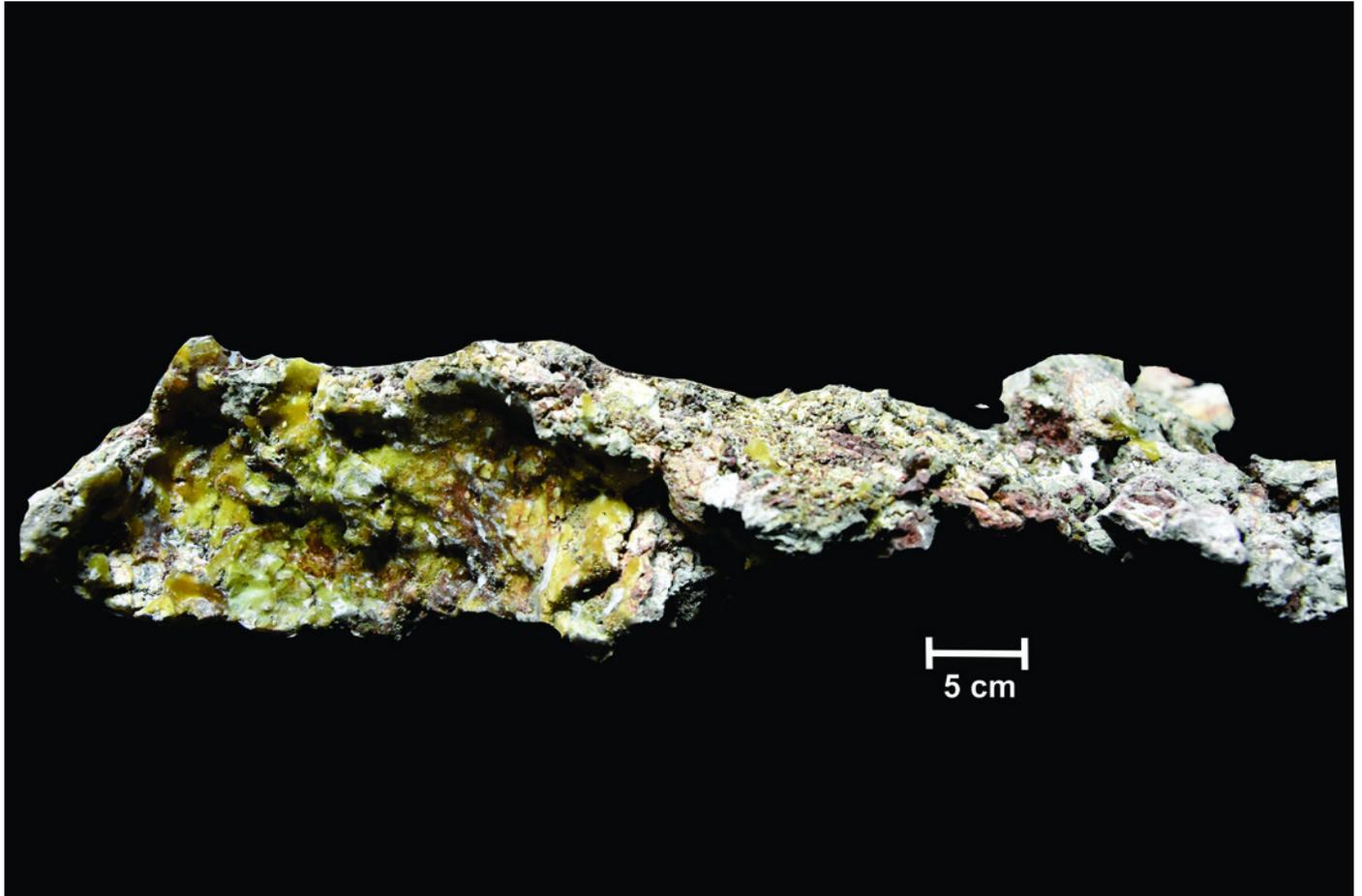


Figure 5

Dorsal view of poorly preserved left clavicle of ISI A 202 *Compsocerops tikiensis*.

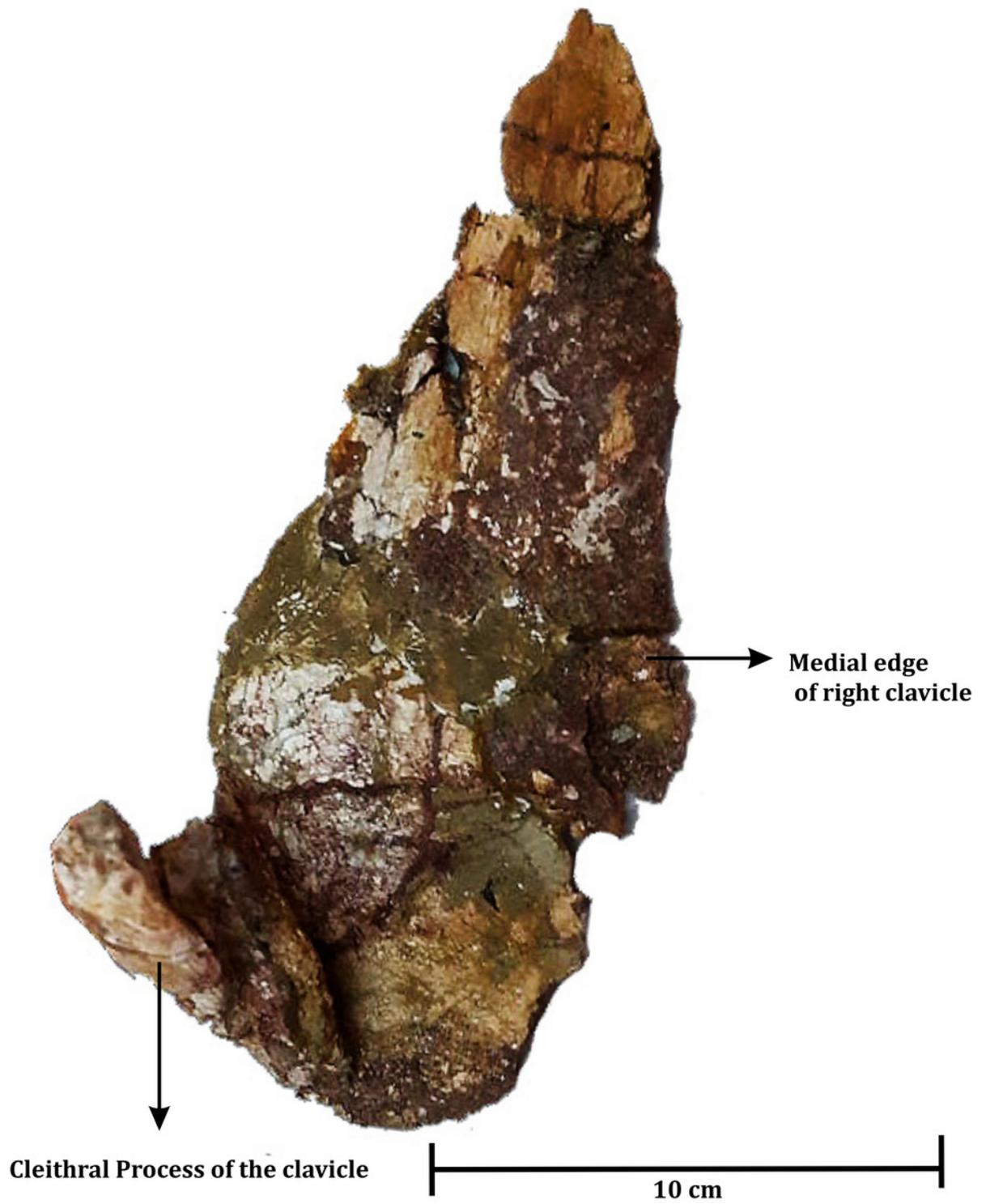


Figure 6

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.

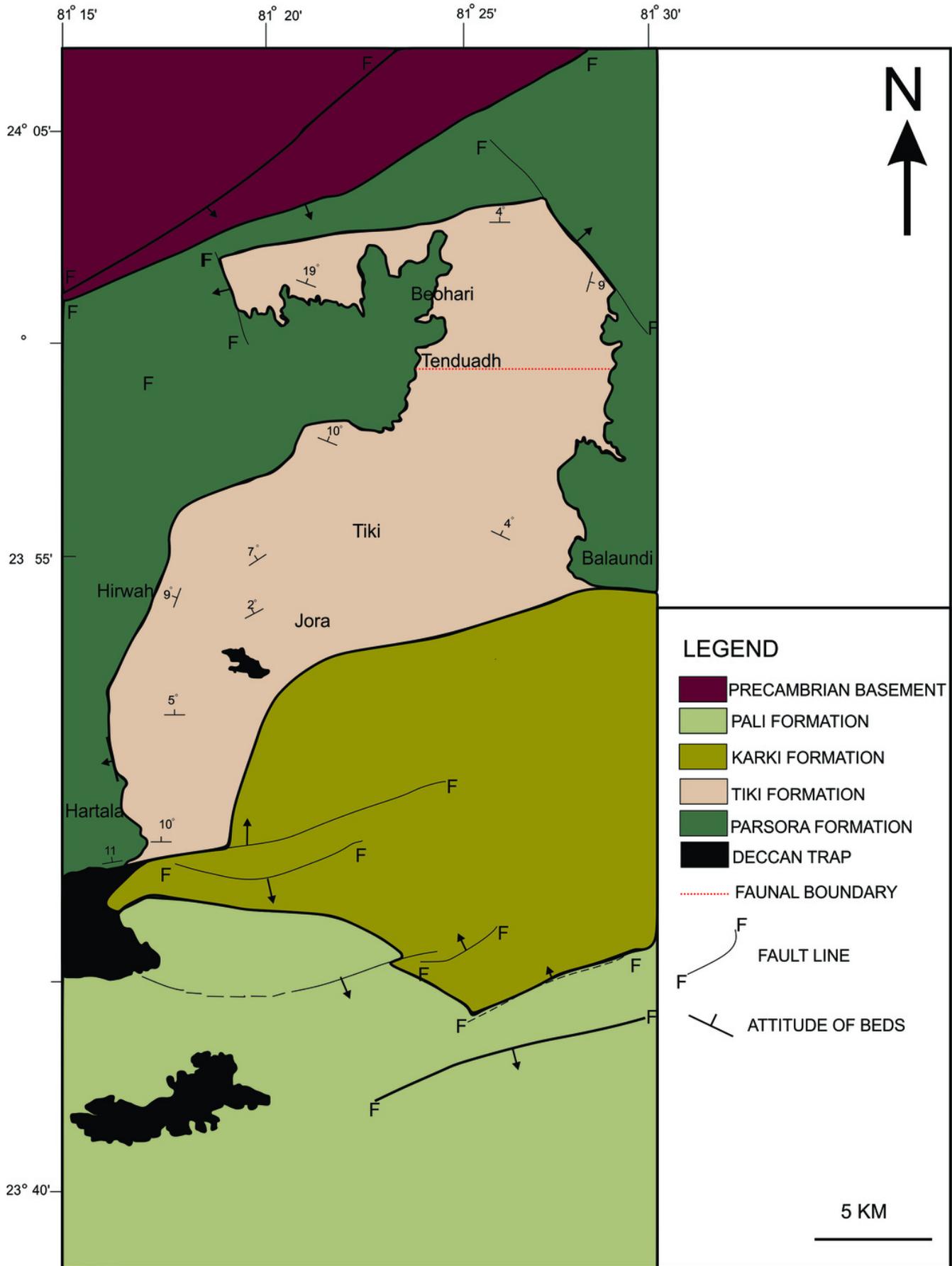


Figure 7

Field photograph showing the exposure of *Compsocerops tikiensis* embedded in mudstone in the Upper part of the Tiki Formation. Image taken by the authors during field season 2019.



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).

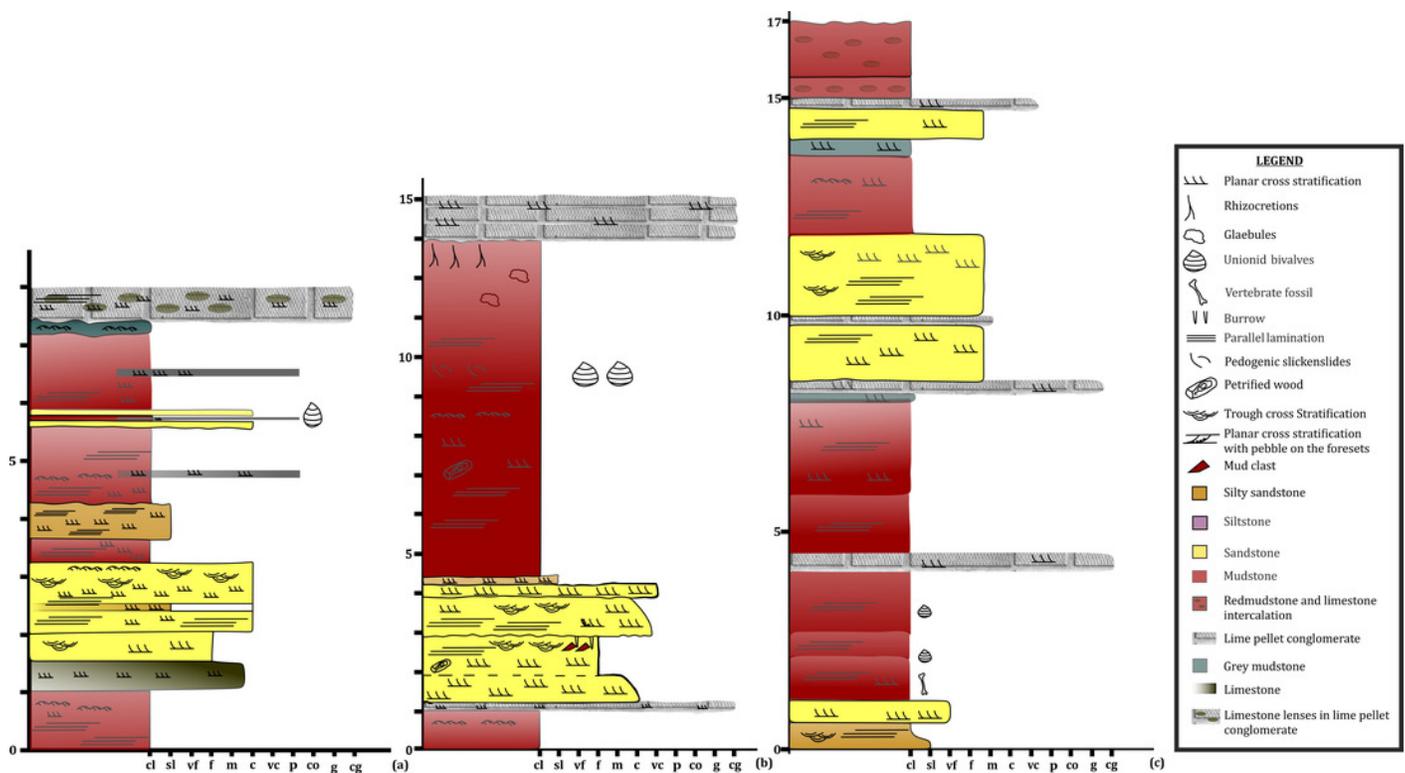


Figure 9

Field photograph of the sand-mud alternation in the Tiki Formation near Tenduadh. Photograph taken by the authors during field season 2019.

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.

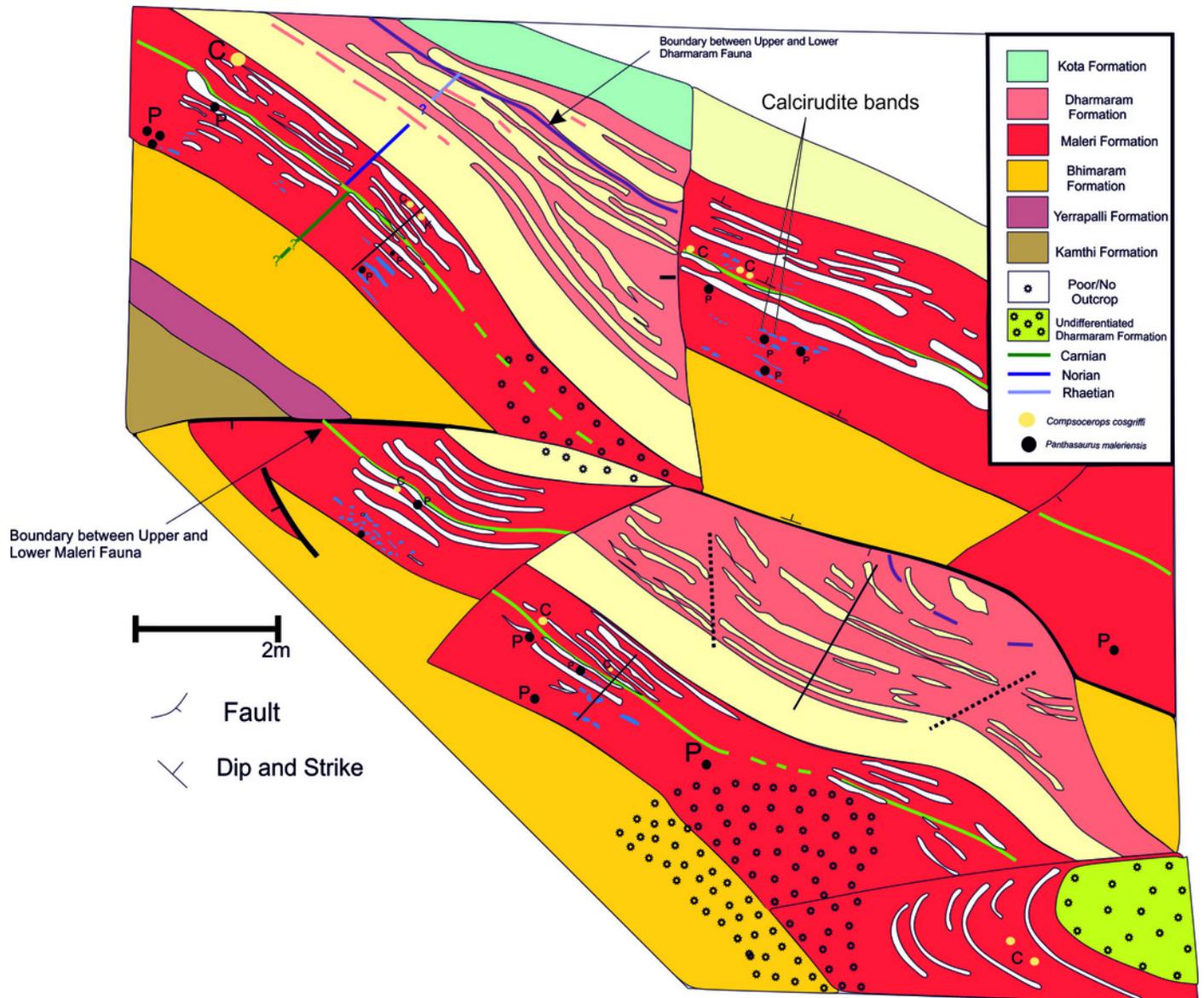


Figure 11

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

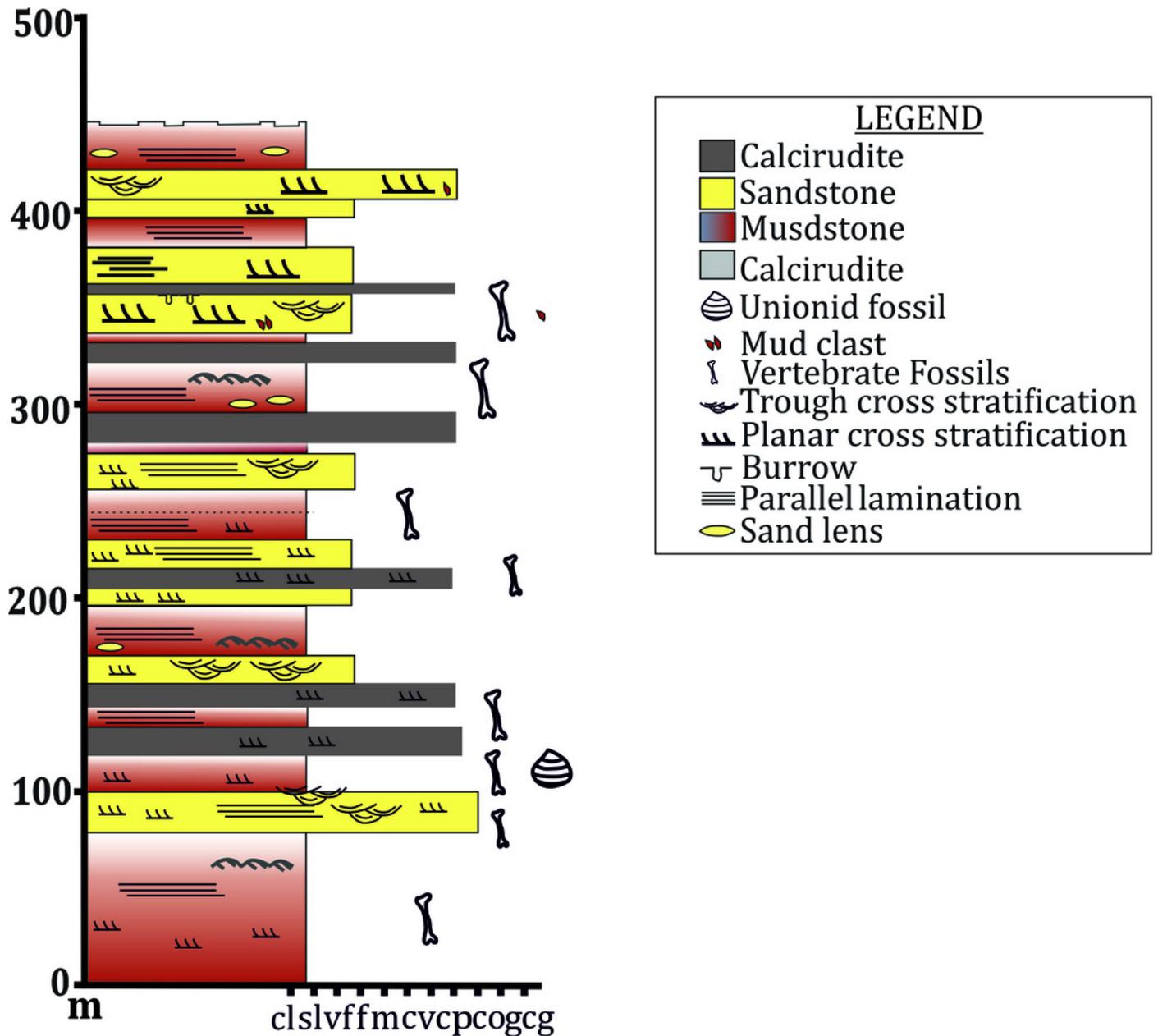


Figure 12

Field photograph showing the abundance of red mudstone in the basal part of the Maleri Formation. Image taken by the authors during field season 2015 at Pranhita- Godavari Valley.

