Journal of Vertebrate Paleontology e2232833 (18 pages)

DOI: 10.1080/02724634.2023.2232833

ARTICLE

A NEW CLEVOSAURID (LEPIDOSAURIA: RHYNCHOCEPHALIA) FROM THE UPPER TRIASSIC OF INDIA

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ABSTRACT—A new clevosaurid rhynchocephalian is described from the Upper Triassic Tiki Formation of the Rewa Gondwana Basin of India. The material is based on several partial craniomandibular elements containing acrodont and fully ankylosed tooth implantations and on the basis of multiple diagnostic features is assigned to a new taxon, *Clevosaurus nicholasi*. Phylogenetic analysis nests the Tiki rhynchocephalian within the clade Clevosauridae, where it is recovered as an early-diverging taxon basal to the other clevosaurs except for a clade comprising *C. convallis* + *Sigmala sigmala*. The autapomorphic characters of *Clevosaurus nicholasi* include a very robust dentary with an obliquely angled narrow lip of the secondary bone at the symphysis, anteriorly bifurcated Meckelian canal, a sub-dental shelf on the dentary, acrodont marginal anterior teeth, and absence of or smooth lateral and medial wear facets on the marginal dentary and maxillary teeth, respectively. The Late Triassic rhynchocephalian record of the Gondwana is relatively sparse in comparison with that of the Laurasian regions, and the new clevosaur represents the first Late Triassic record from India. Based on the paleobiogeographic distribution, a possible Gondwanan origin for Clevosauridae is hypothesized.

http://zoobank.org/urn:lsid:zoobank.org:pub:385F1A20-9701-4F80-A1F6-8AAE3D3A780E

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Citation for this article: Bhat, M. S., Datta, D., Ray, S., & Datta, P. M. (2023) A new clevosaurid (Lepidosauria: Rhynchocephalia) from the Upper Triassic of India. *Journal of Vertebrate Paleontology.* https://doi.org/10.1080/02724634.2023.2232833

Submitted: September 27, 2022
Revisions received: June 13, 2023
Accepted: June 29, 2023

INTRODUCTION

Rhynchocephalia are a monophyletic group of small- to large-sized lizard-like diapsid reptiles (Daugherty et al., 1990; Evans et al., 2001; Evans & Jones, 2010; Fraser, 1988; Romo-de-Vivar-Martínez & Soares, 2015), represented today by a solitary genus *Sphenodon* with only one living species, *S. punctatus* (the tuatara of New Zealand sensu Jones & Cree, 2012; Simões et al., 2022). Rhynchocephalia consists of two groups, the basally branching *Gephyrosaurus* displaying pleurodont tooth implantation, and the more derived Sphenodontia (Gauthier et al., 1988) with acrodont and fully ankylosed teeth (Chambi-Trowell et al., 2021; Evans, 1980; Säilä, 2005; Sues & Schoch, 2021), which together with Squamata form the clade Lepidosauria (Gauthier et al., 1988). The crown-group Squamata has an almost worldwide distribution at present (~11,000 extant species; Burbrink et al., 2020) and a rich and diverse fossil record dating back to the Middle Jurassic (Evans, 1998). Interestingly, the rhynchocephalians were taxonomically and ecologically diverse and cosmopolitan during most of the Mesozoic (Evans, 1988; Evans et al., 2001; Heckert et al., 2008; Jones et al., 2009; Kligman et al., 2021). These became nearly extinct during the early Cretaceous in Laurasia, and were replaced by the diversifying squamates (Carroll, 1988). In contrast, these remained abundant in Gondwana until the Late Cretaceous (Apesteguía & Novas, 2003). Their fossils are known from Europe, North America, China, South Africa, Argentina, Brazil, Morocco, Zimbabwe, and India (DeMar, Jr. et al., 2022; Evans et al., 2001; Evan & Jones, 2010; Jones et al., 2009). Rhynchocephalians thrived in aquatic and terrestrial niches and included small, gracile, terrestrial insectivores such as *Gephyrosaurus* (Evans, 1980, 1981), large, robust, terrestrial herbivores (e.g., *Priosphenodon*; Apesteguía & Novas, 2003; LeBlanc et al., 2020), and aquatic forms with elongated bodies and short limbs as in *Pleurosaurus* (Anantharaman et al., 2022; Carroll, 1985; Evans & Jones, 2010; Jones, 2008). Generally, these are characterized by a diapsid skull, anteriorly elongated pterygoid, an immobile quadrate firmly overlapping the pterygoid, and a diverse array of tooth morphologies that suggest a wide range of dietary preferences and ecological adaptations (Evans et al., 2001; Evans & Jones, 2010; Fraser, 1982; Fraser & Walkden, 1983; Herrera-Flores et al., 2017; Jones, 2008, 2009; Meloro & Jones, 2012; Säilä, 2005).

The earliest record of the rhynchocephalian is from the Middle Triassic (Ladinian) Erfurt Formation of Baden-Württemberg,

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Published online 03 Aug 2023