

## Why so many dipnoans? A multidisciplinary approach on the Lower Cretaceous lungfish record from Tunisia



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### ABSTRACT

The Lower Cretaceous record of vertebrates from Africa is problematic as the majority of fossil localities lack adequate stratigraphic and paleoecological data when compared with coeval Laurasian deposits. Thereby, our comprehension of paleocommunities and paleobiogeographic patterns may be affected by the lack of multidisciplinary approach. Among taxonomically and paleoecological significant clades, lungfishes (Sarcopterygii, Dipnoi) are commonly found in the Cretaceous fresh water, brackish and marginal-marine deposits of Gondwana, although identifiable elements are limited to isolated tooth plates. We provide the first taxonomic identification of dipnoans from the Ain el Guettar Formation of southern Tunisia (Oum ed Diab member, Albian). Identification of tooth plates based on morphological parameters and phylogenetic analyses indicates the co-occurrence in a discrete stratigraphic unit of at least five lineages referable to *Equinoxiodus*, *Neoceratodus*, *Asiatoceratodus* and/or *Ferganoceratodus*, *Ceratodus*, and *Lavocatodus*. This unusually high diversity is unparalleled in the fossil record and is also challenged by an actualistic comparison with extant taxa. We suggest that a series of taphonomic factors significantly inflated observed lungfish diversity in the estuarine and marginal-marine deposits of the Oum ed Diab member. Therefore, we recognize the fossil fauna as representative of a larger, inland paleo-hydrographic system. This study confirms the paleoecological scenario resulted from the analyses on terrestrial reptiles from the Oum ed Diab member.

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### 1. Introduction

Despite the extensive record of lungfish taxa throughout the Paleozoic, Mesozoic and Cenozoic, the record of Cretaceous Gondwanan dipnoans is both stratigraphically and geographically incomplete being primarily represented by isolated tooth plates, rarely associated to more complete remains (Agnolin, 2010; Soto and Perea, 2010; Clack et al., 2011; Cleason et al., 2014). Recent studies based on a widely accepted set of diagnostic morphologic parameters have constrained known taxa to five lineages, corresponding to Linnean-rank families (i.e. *Asiatoceratodontidae*, *Ceratodontidae*, *Lepidosirenidae*, *Neoceratodontidae*, and *Ptychoceratodontidae*), the paleogeographic distribution of which is largely discussed (Agnolin, 2010; Soto and Perea, 2010; and references therein). Conversely, only a few studies have discussed the taphonomic and paleoecologic implication of the co-occurrence in discrete units, or even in single fossil localities, of multiple dipnoan taxa, primarily limiting the discussion to extant species.

In this study, we describe surface-collected dipnoan tooth plates from the Lower Cretaceous deposits of the Tataouine basin of southern Tunisia (Fig. 1).

The Tunisian material offers the opportunity to evaluate a diverse non-tetrapod sarcopterygian community including both coelacanthid and dipnoans, the latter represented by several genera and species. Based on comparison with both the fossil record and present day ecology of lungfish species, such high diversity is unexpected within a single formation. The aim of this study is twofold: first, provide taxonomic information on the “mid-Cretaceous” dipnoans of southern Tunisia, and second, discuss this unique assemblage as a proxy for taphonomic and paleoecological implications. The combination of new parameters for the description of dipnoan tooth plates, high-resolution stratigraphic and sedimentological information, and phylogenetic analyses, provides new tools to interpret unusual assemblages in several Saharan and other Gondwanan localities.

### 2. Material and methods

Dipnoan tooth plates discussed here ( $n = 42$ ) were surface collected from the Albian Oum ed Diab member of the Ain el Guettar Formation beds exposed in the Tataouine region of southern Tunisia. Isolated plates are representative of four localities covering more than 80 km

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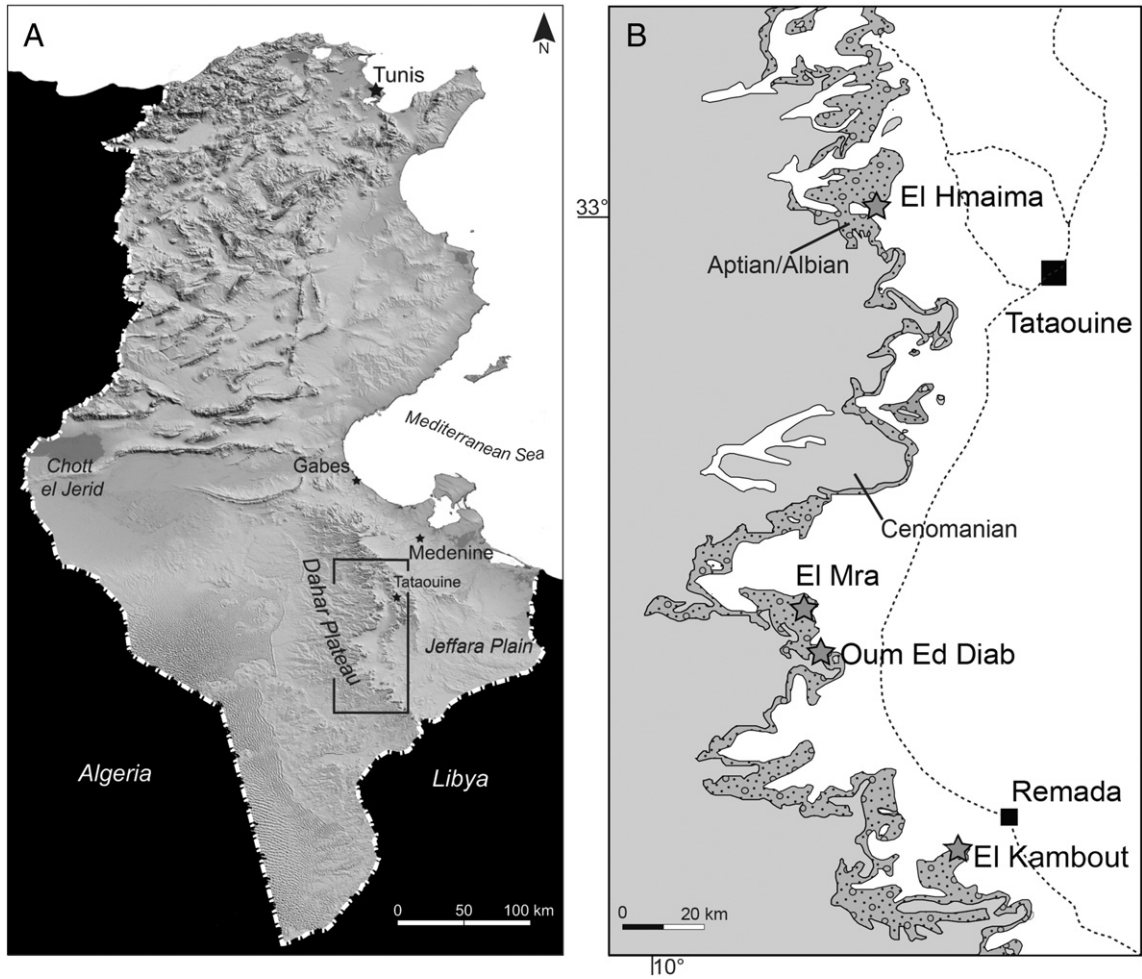


Fig. 1. (A) Reference map of Tunisia showing the study area in the Tataouine region. (B) Simplified geological map of the Dahar Escarpment indicating the El Hmaima, El Mra, Oum ed Diab, and El Kambout localities.

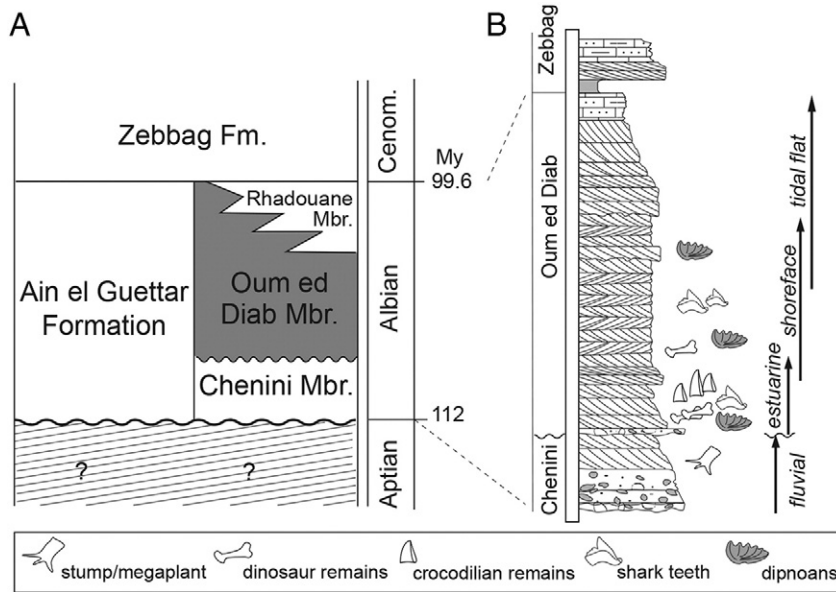


Fig. 2. (A) Stratigraphic nomenclature for the Aptian–Cenomanian deposits of southern Tunisia. Specimens discussed in this study were surface collected from the Albian beds Oum ed Diab member of the Ain el Guettar Formation. (B) Simplified field log showing facies interpretation and the stratigraphic occurrence of vertebrate remains and lungfish in the Oum ed Diab member.

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