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## AUSTRALIA'S OLDEST CROCODILE EGGSHELLS

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### ABSTRACT

Mekosuchine crocodiles were a significant clade of endemic predators from Australia during the Cenozoic. Despite there is an abundant skeletal fossil record of this group, there has been no fossil evidence relating to their reproductive biology. Here, we describe Australia's oldest crocodylian eggshells from the early Eocene Tingamarra Local Fauna from Murgon (Australia). These eggshells are tentatively attributed to the genus *Kambara*, copious in the Tingamarra deposits and being the only crocodylian genus described in the area.

*Keywords:* Cáscaras de huevo, Mekosuchinae, Eoceno, Australia, Biología reproductiva.

### 1. INTRODUCTION

Mekosuchine crocodylians were the predominant predators among other terrestrial species throughout most of the Cenozoic era in Australia. Their decline commenced around the middle Pliocene with the arrival of crocodylines and gavialoids, although both groups coexisted during the Pliocene and up to the late Pleistocene (Willis, 1997; Mead *et al.*, 2002). This indigenous group of foundational crocodylians (Rio & Mannion, 2021) underwent a successful radiation during the late Oligocene and early Miocene, manifesting in various forms such as ziphodont mekosuchine crocodiles like *Quinkana* spp. (Molnar, 1981; Willis & Mackness, 1996; Wroe, 2002; Sobbe *et al.*, 2013) and semi-terrestrial, semi-arboreal mekosuchines like species of *Trilophosuchus* (Willis, 1993; Mead *et al.*, 2002). In the Quaternary, they colonised sever-

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al South Pacific islands, including New Zealand, Vanuatu, and New Caledonia (Scanlon, 2014). Mekosuchines became extinct during the Late Pleistocene mainly from climatic changes, habitat degradation and/or trophic collapse and to a lesser extent predation from humans (Ristevski *et al.* 2023).

The earliest mekosuchine records were unearthed at the early Eocene Tingamarra Local Fauna in Murgon, (Salisbury & Willis, 1996). Abundant cranial and postcranial elements of two mekosuchine species, *Kambara murgonensis* (Willis *et al.*, 1993), and *Kambara implexidens* (Salisbury & Willis, 1996), along with hatchling-sized skeletal elements and eggshells, were discovered at this site (Salisbury & Willis, 1996). This study describes the first mekosuchine eggshells, the oldest found in Australia.

## 2. GEOGRAPHICAL AND GEOLOGICAL SETTING

The Tingamarra deposits are located near Murgon, approximately 270 km northwest of Brisbane, Queensland, Australia. They are part of the 100-meter-thick Oakdale Sandstone Formation (Murphy *et al.*, 1976; Cranfield *et al.*, 2001), consist of green lacustrine clays and muds deposited during the early Eocene ( $54.6 \pm 0.5$  Ma) in a lake and/or swamp environment (Godthelp *et al.*, 1992; Salisbury & Willis, 1996).

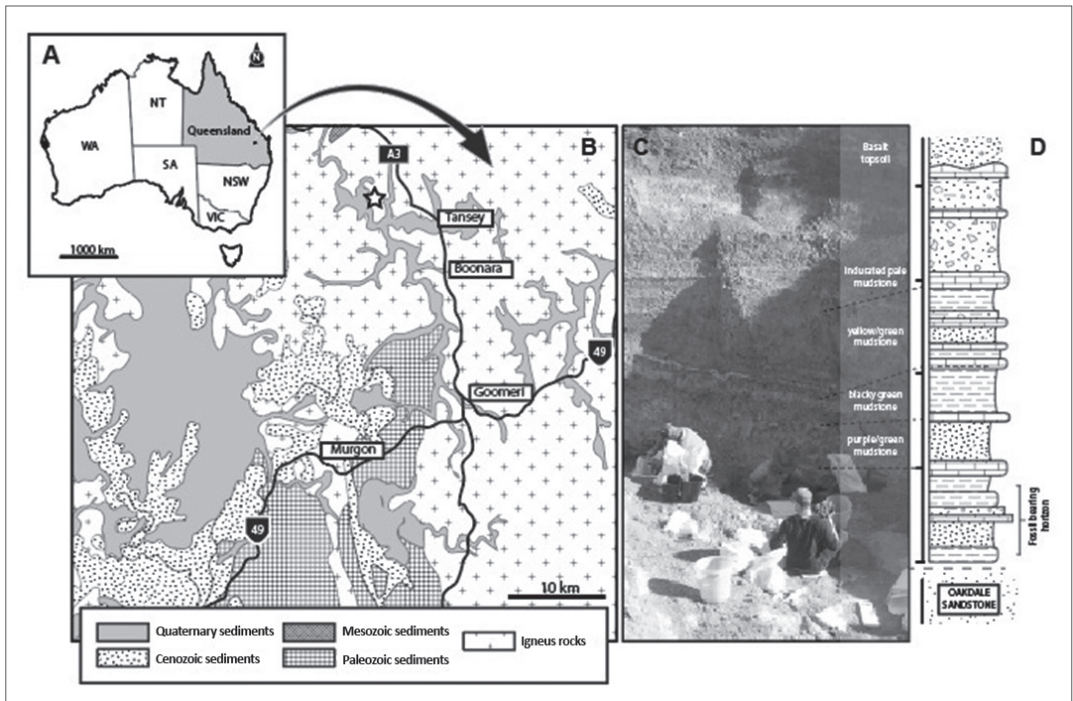


Figure 1. Geographic and geological location of the Tingamarra Local Fauna – Murgon site (Queensland, Australia).

The Tingamarra deposits features a distinctive assemblage predating the final breakup of Gondwana, including Australia's oldest marsupials, frogs, madtsoiid snakes, non-marine birds (including the world's oldest songbirds), the Southern Hemisphere's oldest bat, an archaic condylarth-like eutherian mammal, trionychid turtles, and the earliest record of mekosuchine crocodylians (Godthelp *et al.*, 1992; Cook *et al.*, 2013).

### 3. METHODS

The 13 fossil eggshells examined in the present work were originally collected by the School of Biological, Earth and Environmental Science, University of New South Wales (Australia) during the 1990s expeditions, from screen-washing off the Tingamarra clay, and were stored at the University of New South Wales (Godthelp *et al.*, 1992; Long *et al.*, 2002; Cook *et al.*, 2013).

The eggshells were cut in standard petrographic radial thin-sections (30 microns in thickness). The ultra, micro, and macro features of a single eggshell were captured from the petrographic thin sections under DSX1000 polarised using a light Digital Microscope and from a single eggshell under a Hitachi S-3500N Scanning Electron Microscope (SEM) (Mikhailov, 1997). Morphometric ranges of standard microstructural eggshell characters (Mikhailov, 1997) were obtained from polarised light and petrographic calibrated pictures with ImageJ software (Rasband, 1997).

The descriptive terminology for crocodylomorph eggshell microstructure follows the approaches of Moreno-Azanza *et al.* (2014), Marzola *et al.* (2015), and Jackson & Varricchio (2016).

### 4. RESULTS AND DISCUSSION

Eggshells have an average thickness of 350  $\mu\text{m}$ . The discrete trapezoid eggshell units are nearly as wide as tall, with the interstices limited to the lower fourth of the shell thickness. There is a pronounced horizontal tabular ultrastructure in the outer layer of the eggshell, which bestows a characteristic book-like looking to this region of the shell. Atypical in crocodylians, there are several vesicles of 0,01  $\mu\text{m}$  scattered along the middle layer of CL. The combination of these features is consistent with the described crocodylian eggshell morphology (Hirsch, 1985; Moreno-Azanza *et al.*, 2014; Marzola *et al.*, 2015).

Assigned to the genus *Kambara*, the only crocodile from the Early Eocene period in the area, the earliest crocodylian eggshells found in Australia, along with a combination of adult mekosuchines and hatchlings, suggest that the Murgon site could be a possible nesting site for crocodiles.

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