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A Late Cretaceous madtsoiid snake from Romania associated with a megaloolithid egg nest — Paleoecological inferences

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ABSTRACT

Here we report on the taphonomy and paleoecological implications of the first record of a small madtsoiid snake (*Nidophis insularis*) closely associated with a megaloolithid dinosaur egg nest. Taphonomic and sedimentologic evidence suggest that the snake was buried autochthonously within or nearby the egg nest, with at least partially articulated skeleton. Count of growth rings on the vertebral zygapophyses indicates that the holotype of *Nidophis* belonged to an adult individual approaching the limit of its maximum body size of about 1 m length. The presence of layers of arrested growth on the zygapophyses, together with other independent data (e.g., paleomagnetic data, sedimentology, paleosol development stage, stable isotope geochemistry) indicates that *Nidophis* lived under a semi-arid, seasonally variable subtropical climate, having alternative periods of active feeding. The trunk vertebrae with relatively low neural spines and without prezygapophyseal accessory processes indicate a relatively heavy-bodied, slowly-moving animal, one that probably had a semifossorial habit and was an active forager, but definitively not a dinosaur nest raider as suggested for certain large madtsoiid snakes (the Indian *Sanajeh*). Potential prey items, available around the dinosaur nesting area, probably ranged from small squamate eggs to various small vertebrates. Finally, one anterior trunk vertebra of the holotype displays distinct bite marks left by a small-sized and pointed-toothed predator, most probably a crocodyliform or a theropod, thus documenting that madtsoiids were also preyed upon.

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1. Introduction

The Squamata clusters a monophyletic group of reptiles which includes lizards, snakes and amphisbaenians. The snakes, with more than 3200 species (Uetz, 2013), have deviated from the ancestral four-legged lizard body plan by extreme elongation of vertebral column and limblessness. Attainment of macrostomatan condition of derived alethinophidians represented a major step in the diversification of snakes, by allowing the ingestion of very large prey, contrary to small-gaped fossorial scolecophidians and fossorial alethinophidians (Cundall and Greene, 2000; Vidal and Hedges, 2009). Although the emergence of the most major squamatan crown-groups, including snakes, was considered to have taken place in the Cretaceous (Jones et al., 2013) as an adaptive response to circumstances of major continental breakup and drift, warm global climate, and rapid diversification of terrestrial biotas (e.g., Lloyd et al., 2008; Meredith et al., 2011), new discoveries suggest snakes separated from lizards earlier in time, before or during the Middle Jurassic (Caldwell et al., 2015). Nevertheless, the reconstruction of the early history of alethinophidian snakes is obscured by the scantiness of their fossil record throughout the Late Cretaceous. As currently recognized, most snake assemblages that include members of the exclusively fossil Madtsoiidae were restricted to Gondwanan landmasses (e.g., Rage and Werner, 1999; Rage et al., 2004; de la Fuente et al., 2007; Cavin et al., 2010; LaDuke et al., 2010; Mohabey et al., 2011; Vasile et al., 2013; Albino and Brizuela, 2014; Pritchard et al., 2014). Recent reports of madtsoiid snakes from the Maastrichtian of the Haţeg Basin (Folie and Codrea, 2005; Vasile et al., 2013), in addition to those from the Campanian of Champ-Garimond, southeastern France (Sigé et al., 1997) and from the upper Campanian or lower Maastrichtian of Laño, northern Spain (Astibia et al., 1990; Rage, 1996) imply a more intricate European history of this Gondwanan-related group (Csiki-Sava et al., 2015).

Nidophis insularis Vasile, Csiki-Sava and Venczel 2013, discovered at the Tuştea dinosaur nesting site, in the northern part of

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Haţeg Basin (Fig. 1A), and representing currently the most complete member of this group known from Laurasia, shares with other madtsoiids consistent presence of parazygantral and paracotylar foramina in trunk vertebrae. Among Madtsoiidae it was diagnosed as possessing a relatively short and wide vertebral centrum with sharp hemal keel, a moderately high neural spine showing a posterior tubercle, and a wide, dorso-ventrally compressed zygosphene with a markedly trilobate anterior edge (Vasile et al., 2013). Phylogenetic assessments place *Nidophis* close to the other small European madtsoiid, the late Campanian–early Maastrichtian *Herensugea* from Spain, and tentatively identify two major clades of madtsoiids, one including mainly small-bodied taxa, and a second with medium-large-to-gigantic forms. Intriguingly, *Nidophis*, a member of the small-bodied madtsoiid clade (Vasile et al., 2013), was found associated with a *Megaloolithus* egg nest. Herein we 1) investigate the taphonomy of the megaloolithid-madtsoiid snake co-occurrence from Tuştea, 2) estimate the body size and assess the presence of seasonal growth in *Nidophis*, 3) report physical evidence of predation upon this small madtsoiid, and 4) outline the paleoecological implications of this discovery.

2. Material and methods

The snake material discussed in this contribution, consisting of mainly disarticulated vertebrae and ribs, was found associated with the megaloolithid egg nest no. 20 from the Tuştea dinosaur nesting site (Grigorescu et al., 2010). This nest has been excavated in the summer of 2007, and was removed from the field encased in a plaster and burlap jacket (Fig. 1B, C). The snake material was discovered while screen-washing the relatively small amount (around 170 kg) of matrix resulted from the preparation of the nest.

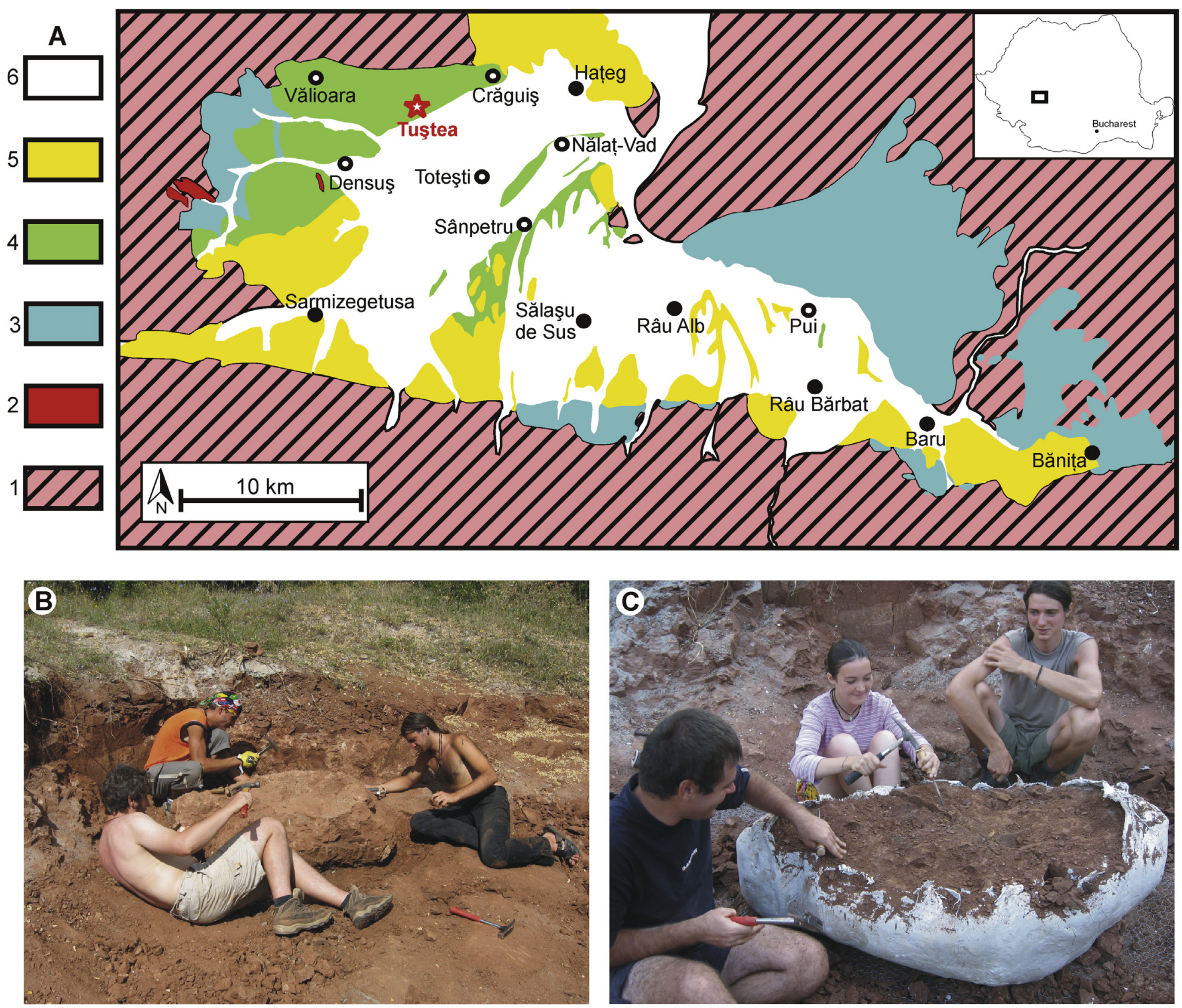

Fig. 1. Location of the Tuştea nesting site within the Haţeg Basin and photographs of nest no. 20 associated with the madtsoiid snake *Nidophis insularis*. **A**: Geological map of the Haţeg Basin; the star marks the location of the Tuştea nesting site. Inset shows the position of the Haţeg Basin in southwestern Romania. Legend: **1**. Crystalline basement; **2**. Banatitic (upper Cretaceous to Paleogene) igneous rocks; **3**. Pre-Maastrichtian sedimentary units; **4**. Maastrichtian continental deposits; **5**. Cenozoic sedimentary units; **6**. Quaternary deposits; **B**: Excavation of nest no. 20 from the Tuştea nesting site; **C**: Removal of sediment from the base of nest no. 20 before being completely encased in a plaster and burlap jacket for protection during transport.

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