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# First fossil gravid turtle provides insight into the evolution of reproductive traits in turtles

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Here we report on the first discovery of shelled eggs inside the body cavity of a fossil turtle and on an isolated egg clutch, both referable to the Cretaceous turtle *Adocus*. These discoveries provide a unique opportunity to gain insight into the reproductive traits of an extinct turtle and to understand the evolution of such traits among living turtles. The gravid adult and egg clutch indicate that *Adocus* laid large clutches of rigid-shelled spherical eggs and established their nests near rivers, traits that are shared by its closest living relatives, the soft-shelled turtles. *Adocus* eggshell, however, was probably more rigid than that of living turtles, based on its great thickness and structure, features that may represent unique adaptations to intense predation or to arid nest environments. In light of the reproductive traits observed in *Adocus*, the distribution of reproductive traits among turtles reveals that large clutches of rigid-shelled eggs are primitive for hidden-necked turtles (cryptodirans) and that spherical eggs may have evolved independently within this group.

**Keywords:** *Adocus*; turtle; egg; reproduction; eggshell; Trionychia

## 1. INTRODUCTION

Fossil egg remains have been attributed to turtles based on similarity of eggshell structure, egg size and egg shape to extant turtle eggs (Hirsch 1983). Such fossils, however, are uncommon and consist primarily of isolated eggs or eggshell fragments (e.g. Hirsch 1983, 1996; Kohring 1999), with the exception of a few egg clutches (e.g. Winkler & Sánchez-Villagra 2004; Jackson & Schmitt 2007; Jackson *et al.* 2008). Because fossil turtle eggs have never been ascribed to a particular taxon due to a lack of intimately associated skeletal remains with eggs, virtually nothing is known about the reproductive traits of extinct turtles.

Here we report on the first fossil turtle to preserve shelled eggs within its body cavity (see Joyce & Zelenitsky 2002 for possible egg pseudomorphs) and

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on an egg clutch, both referable to *Adocus* sp. (Cryptodira: Adocidae). Because adocids and their sister taxon Trionychia (i.e. a clade that includes modern soft-shelled turtles) are basal cryptodirans (Danilov & Parham 2006, 2008; see the electronic supplementary material), these fossil specimens not only provide the first direct information on the reproductive characteristics of a fossil turtle taxon, but also give insight into the evolution of reproductive traits among living turtles.

## 2. GEOLOGICAL SETTING

Both fossil specimens are from the Upper Cretaceous (late Campanian) Judith River Group of southeastern Alberta. The gravid *Adocus* specimen (TMP 1999.63.2) was discovered in a mud-filled freshwater estuarine channel (Eberth & Brinkman 1997) in the Lethbridge Coal Zone of the uppermost Dinosaur Park Formation. The *in situ* egg clutch (TMP 2008.27.1) was recovered from a sandy siltstone representing well-drained levee deposits in the uppermost Oldman Formation. Based on the geographical and stratigraphical relationships between the Oldman and Dinosaur Park formations in southeastern Alberta, the two specimens are inferred to be roughly coeval, with an age of *ca* 75 Myr ago (Eberth & Hamblin 1993).

## 3. IDENTIFICATION AND DESCRIPTION

Our identification of the gravid turtle as *Adocus* sp. is based on the highly diagnostic honeycomb-like carapace and scute sculpture patterns. Necessity for revision of the alpha taxonomy of Cretaceous North American adocids (Meylan & Gaffney 1989) precludes assignment of this specimen to a particular species. The *in situ* egg clutch is also attributed to *Adocus* sp. based on similarity of the eggs with those inside the gravid adult. Here, we describe both macroscopic and microscopic features of the eggs for *Adocus* (see the electronic supplementary material for materials and methods).

The dorsoventrally crushed gravid *Adocus* has a preserved carapace length of 310 mm, with an estimated total length of 405 mm (figure 1a). Eggshell fragments are exposed where the carapace is missing. Curvature of eggshell fragments indicates that the eggs were originally spherical, and approximately 35–40 mm in diameter. Based on the distribution of eggshell fragments, the remains of at least five eggs can be recognized (figure 1a). CT scans reveal that eggshells are also present under the carapace. Additional eggs would have been present in the missing posterior half of the body, which indicates that the total number of eggs produced by that individual would have been greater than the number recognized.

Eggs of the *in situ* clutch (TMP 2008.27.1) are distributed over an oval-shaped area (480 × 350 mm), with some eggs overlapping others (figure 1b). All eggs were completely crushed, except for three. Based on egg and eggshell distribution, the clutch is estimated to have contained 26 eggs. Two complete, relatively uncrushed eggs have diameters of 40 × 42 mm and 40 × 43 mm, indicating that the eggs were originally spherical or subspherical (figure 1c).

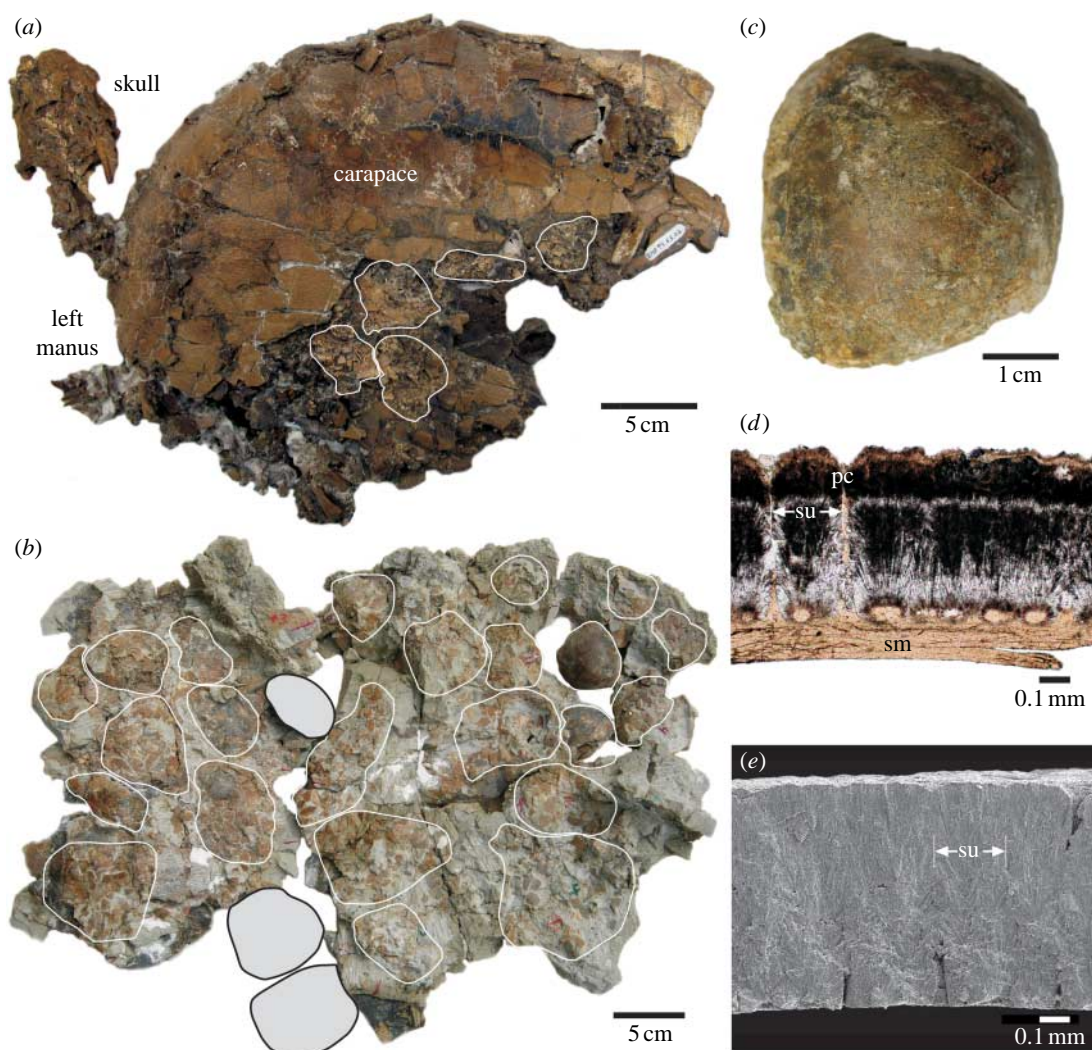


Figure 1. *Adocus* specimens showing: (a) gravid adult (TMP 1999.63.2) in dorsal view, (b) egg clutch (TMP 2008.27.1) in plan view, (c) spherical egg from clutch, (d) eggshell in thin section in plane-polarized light (TMP 1999.63.2) and (e) eggshell fragment under scanning electron microscopy (TMP 2008.27.1). Abbreviations: pc, pore canal; sm, shell membrane; su, shell unit. White outlines represent egg and eggshell clusters. Grey-shaded areas represent eggs removed from clutch.

Thickness of the *Adocus* eggshell differs between the two specimens. Eggshell fragments in the gravid specimen are thinner (0.50–0.65 mm,  $n=70$ ) than those from the clutch (0.73–0.81 mm,  $n=86$ ), presumably because eggshell formation was not complete in the gravid specimen.

The eggshell structure in both specimens is well preserved and still consists of authigenic aragonite. The eggshell is rigid and has a smooth outer surface that lacks ornamentation (figure 1c). The shell units that comprise the *Adocus* eggshell are domed, 2.5–3.5 $\times$  higher-than-wide, and feather laterally in the outer half of the shell (figure 1d,e). In *Adocus* eggshell, pore canals occur between the shell units, although they are rare (figure 1d). Some eggshell fragments in the gravid female preserve a replaced organic shell membrane, approximately one-third the thickness of the calcareous portion of the shell, at the base of the shell units (inner shell surface; figure 1d). Similarity in egg size, shell thickness and eggshell microstructure between the *Adocus* specimens described herein and a turtle clutch from contemporaneous deposits of Montana (Jackson & Schmitt 2007) suggests that the latter is also referable to *Adocus*.

#### 4. DISCUSSION

Features of the eggs inside the gravid *Adocus* reveal that the female died during egg formation, shortly before laying her eggs. The presence of both the organic shell membrane and the calcareous portion of the eggshell indicate that the eggs were in the shell-forming region of the oviducts at the time of death (Aitken & Solomon 1976). The fact that the eggshell of the gravid turtle is nearly as thick as that of the separately collected clutch and that the shell units show feathered structures (which occur only in the outer portion of the eggshell in *Adocus*) indicates that the eggshell was in the later stages of formation. Based on the duration of eggshell formation in extant turtles (Miller 1982), the gravid female probably died within days of oviposition.

The number of eggs produced by the gravid *Adocus* and the carapace length of the female that laid the egg clutch can be estimated based on the correlation between body size and clutch size among extant turtle species (Moll 1979). A least-squares regression of clutch size to carapace length in extant turtles predicts that the gravid *Adocus* could have produced 19 eggs and that the isolated clutch of 26

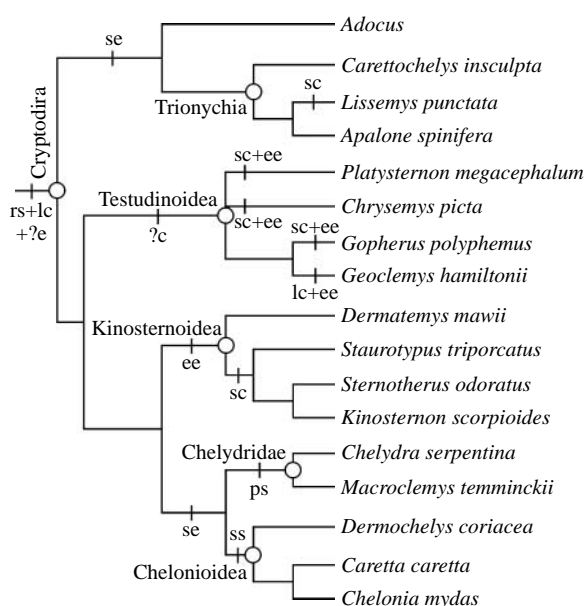


Figure 2. Distribution of reproductive traits in cryptodiran turtles. Abbreviations: ee, elongate eggs; ?e, unknown egg shape; lc, large clutch size (more than 15 eggs); ps, pliable-shelled eggs; rs, rigid-shelled eggs; sc, small clutch size (less than 15 eggs); se, spherical eggs; ss, soft-shelled eggs. The results show that large clutches of rigid eggs are primitive for cryptodirans, whereas round eggs may have arisen independently several times. Node-based taxa are represented by a circle. Phylogenetic tree is based on Danilov & Parham (2006, 2008). Sources of data are provided in the electronic supplementary material.

eggs would have been produced by a female with a carapace length of 495 mm (see the electronic supplementary material).

The egg clutch of *Adocus* was laid in a sandy siltstone of well-drained levee deposits, proximal to a river channel. The eggs of this taxon were rigid shelled, as evidenced by the interlocking nature of tall, adjacent shell units. The lateral feathering of the crystallites in *Adocus* eggshell and its extreme thickness relative to extant turtles (see the electronic supplementary material) probably strengthened the shell. Rigid eggshell is thought to have evolved independently in different turtle clades to prevent predation, microbial infection and desiccation of the eggs (Iverson & Ewert 1991). Based on the thickness of the *Adocus* eggshell and its low number of pore canals, the eggs would have had a low rate of vapour conductance (Ackerman 1980), features that are inferred to be adaptations for incubation in dry nesting conditions in some fossil turtle eggs (Jackson *et al.* 2008).

The reproductive characteristics of *Adocus* elucidated here give insight into the evolution of such characteristics among living turtles. Based on the phylogenetic distribution of reproductive traits (figure 2; see the electronic supplementary material), rigid-shelled eggs and large clutch sizes (more than 15 eggs) are shown to be primitive characteristics for cryptodiran turtles, whereas the primitive condition for egg shape of these turtles is ambiguous. Spherical egg shape may have evolved independently in cryptodirans, although verification of this hypothesis awaits resolution of testudinoid interrelationships (figure 2).

In addition to retaining the primitive cryptodiran traits of large clutch sizes and rigid-shelled eggs, *Adocus* and modern trionychnians (Ewert 1979; Packard & Hirsch 1986; Webb *et al.* 1986; Iverson *et al.* 1993) both lay spherical eggs (figure 2). These shared reproductive traits indicate that they would have been present in the most recent common ancestor of *Adocus* and trionychnians. However, the great thickness and the nature of the eggshell structure unique to *Adocus* may represent either primitive reproductive characteristics of the clade *Adocus* + Trionychia that were lost in trionychnians or unique traits of *Adocus* (or adocids) that may have evolved in response to intense predation or to arid nest environments.

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