

Avian Paternal Care Had Dinosaur Origin

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The repeated discovery of adult dinosaurs in close association with egg clutches leads to speculation over the type and extent of care exhibited by these extinct animals for their eggs and young. To assess parental care in Cretaceous troodontid and oviraptorid dinosaurs, we examined clutch volume and the bone histology of brooding adults. In comparison to four archosaur care regressions, the relatively large clutch volumes of *Troodon*, *Oviraptor*, and *Citipati* scale most closely with a bird-paternal care model. Clutch-associated adults lack the maternal and reproductively associated histologic features common to extant archosaurs. Large clutch volumes and a suite of reproductive features shared only with birds favor paternal care, possibly within a polygamous mating system. Paternal care in both troodontids and oviraptorids indicates that this care system evolved before the emergence of birds and represents birds' ancestral condition. In extant birds and over most adult sizes, paternal and biparental care correspond to the largest and smallest relative clutch volumes, respectively.

Avian reproduction differs from that of other vertebrates in the extensive contribution of males to the care of eggs and young. Males participate in parental care in more than 90% of extant bird species (1). By comparison, males contribute to parental care in fewer than 5% of mammalian species and even more rarely among extant non-avian reptiles (1). The origin of this paternal contribution as well

as the overall parental care system in ancestral birds remains controversial (2, 3). Maternal care predominates in crocodylians (the closest living sister taxon to birds), and the two major clades of extant birds use differing parental care systems. Neognathes (i.e., galliforms through passerines) typically exhibit biparental care, with females and males variably sharing incubation and care of the young (1–3). In contrast, males

of nearly all Paleognathes (ratites, tinamous) incubate and care for the young alone (4). Cretaceous troodontid and oviraptorid dinosaurs share a close ancestry with birds and display some of their reproductive attributes, including multilayered eggshells, asymmetric eggs, and monoautochronic ovulation (5). Additionally, adult *Troodon formosus*, *Oviraptor philoceratops*, and *Citipati osmolskae* have been discovered on top of egg clutches, with some specimens retaining avian-like brooding postures (5, 6). We assessed the parental care system of these dinosaurs with the use of clutch volume–adult body mass models and bone histology data from brooding adults (7).

Complete egg clutches for *Troodon* and the oviraptorids contain 22 to 30 large eggs (7). Total clutch volumes far exceed those of extant crocodylians, more closely matching those of polygamous ratites with similar adult size (Fig. 1). We generated regression models describing the adult

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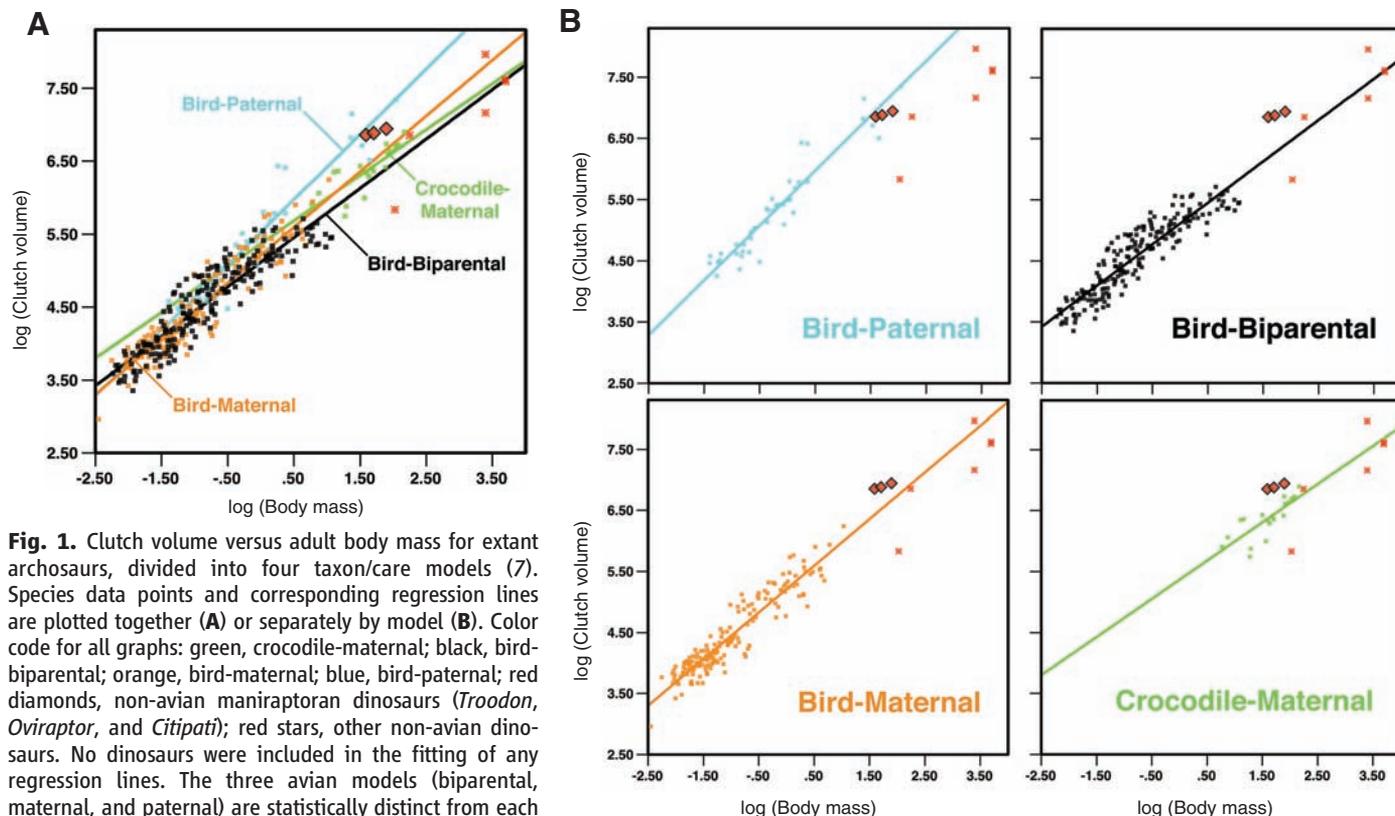


Fig. 1. Clutch volume versus adult body mass for extant archosaurs, divided into four taxon/care models (7). Species data points and corresponding regression lines are plotted together (A) or separately by model (B). Color code for all graphs: green, crocodile-maternal; black, bird-biparental; orange, bird-maternal; blue, bird-paternal; red diamonds, non-avian maniraptoran dinosaurs (*Troodon*, *Oviraptor*, and *Citipati*); red stars, other non-avian dinosaurs. No dinosaurs were included in the fitting of any regression lines. The three avian models (biparental, maternal, and paternal) are statistically distinct from each other (table S2). For birds, paternal care is associated with relatively larger clutch volumes than either biparental or maternal care over most body sizes; biparental care is associated with the smallest relative clutch volumes. The bird-paternal regression most likely accounts for the clutch volume–body mass relationship in *Troodon* and the two oviraptorids.

clutch volume–adult body mass relationships of 433 extant archosaurs (crocodilians and birds) divided into four taxon/care groups: crocodile-maternal, bird-maternal, bird-biparental, and bird-paternal (Fig. 1 and tables S1 and S5). (For this analysis we defined “clutch” as the complete collection of eggs in a nest, regardless of their parentage.) We used corrected Akaike information criterion values (8) to assess which taxon/care group regression model best described the data from the three maniraptoran theropods

(7). Of the four regression models, the dinosaur ratios most closely matched bird-paternal care (Fig. 1) (7). Akaike weights for the four models were bird-paternal, 0.45; bird-maternal, 0.24; crocodile-maternal, 0.19; and bird-biparental, 0.12. Thus, clutch volume–adult body mass ratios of these dinosaurs are 1.8, 2.4, and 3.6 times more likely to fit the bird-paternal model than the bird-maternal, crocodile-maternal, and bird-biparental models, respectively (table S4). Although relatively large clutch volumes occur in

lepidosaurs with maternal care (9–11), a lepidosaur-maternal care model is inappropriate for these three non-avian dinosaurs. Maternal care occurs in only a small percentage of extant lepidosaurs (1, 12) and represents a derived condition within the clade (2, 13); further, lepidosaurs produce parchment-like eggshells and generate their clutches en masse, whereas troodontids, oviraptorids, and extant birds share hard-shelled eggs with multi-layered microstructure and iterative egg production (5, 14).

Female archosaurs extract substantial amounts of calcium and phosphorus from their skeletal tissues during egg formation (15, 16). Consequently, the long bones of reproductively active crocodilians and possibly the primitive theropod *Syntarsus* (17) exhibit extensive resorption cavities within the cortex (15). Many birds possess medullary bone, a complex of irregular bone tissue deposited along the interior endosteal surface of long bones (16). Although medullary bone is largely resorbed during egg laying, birds can retain some medullary bone days to weeks after ovulation (16). Medullary bone was recently reported in the dinosaurs *Tyrannosaurus* (18), *Allosaurus*, and *Tenontosaurus* (19); each represents a clade more distantly related to birds than either troodontids or oviraptorids (20).

Histologic examination (7) of femoral, tibial, and metatarsal cross sections from an adult *Troodon* discovered in direct contact with an egg clutch (5) revealed minimal secondary remodeling, with no medullary bone or evidence of active bone resorption through the diaphyseal length (Fig. 2, A, C, and D). A distal femur and fibula from an adult *Citipati* specimen found in brooding posture also lack medullary bone or large resorption cavities (Fig. 2B). A variety of additional elements from six other brooding maniraptoran adults (21) similarly display no reproductive tissues. If these dinosaurs used long bone tissues as sources of calcium and phosphorus, as in crocodilians, then the absence of resorption cavities implies that the clutch-associated adults were male. If they relied on medullary bone as in birds, the absence of such tissues suggests that these adults were males or postreproductive or nonreproductive females. Some modern birds lack medullary bone, relying instead on dietary intake of minerals for egg production (22). Given their proportionately large eggs (23) and clutches, this strategy seems unlikely for *Troodon* and oviraptorids in the absence of paternal care (24). Thus, histologic examination of *Troodon* and *Citipati* clutch-associated adults provides no evidence to falsify paternal care.

Relatively large clutch volumes like those found in *Troodon* and oviraptorids occur only among extant archosaurs with polygamous mating systems and extensive male care—for example, *Struthio* (ostrich), *Dromaius* (emu), and *Rhea* (4). The presence of a paleognath-like reproductive strategy within these non-avian dinosaurs supports an earlier hypothesis that large *Troodon* clutches represent communal nests (25).

Fig. 2. Bone histology of

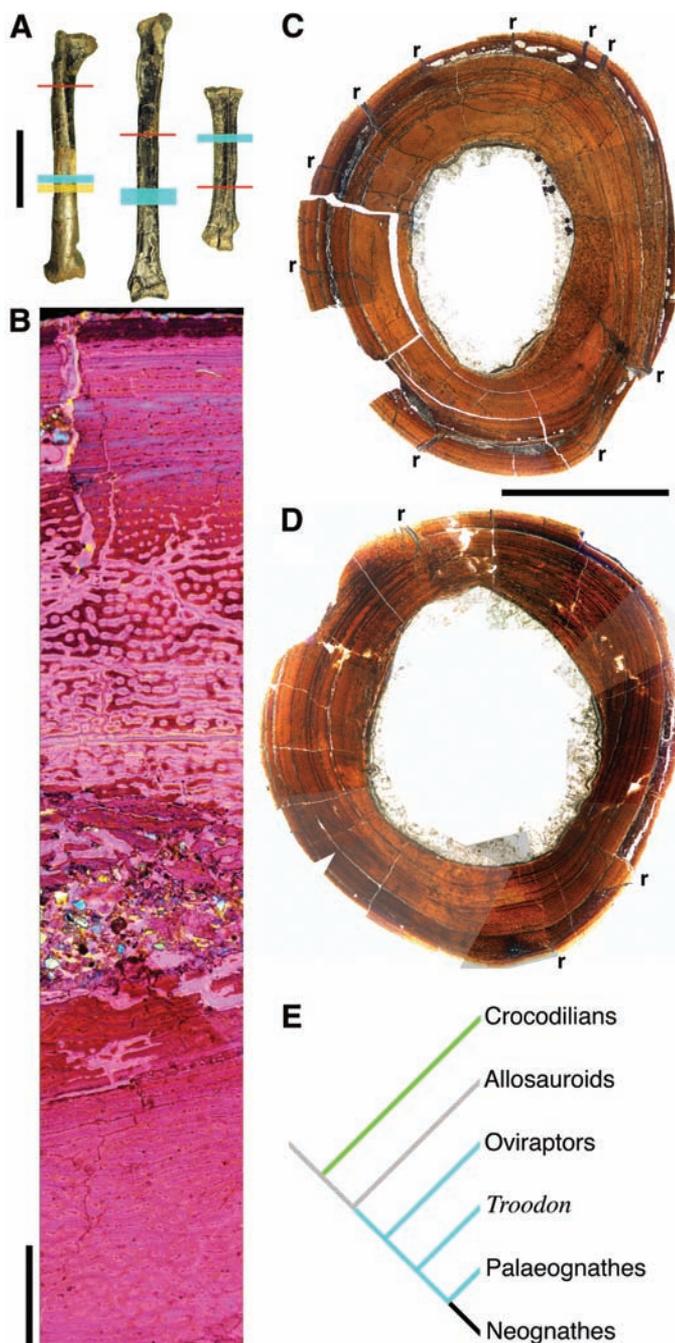
clutch-associated *Troodon formosus* and *Citipati osmolskae* adults. (A)

Troodon (Museum of the Rockies, MOR 748) right femur, tibia, and metatarsus (from left to right). Histologic examinations were conducted on an incomplete left leg. Color bars indicate relative position of thin-section microscope samples (blue, *Troodon*;

yellow, equivalent position of *Citipati* sample) and fracture planes (red, *Troodon*) examined with dissecting scope. Scale bar, 10 cm. (B) Cross section of *Citipati* (Institute of Geology, Mongolia, IGM 100/979) femur from endosteum to periosteum (at top) showing fibrolamellar bone with lines of arrested growth, an external fundamental system, and no reproductive-associated tissues. Fractured zone with matrix and bone shards marks the middle of the section. Scale bar, 1 mm.

(C and D) *Troodon* (MOR 748) tibia (C) and femur (D) composite cross sections consisting predominantly of fibrolamellar bone with minor amounts of endosteal lamellar bone. Both lack medullary bone and cortical erosion rooms. Fossil root or fungal traces (r) invade both bones; branching systems with largely micritic fill penetrate the exterior cortex, producing peripheral bands of irregular erosion and dark staining. Root damage, limited in the femur (right side), extends as a nearly complete circumferential band in the tibia. Scale bar, 10 mm. (E)

Distribution of parental care systems (green, maternal; blue, paternal; black, biparental; gray, equivocal) in modern archosaurs and three clades of non-avian theropod dinosaurs.



Distribution of parental care systems (green, maternal; blue, paternal; black, biparental; gray, equivocal) in modern archosaurs and three clades of non-avian theropod dinosaurs.

Large clutch volume–adult body mass ratios do not occur in dinosaurs more distantly related to birds, such as allosauroids (26). Troodontids and oviraptorids further differ from other more basal dinosaurs in featuring relatively larger eggs, monoautochronic ovulation, and brooding (5, 6, 23). Consequently, two factors may have contributed to the evolution of paternal care: (i) increased energy demands of larger, sequentially ovulated eggs, necessitating females to focus strictly on their own feeding and egg laying (24, 27), and (ii) greater thermal incubation needs of embryos, requiring an attendant brooding adult (28). Because maternal and biparental care systems occur within extant crocodylians, the nature of parental care within more basal theropods and dinosaurs in general remains ambiguous.

Paternal care in both troodontids and oviraptorids (Fig. 2E) implies that this reproductive system originated before the origin of flight and was primitive for Aves. Biparental care of Neognathes would then represent a derived condition. Although paternal care has previously been suggested as the ancestral condition for extant birds (3, 24, 27, 29), it has largely been envisioned as evolving within primitive birds, potentially in conjunction with superprecocial chicks (24, 27). In extant birds, the three parental care strategies correspond to statistically distinct clutch volume–adult body mass relationships (table S2), with paternal care associated with the

largest clutches, maternal care with intermediate-size clutches, and biparental care with the smallest clutches for most adult sizes. This suggests a trade-off in parental investment between overall clutch mass and total parental care.

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Supporting Online Material

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Orbital Identification of Carbonate-Bearing Rocks on Mars

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Geochemical models for Mars predict carbonate formation during aqueous alteration. Carbonate-bearing rocks had not previously been detected on Mars' surface, but Mars Reconnaissance Orbiter mapping reveals a regional rock layer with near-infrared spectral characteristics that are consistent with the presence of magnesium carbonate in the Nili Fossae region. The carbonate is closely associated with both phyllosilicate-bearing and olivine-rich rock units and probably formed during the Noachian or early Hesperian era from the alteration of olivine by either hydrothermal fluids or near-surface water. The presence of carbonate as well as accompanying clays suggests that waters were neutral to alkaline at the time of its formation and that acidic weathering, proposed to be characteristic of Hesperian Mars, did not destroy these carbonates and thus did not dominate all aqueous environments.

Although telescopic measurements hinted at the presence of carbonate on Mars (1–3), subsequent orbiting and landed instruments found no large-scale or massive carbonate-bearing rocks (4, 5). Carbonate in veins within Martian meteorites (6) and possibly at <5% abundance in Mars dust (1, 4) indicates that it is present as a minor phase. The lack of carbonate-bearing rock outcrops is puzzling in light of evidence for surface water and aqueous alteration, which produced sulfate and phyllo-

silicate minerals (5, 7). Carbonate is an expected weathering product of water and basalt in an atmosphere with CO₂ (8, 9), and large-scale deposits, which might serve as a reservoir for atmospheric CO₂, were predicted for Mars (10). Lack of carbonate among identified alteration minerals has compelled suggestions that either (i) a warmer, wetter early Mars was sustained by greenhouse gases other than CO₂ (11, 12); (ii) liquid water on Mars' surface in contact with its CO₂ atmosphere was not present for long enough

to form substantial carbonate (13) (thus implying that minerals such as phyllosilicates must have formed in the subsurface); or (iii) formation of carbonate deposits was inhibited or all such deposits were destroyed by acidic aqueous activity (14, 15) or by decomposition (16). Here we report the detection of carbonate in a regional-scale rock unit by the Mars Reconnaissance Orbiter's (MRO's) Compact Reconnaissance Imaging Spectrometer for Mars (CRISM) and discuss the implications for the climate and habitability of early Mars.

In targeted mode, CRISM acquires hyper-spectral images from 0.4 to 4.0 μm in 544 channels at a spatial resolution of 18 meters per pixel (17). In addition to diverse hydrated silicates (18), CRISM identified a distinct, mappable

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ERRATUM

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Reports: “Avian paternal care had dinosaur origin” by D. J. Varricchio *et al.* (19 December 2008, p. 1826). Incorrect Akaike weights and evidence ratios were used in the comparison of clutch volume–body mass data of three nonavian dinosaurs (Troodon, Citipati, and Oviraptor) to four a priori models generated from extant archosaurs. Erroneous Akaike information criterion values were calculated using base 10 rather than the natural logarithm. The corrected Akaike weights for the four models are bird-paternal, 0.698; bird-maternal, 0.174; crocodile-maternal, 0.093; and bird-biparental, 0.036. Thus, clutch volume–adult body mass ratios of these dinosaurs are 4.0, 7.5, and 19.5 times more likely to fit the bird-paternal model than the bird-maternal, crocodile-maternal, and bird-biparental models, respectively. These corrected values do not alter but instead lend greater support to the original interpretation.

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