Evidence for heterothermic endothermy and reptile-like eggshell mineralization in *Troodon*, a non-avian maniraptoran theropod

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The dinosaur–bird transition involved several anatomical, biomechanical, and physiological modifications of the theropod bauplan. Non-avian maniraptoran theropods, such as *Troodon*, are key to better understand changes in thermophysiology and reproduction occurring during this transition. Here, we applied dual clumped isotope (Δ_{47} and Δ_{48}) thermometry, a technique that resolves mineralization temperature and other nonthermal information recorded in carbonates, to eggshells from *Troodon*, modern reptiles, and modern birds. *Troodon* eggshells show variable temperatures, namely 42 and 29 ± 2 °C, supporting the hypothesis of an endothermic thermophysiology with a heterothermic strategy for this extinct taxon. Dual clumped isotope data also reveal physiological differences in the reproductive systems between *Troodon*, reptiles, and birds. *Troodon* and modern reptiles mineralize their eggshells indistinguishable from dual clumped isotope equilibrium, while birds precipitate eggshells characterized by a positive disequilibrium offset in Δ_{48}. Analyses of inorganic calcites suggest that the observed disequilibrium pattern in birds is linked to an amorphous calcium carbonate (ACC) precursor, a carbonate phase known to accelerate eggshell formation in birds. Lack of disequilibrium patterns in reptile and *Troodon* eggshells implies these vertebrates had not acquired the fast, ACC-based eggshell calcification process characteristic of birds. Observation that *Troodon* retained a slow reptile-like calcification suggests that it possessed two functional ovaries and was limited in the number of eggs it could produce; thus its large clutches would have been laid by several females. Dual clumped isotope analysis of eggshells of extinct vertebrates sheds light on physiological information otherwise inaccessible in the fossil record.

dual clumped isotope thermometry | dinosaur–bird transition | eggshell mineralization | amorphous calcium carbonate

Dinosaurs are part of a diverse group, known as the Archosauria, and are evolutionary intermediates [i.e., phylogenetically bracketed, sensu Witmer (1)] between the only known living archosaurs, crocodiles, and birds (Fig. 1). Consequently, some of their anatomical, reproductive, and physiological characters are shared with reptiles and/or birds, whereas others are transitional between the two. Although modern reptiles and birds can potentially represent analogs to infer aspects of dinosaur paleobiology, these two living groups tend to have a radically different biology (2, 3). One striking difference is their thermophysiology: Reptiles are ectotherms (internal body temperature is directly influenced by the surrounding environment), whereas birds are endotherms (body temperature is kept constant by heat produced through high metabolic rates) (4). Another major difference concerns their reproductive systems. Reptiles produce small eggs relative to their body size (5, 6), have two functional ovary-oviduct systems (7), and their oviposition strategies, although diverse, usually involve simultaneous production of multiple eggs in both ovaries (anoline lizards are an exception as they alternate production from one ovary to the other) (8). As the closest living reptiles to dinosaurs, crocodylians are of particular interest: While sharing many generalized reproductive traits with reptiles, they possess a more specialized trait known as "archosaurian assembly line," where different eggshell layers form in different portions of the oviduct (9). Birds also possess this trait, but they generally produce fewer, relatively large eggs (10) that are formed iteratively (rather than "en masse") via a single ovary-oviduct system (11). Another difference between living reptiles and birds reflects the influence of thermophysiology on reproduction. Reptiles, as ectotherms, generally incubate their eggs at environmental temperature and/or utilize heat generated by plant decomposition in buried nests. In contrast, nearly all bird species, as endotherms, use body heat for contact incubation of exposed eggs (open nests) in a behavior known as brooding.

Although direct investigation of the reproductive system of dinosaurs is generally challenged by absence of conclusive soft-tissue evidence, comparative analysis of the eggs of dinosaurs, reptiles, and birds can provide insight into this important aspect of dinosaur

Significance

The dinosaur–bird transition is among the most fascinating events in evolutionary history, but several biological aspects such as changes in reproductive system, nesting strategy, and body temperature are still poorly understood. Dual clumped isotope thermometry (Δ_{47} and Δ_{48}) can shed light on these biological aspects in fossils. Our results show that eggshells of modern reptiles and birds differ in their isotopic compositions. Interestingly, analyses of eggshells of *Troodon*, a non-avian theropod, reveal that it retained a slower, reptile-like mineralization to produce its eggs, despite having already evolved the capacity of changing its body temperature (heterothermic endothermy) like modern birds. Our findings also suggest that *Troodon* possessed two functional ovaries and that their nests were shared by multiple females.

biology. Most dinosaurs are considered to have laid eggs "en masse", incubating them in covered nests like reptiles (12). However, certain derived theropods (e.g., oviraptorids) appear more transitional: They laid eggs iteratively and "brooded" them [it is unclear whether they used body heat for incubation (21, 22)] in open or semi-open nests more similar to birds (23, 24), but they retained two functional oviducts like reptiles (24, 25). For *Troodon*, a derived theropod very close to the origin of birds (Fig. 1), exhibiting many bird-like egg characteristics (e.g., two-layered eggshell, asymmetric egg shape) (26–29), the evidence for the number of functional ovaries in its reproductive system remains inconclusive(24, 26).

With respect to thermophysiology, recent studies suggest the presence of high metabolic rates in most dinosaurs (18, 30), but estimates of absolute body temperature are required to understand their thermoregulatory strategy. Clumped isotope thermometry (i.e., measurement of Δ_{47}, which allows reconstruction of carbonate precipitation temperature without prior knowledge of the original fluid isotopic composition) has already been used to reconstruct dinosaur body temperatures (19, 31–35). Specifically, studies on non-avian theropods indicate that some might have possessed body temperatures lower than modern birds but higher than ambient temperature, while others might have possessed body temperature

very close to those of birds (19, 31, 34). However, confirmation that previous Δ_{47}-derived body temperature estimates were not biased by disequilibrium processes, potentially occurring during mineralization, is still needed. Dual clumped isotope thermometry is a recently developed technique combining measurements of Δ_{47} and Δ_{48} (36): These two values are bound together by a temperature-dependent equilibrium relationship, deviations from which reflect isotopic disequilibrium. Therefore, this technique allows us not only to validate Δ_{47}-based temperatures but also to better understand the underlying mineralization processes causing isotopic disequilibrium patterns (37, 38). Here, we apply the dual clumped isotope thermometer to eggshells of *Troodon*, as well as to modern reptiles, modern birds, and synthetic calcites, to 1) reliably reconstruct the body temperature of *Troodon* and to 2) compare eggshell mineralization processes among derived non-avian theropods, reptiles, and birds, in order to better understand the dinosaur–bird transition.

Results

Dual clumped isotope data are presented in Figs. 2 and 3 and *SI Appendix*, Table S1. *Troodon* eggshells, like reptiles, are characterized by Δ_{47} and Δ_{48} values indistinguishable from the calcite
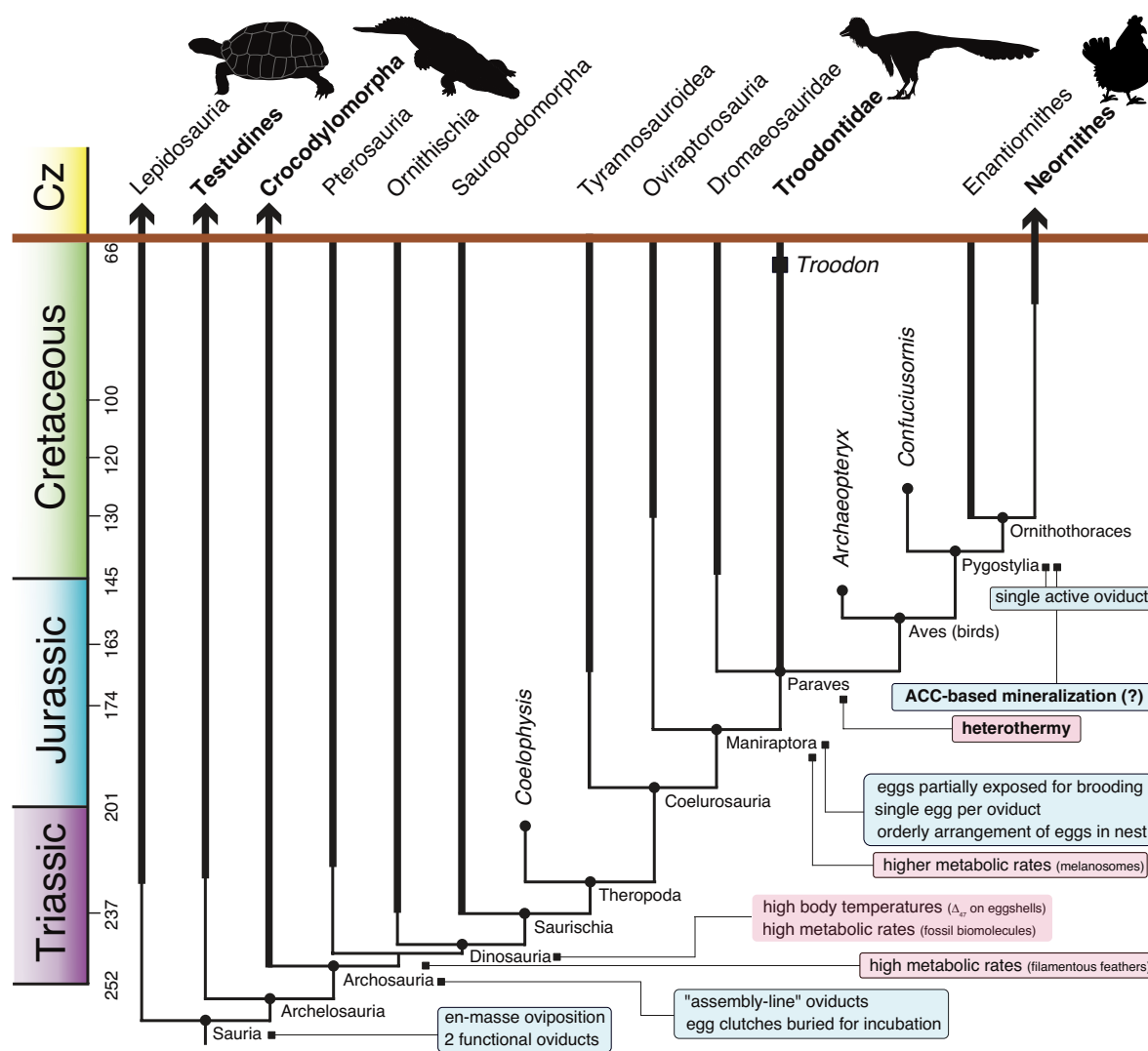

Fig. 1. Cladogram representing the phylogenetic relationship of the organisms analyzed in this study. The phylogenetic relations between taxa are based on Tanaka et al. (12), Xu et al. (13), Zelenitsky et al. (14), Lyson and Bever (15), Zelenitsky and Therrien (16), Yang et al. (17). The thicker lines represent direct fossil evidences, while the thinner lines are indirectly reconstructed temporal distributions. occurrence of reproductive and metabolic traits are based on Wiemann et al. (18), Dawson et al. (19), Li et al. (20), Xu et al. (13). Traits inferred in this study appear in bold font.

equilibrium line, whereas bird eggshells and synthetic calcites show significant departures from it (Figs. 2 and 3). An ANOVA test confirms that *Troodon* and reptiles share equilibrium Δ_{47}-Δ_{48} patterns, while birds exhibit disequilibrium patterns. *Troodon* data are interpreted by comparison with reptiles and birds.

Discussions

Inferred Body Temperatures of Modern Species. The observation that reptile eggshell Δ_{47} and Δ_{48} values plot indistinguishable from the calcite equilibrium line implies that their clumped isotopic compositions were exclusively controlled by temperature. In fact, Δ_{47}-based body temperatures are consistent with monitored ambient temperatures, as expected for the ectotherms analyzed in this study (*Materials and Methods* and *SI Appendix,* Tables S1 and S2). In contrast, bird eggshell Δ_{47} and Δ_{48} values plot off equilibrium and therefore their isotopic compositions are controlled by disequilibrium effects [i.e., rate-limiting kinetics (37)] in addition to temperature. Notably, all Δ_{48} values show significant positive disequilibrium offsets, whereas Δ_{47} values are all indistinguishable from, or very close to, the expected values based on birds' body temperatures (*SI Appendix,* Table. S2) (40).

***Troodon* Was a Heterothermic Endotherm Dinosaur.** All *Troodon* eggshells, sourced from the upper Oldman Formation (upper Campanian, ~76.8 to 74.3 Ma) of southern Alberta—Canada (*SI Appendix,* Fig. S1), have been screened for diagenesis and no evidence of extensive alteration was found (*Materials and Methods,* *SI Appendix,* Tables S2–S4): Eggshells show mostly dark cathodoluminescence images, and they have well-preserved microstructures and present low trace-element contents. From these observations, we consider that the eggshells were not significantly affected by secondary recrystallization (see *SI Appendix* for further discussion) and are thus suitable for

investigation using dual clumped isotope thermometry. *Troodon* eggshells present isotopic equilibrium patterns comparable to reptiles (see *SI Appendix*: ANOVA test), implying that their isotopic composition directly reflects eggshell formation temperature (Figs. 2 and 3) and thus body temperature. Measured Δ_{47} of three *Troodon* eggshells corresponds to temperatures of 42 ($\pm$ 2) °C, fully comparable with body temperatures of modern birds, whereas a fourth eggshell shows a colder temperature of 29 ($\pm$ 2) °C. Notably, this temperature range was reported in previous studies on well-preserved eggshells from non-avian theropods (19, 31, 34). Temperatures of about 42 °C for *Troodon* were obtained by Dawson et al. (19) (on one of the specimens also analyzed here) and are comparable with modern birds, suggesting that *Troodon* possessed the capacity to achieve high metabolic rates, an observation in line with results from previous studies on dinosaur skeletal morphology and bone vascularization (41), melanosome morphology (20), mathematical models (42), and recently discovered metabolism-related biomolecules (18). In addition, high metabolic rates and endothermic thermoregulation represent the only possible explanation for the perennial residence of troodontid hatchlings at paleolatitudes of 80 to 85°N (43–45). Given the high body temperature indicated by several eggshells, it is possible that *Troodon* could have used body heat, at least in part, for egg incubation, not inconsistent with the previously hypothesized brooding behavior in *Troodon* (24). Similarly, high temperatures of 37 to 40 ($\pm$ 3) °C were also obtained from eggshells presumed to belong to more basal theropods (abelisaurids) by Laskar et al. (34). The colder temperature estimated here for *Troodon* (29 °C) also aligns well with those presented in previous studies: Eagle et al. (31) reported temperatures of about 29 to 30 °C in three well-preserved oviraptorids (a group of non-avian maniraptoran theropods more basal than *Troodon,* Fig. 1) and Dawson et al. (19) reported a temperature of 29 °C in two different specimens of *Troodon*. Thus, our data further support the interpretation
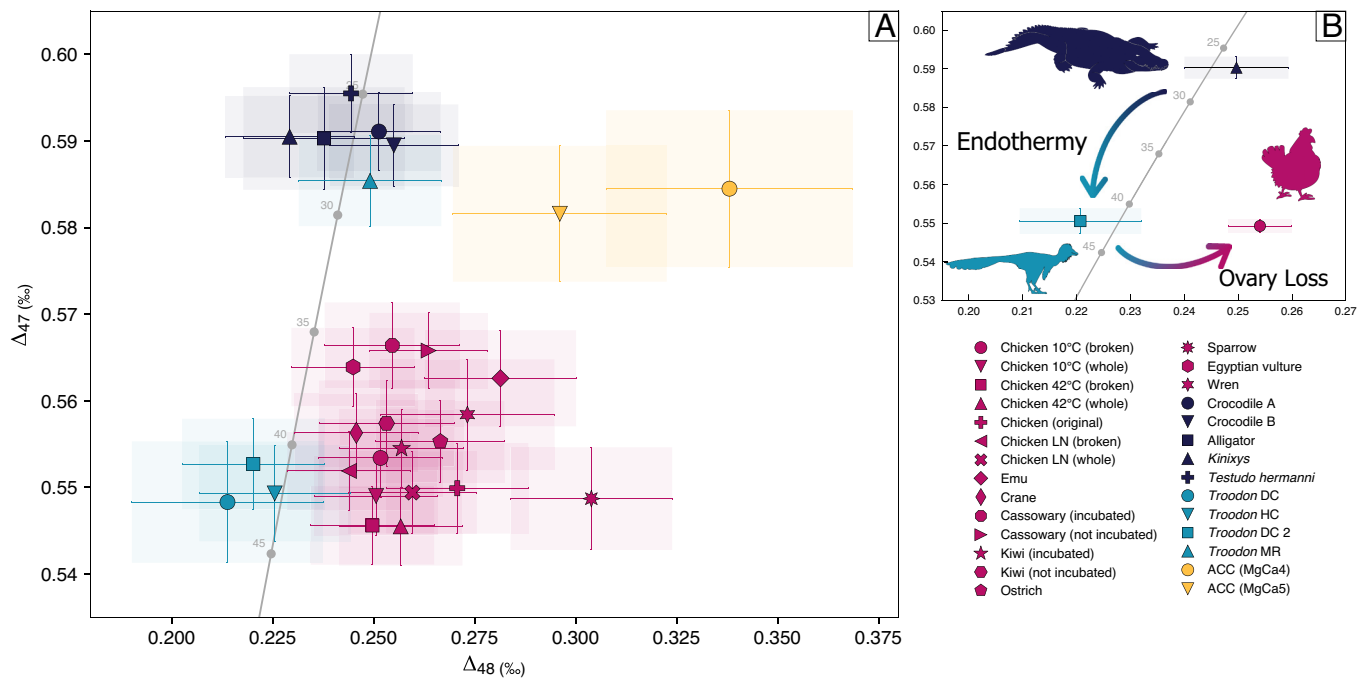

Fig. 2. Comparison of eggshell Δ_{47}-Δ_{48} data of reptiles, birds, and *Troodon*. (*A*) Modern reptiles, birds, and Troodon are grouped in three distinct populations in Δ_{47}-Δ_{48} space. Two high Mg-calcite samples, each derived from the transformation of ACMC at 25 °C, show Δ_{47}-Δ_{48} disequilibrium patterns very similar to birds. All values are reported as CDES 90, relative to the calibration of Fiebig et al. (39). (*B*) Representation of the two major evolutionary steps (endothermy and ovary loss) recorded in our dataset (the average values and relative errors were calculated pooling together data from chicken, *Troodon*, and Crocodylia eggshells).
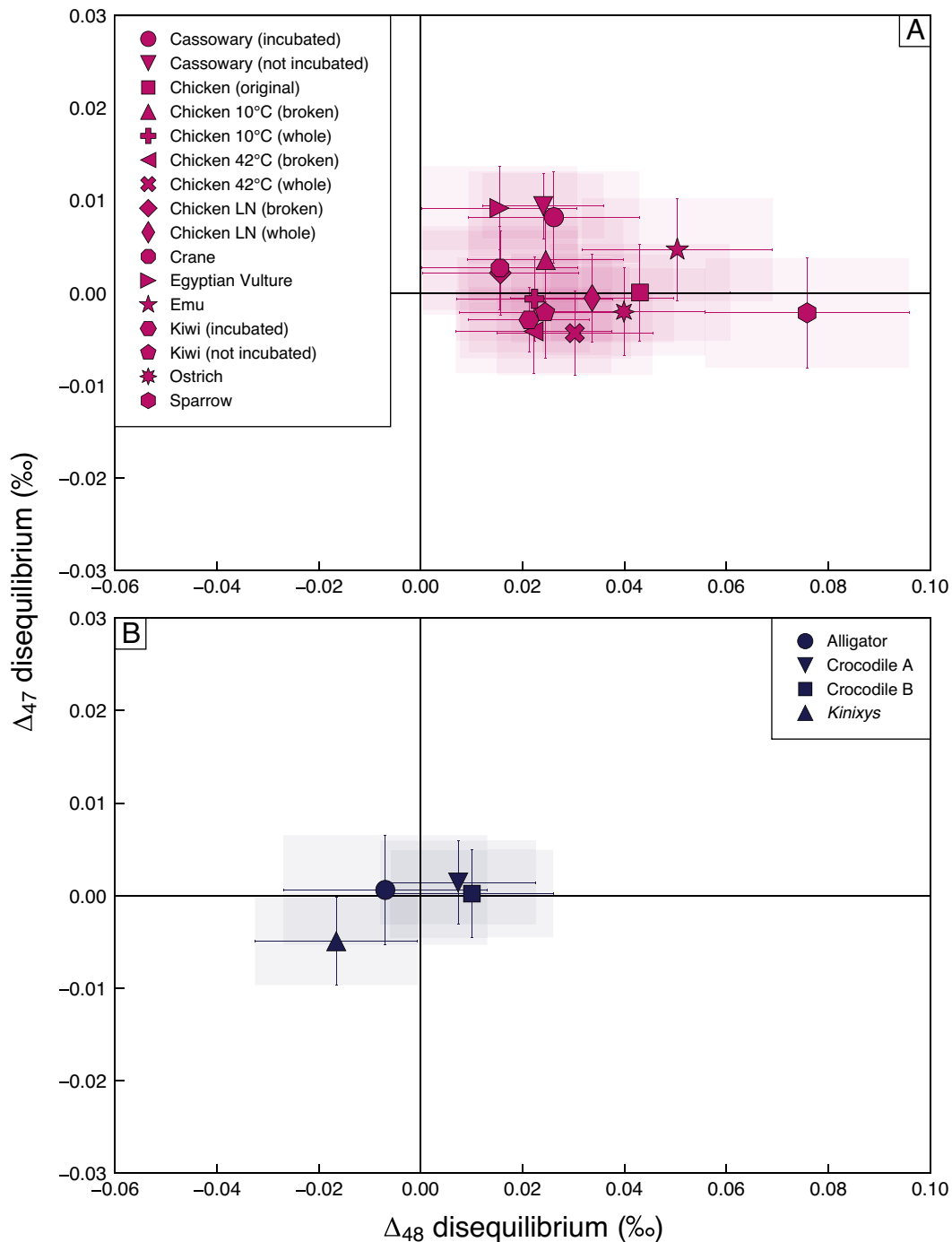
Fig. 3. Extent of Δ_{47}- and Δ_{48}-disequilibrium recorded in eggshells of birds (*A*) and reptiles (*B*). See *Materials and Methods* for details concerning the calculation of Δ_{47} and Δ_{48} disequilibrium values.

originally proposed by Dawson et al. (19) of a heterothermic strategy for *Troodon*.

Heterothermy is a strategy that allows an animal to change its body temperature according to specific needs or environmental inputs. The prevalence of heterothermy among modern taxa (e.g., mammals and birds) and its inherent transitional nature led some authors to postulate that heterothermy might have been a key driver in the establishment of "true endothermy" (46, 47). While it has recently been discovered that some ectotherms can voluntarily increase their body temperature during reproduction (46), the most common strategy for extant endotherms is to reduce metabolic rate to minimize energetic expenditure by entering a

state of torpor (48, 49). Torpor is defined as a drop of at least 5°C in body temperature (48) but the variation amplitude can be up to 9 ± 3 °C (50), thus well in line with *Troodon* reconstructed body temperatures of 29 to 42 °C. Daily bouts of torpor are observed in several taxonomically diverse groups of modern birds (13 out of 30 orders), though complexities in observing this behavior might have led to underestimation of its true taxonomic distribution and diversity (48). In fact, heterothermic endothermy is so phylogenetically widespread that it has been suggested to be a plesiomorphic (ancestral) characteristic for all birds (51–53). This supports our hypothesis that heterothermy, like numerous other traits (13), first evolved among non-avian theropods, specifically in

paravians-like *Troodon*. It must be noted that torpor and reproduction have been often considered incompatible from an energetic point of view (54); however, more recent studies and evidences suggest that use of torpor during reproduction might be foundational to the survival of several species (48). Although torpor is largely used to survive at cold temperatures, it is also applied in response to food scarcity or unpredictable weather (49). During the Campanian, the mean annual temperature in the sample area was reconstructed at 12 to 13 °C (55, 56), with summer months of 25 to 28 °C (19) and cold months of 5 to 8 °C (57, 58), although clumped isotope measurements of penecontemporaneous paleosols from Montana suggest even colder winters (−5 °C) (58). These temperatures appear to be sufficiently low to trigger torpor (48), but a more extensive dataset is needed to conclusively understand the extent and environmental causes of this behavior.

Eggshell Mineralization and Δ_{47}-Δ_{48} Disequilibrium in Birds. To test whether environmental temperature after oviposition has any impact on the eggshell isotopic composition, chicken eggshells were collected and stored at different temperatures prior to analysis (*Materials and Methods*). All Δ_{47} and Δ_{48} values derived from these samples are indistinguishable within error from one another (Figs. 2 and 3). This evidence, paired with the absence of any trace of organic matter contamination (see S6-S7), proves that the rate-limiting process causing positive offsets from Δ_{48} equilibrium in chickens occurs during biomineralization. Generally, disequilibrium isotope signatures in a precipitating calcite are generated if the rate of carbonate precipitation exceeds the rates of isotopic equilibration between dissolved inorganic carbon species, water, and calcite. The high precipitation rate (~0.33 g/h) characterizing chicken eggshell mineralization, unrivaled in nature (59), is enabled by involvement of amorphous calcium carbonate (ACC) (59–61), which facilitates nucleation rates up to 100 times faster than the ion-by-ion mechanism (62). Transmission electron microscopy investigations indicate that ACC is formed within extracellular vesicles present within both uterine epithelial cells and uterine fluid (60, 61). These vesicles are successively guided by proteins to the mineralization site, where ACC is deposited before final transformation to calcite (60, 61). To investigate if the disequilibrium signature could arise from the involvement of ACC in eggshell formation, we analyzed two samples of synthetic high-Mg calcite, produced by direct transformation of amorphous calcium magnesium carbonate (ACMC) at 25 °C. These two samples show a remarkable similarity with the observed Δ_{47}-Δ_{48} disequilibrium patterns in bird eggshells in that Δ_{47} closely corresponds to carbonate formation temperature, whereas Δ_{48} exhibits a significantly positive disequilibrium offset (Fig. 2). Moreover, both synthetic samples are characterized by a positive $\delta^{18}O$ offset (+1‰) from equilibrium (63) comparable with the positive disequilibrium $\delta^{18}O$ offsets measured in chicken eggshells both here and in the study by Lazzerini et al. (64) (*SI Appendix,* Fig. S5). Though, at this stage, the exact process causing isotopic disequilibrium remains unknown, these similarities constitute empirical evidence that the avian-specific isotopic disequilibrium signatures could be indicative of involvement of rapidly grown ACC in eggshell formation. This contention agrees with the absence of the disequilibrium signature in eggshells from reptiles, which mineralize much slower and less effectively than birds and for which ACC involvement has not been documented to date.

Implications for the Dinosaur–Bird Transition. Although birds are known to possess one functional ovary (a second one is present but vestigial) (11), it is uncertain whether the evolutionary reduction

from two functional ovaries (the ancestral condition for all amniotes, Fig. 1) initially occurred among non-avian theropods during the dinosaur–bird transition or among birds. For birds, this functionality loss has been explained as a way to reduce their body mass, thus facilitating more efficient flight (11). Since birds produce larger, more calcified eggs (11) than non-avian theropods, the loss of an ovary would lead to an inevitable increase in the time necessary to lay a clutch of the same number of eggs (clutch size). If not counterbalanced by other adaptations, this condition might expose birds to adverse natural events and predators for longer time (65, 66), thus potentially reducing their reproductive success. In this sense, switching to an ACC-based mineralization can be interpreted as a strategy to produce calcite faster, increasing the overall mineralization and counterbalancing the ovary loss.

No definitive evidence has been found so far concerning the presence of two functional ovaries in *Troodon*, uncertainties stemming from the low preservation potential of soft tissues (e.g., reproductive organs), and complexities in their correct interpretation [see Zheng et al. (67) and Mayr and Manegold (68)], which force reliance on indirect inferences (24, 26). One study indicates that *Troodon* retained two functional ovaries, implying the reduction occurred in birds (24), whereas a later study indicates that *Troodon* had one functional ovary, suggesting the reduction occurred instead in non-avian dinosaurs close to birds (26). As observed in reptiles, *Troodon* eggshells do not present the isotopic disequilibrium signature characteristic of birds. It is therefore reasonable to interpret the equilibrium isotopic composition of *Troodon* eggshells as evidence for the absence of an ACC-based mineralization. By consequence, the observation of a slow, reptile-like mineralization implies that these non-avian theropods possessed two functional ovaries, supporting the hypothesis that ovary loss initially occurred in the bird lineage (11).

The Link between Mineralization Effort and Δ_{48} Disequilibrium. Since the exact duration of eggshell mineralization (different from the whole egg production) is unknown for almost all animals studied herein and considering that crocodilians mineralize multiple eggs simultaneously, we compare the different mineralization processes by estimating the mineralization effort (grams of calcite per clutch size, divided by animal body mass) each animal has to exert to produce a full clutch. Reptiles are all characterized by very low mineralization efforts (below 0.006) and no Δ_{48} disequilibrium, while birds have higher efforts (above 0.008) and a marked Δ_{48} disequilibrium (Fig. 4). One potential explanation for the observed difference is that laying a clutch of bigger size or producing more calcified eggs would require too much time to be advantageous for a reptile-like mineralizer, whereas both could be achieved by the ACC-based, bird-like mineralization. Based on the absence of Δ_{48} disequilibrium, it can also be assumed that *Troodon* mineralization efforts were either equal to those of modern reptiles or at least lower than that in modern birds. That is, it is possible to estimate the number of eggs produced by an individual *Troodon*. Previous studies on *Troodon* allow us to estimate its body mass at about 50 kg (24) and that each egg contained 50 to 60 g of calcite (egg surface area minus pore area per thickness per calcite density) (69). Consequently, previous calculation can be used to estimate the clutch size for a single *Troodon* individual at four to six eggs (Fig. 4). This supports the hypothesis that *Troodon* nests, which can contain up to 24 eggs, were likely communal (70), contributed to by four to six females. This number finds its analogues in modern birds like ostriches, which also share communal nests with two to seven
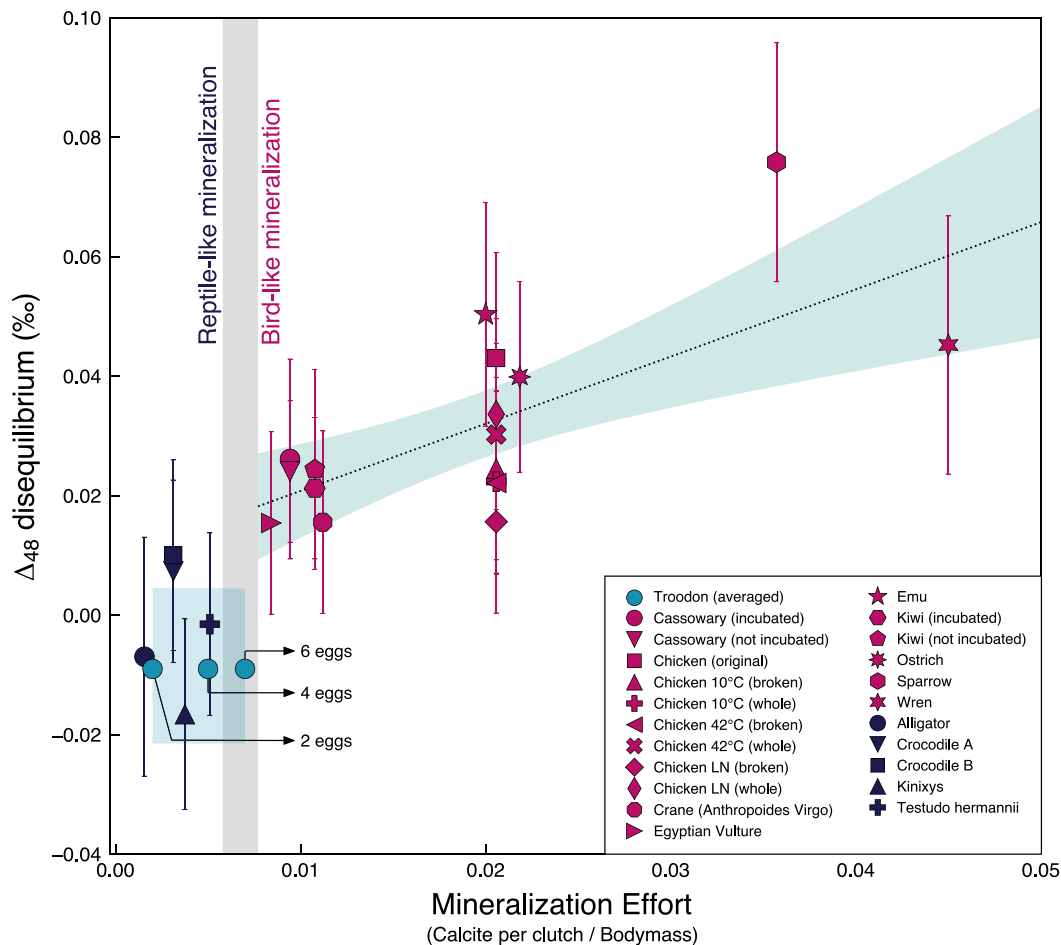
Fig. 4. Relationship between Δ_{48} disequilibrium values and mineralization effort. *Troodon* dots are based on the average Δ_{48} disequilibrium and the mineralization effort according to different clutch size. The two populations of mineralization effort are significantly different (*P*-value = 0.017).

hens per nest (71). Although a clutch size of two eggs for a single *Troodon* individual is theoretically possible according to our calculations, this would result in an unusually high number of individuals (n = 13), contributing to a single nest, a condition that has no modern analogs.

Hypothesis on the (re-)evolution of ACC in Vertebrates. ACC-based (also known as particle-by-particle in opposition to the "traditional" ion-by-ion) calcification has evolved convergently in several invertebrate groups that possess the capacity of simultaneously using both calcification pathways, although one of the two processes always appears to be quantitively dominant (72). Given that ACC-based calcification is present in tunicates (72), the sister taxon to vertebrates, it would be reasonable to expect the toolkit necessary for ACC precipitation to be present in all vertebrates, thus opening the question of why reptiles and non-avian dinosaurs appear to not rely on it. It should be considered that ACC allows a much faster precipitation (up to 100 times faster) (62), but it also requires a much faster mobilization of calcium. While marine invertebrates have access to a virtually infinite pool of dissolved Ca^{2+} in the ocean, terrestrial vertebrates are forced to rely on food intake and bone resorption, which may have a limiting effect on the rate by which the organism can mobilize it. That is, ACC precipitation does not need to (re-)evolve in vertebrates, but it would need to be uninhibited by an increased Ca^{2+} availability. It might be argued that when the second ovary is lost under the evolutionary pressure to reduce weight for improved flight performance (11), the resulting higher

concentration of resources in just one oviduct could have allowed an ACC-based precipitation of calcite. In another possible scenario, ACC-based precipitation could have been facilitated by increased calcium availability thanks to improved intestinal absorption and/or an exaptation of the medullary bone [although Prondvai (73) questioned its role during eggshell formation]. The latter hypothesis is supported by the observation that, during reproduction, Ca^{2+} blood concentrations are much higher in birds than in reptiles [14 (74) vs. 6.6 (75) mM/L, respectively].

Conclusions

Dual clumped isotope analysis on modern and fossil eggshells reveals that the non-avian *Troodon* was not only able to achieve high body temperatures like modern endotherms (~42 °C), but that it was also a heterotherm, capable of voluntarily reducing its metabolic rate like modern birds. Our data also demonstrate that *Troodon* retained slow, reptile-like eggshell mineralization, likely not relying on ACC as precursor phase. Based on this evidence, we argue that *Troodon*, like reptiles, possessed two fully functional ovaries and could produce only a limited number of eggs (n = 4 to 6). Crucially, our study highlights that dual clumped isotope thermometry can be used to extract physiological information from mineralized fossil material, expanding our toolset to reconstruct physiological information for extinct taxa, especially in the absence of reliable soft-tissue evidence.

Materials and Methods

Sample Material—Bird Eggshells. Six chicken eggs were collected from a local producer (Frankfurt am Main, Germany). In order to obtain freshly laid eggs, the collection took place immediately after oviposition. Two eggs were stored in liquid N_2 (-196 °C), two eggs were stored inside an incubator kept at 42 °C, and two were stored inside a second incubator kept at 10 °C. For each pair of eggs, one was broken to separate the eggshell from the albumen, while one was kept intact. Intact eggs and eggshells were stored for 14 d at these respective temperatures before preparation for isotopic analysis. An additional chicken eggshell from New Haven (Connecticut, USA), collected in 2012 and analyzed by Dawson et al. (19) was added to the analytical session. Sparrow (*Passer domesticus*), Wren (*Troglodytes aedon*), and Emu (*Dromaius novaehollandiae*) eggshell aliquots were also originally analyzed by Dawson et al. (19). Two eggshells of Kiwi (*Apteryx australis*) and two of Cassowary (*Casuarius casuarius*) were provided by the Frankfurt Zoo. For both species, one egg was incubated by the producing animal, whereas the other was not. Ostrich (*Struthio camelus*) eggshell was provided by an ostrich farm in the Little Karoo region of South Africa.

Sample Material—Reptile Eggshells. Terrestrial ectotherms are known to be subject of daily body temperature fluctuations (76, 77), so determination of mineralization temperatures is less straightforward. To avoid complications, reptile eggshells were selected to present the minimum possible variance: Being ectotherms, all body temperature variations in reptiles must be driven by external factors and thus, if the environmental temperature is stable so will be the body temperature. Eggshell from *Kinixys belliana* (turtle) was provided by the Leipzig Zoo (Germany) where the animal was kept in a terrarium, which in winter is kept at the minimum constant temperature of 24 °C. The analyzed egg was collected in January 2021. Crocodile eggshells (*Crocodylus rhombifer*) were provided by Zoo Hoyerswerda (Germany). These reptiles were kept at a constant air temperature of 26 to 28 °C while water was kept at 25 °C. *Testudo hermanni* (turtle) eggshell was collected from a terrarium of a private household in June 2020 (Heidelberg, Germany) and thus no meaningful daily variations should be expected. However, it must be noted that no temperature measurements are available for this eggshell. Alligator (*Alligator mississippiensis*) eggshell was originally collected by Dawson et al. (19), from the Rockefeller State Wildlife Refuge (USA) in June 2004, at an average environmental temperature of 27 °C. This is the only reptile in our dataset that was not kept in captivity under controlled temperatures. However, as it has been shown by Seebacher et al. (78), the amplitude of body temperature daily variations for this species is much lower in summer (1 to 4 °C, June/July) than in winter (5 to 8 °C, February), with an evident correlation with body mass: The larger the mass, the lower the amplitude. It is therefore reasonable to expect eggs to be mineralized at a relatively constant temperature, comparable to the average environmental temperature of 27 °C.

Sample Material—*Troodon* Eggshells. The non-avian dinosaur eggshells of *Troodon formosus* were supplied by the Royal Tyrrell Museum of Palaeontology in Alberta (Canada). The eggshell fragments belong to the ootaxon *Prismatoolithus levis*, which have been classified as *Troodon* based on embryonic remains present in association with the eggs (79, 80). *Troodon* DC (TMP 2008.75.127) eggshell was collected in Devil's Coulee. *Troodon* DC is the only specimen that was previously analyzed and screened for diagenesis by Dawson et al. (19). *Troodon* DC 2 (TMP 1996.48.7) was also collected in Devil's Coulee, *Troodon* HC (TMP 1994.99.13) comes from Hutterite Coulee, and *Troodon* MR (TMP 2008.75.31) was found in the southern portion of the Milk River Natural Area (*SI Appendix*, Fig. S1). All four samples were found in the Oldman Formation, a portion of the Belly River Group (southern Alberta, Canada) of late Campanian age (76.8 to 74.3 Ma according to radiometric dating of volcanic ashes). The deposits are typical of an ephemeral fluvial system (from mudstones to sandstones) with additional paleosol-related carbonate concretions indicative of arid climate with occasional wetlands (81, 82). Since all *Troodon* eggshells were collected in almost coeval deposits in southernmost Alberta, it can be assumed that the animals lived under the same environmental conditions. All eggshells were found in the same formation and they were thus overlain by roughly the same stratigraphic succession and subjected to similar burial histories. As reported in the study by Dawson et al. (19), vitrinite-based studies suggested burial temperature below 80 °C for southern Alberta.

Sample Material—Synthetic Carbonates. The high-Mg calcite samples analyzed ("CaMg4 180 min" and "CaMg5 180 min") were previously described by Dietzel et al. (63). Both samples were first precipitated as ACMC at a temperature of 25 °C, but then transformed into high-Mg calcite in the same aqueous solution and at the same temperature. CaMg4 and CaMg5 were sampled from the solution after 180 min. In these runs, transformations of ACMC precursor into high-Mg calcite were complete after a period of 26 to 35 min. Mg-content of CaMg4 and CaMg5 is 16.9 and 13.0 mol%, respectively.

Organic Matter. Portions of material from Kiwi and Cassowary were treated overnight using 3 to 4% NaOCl to remove organic matter eventually present in the sample. Since no difference was found in the isotopic composition between treated and untreated samples (*SI Appendix*, Figs. S6 and S7), both datasets were pooled together.

Cathodoluminescence. Thin sections of fossil eggshells were produced at Goethe University Frankfurt and screened for alteration using an 8200MKII Technosyn cathodoluminescence microscope provided by Geozentrum Nordbayern in Erlangen (*SI Appendix*, Figs. S2–S4).

Trace Element Distributions. All data presented here were collected using the Laser Ablation-Inductively Coupled Plasma-Mass Spectrometry (LA-ICPMS) setup at the Frankfurt Isotope & Element Research Center (FIERCE), Goethe University Frankfurt. The measurements were acquired using a Thermo-Scientific Element XR ICP-MS coupled to a RESOlution ArF Excimer (193 nm) laser ablation system (Applied Spectra Inc.), equipped with a S-155 two-volume ablation cell (83) (Laurin Technic Pty. Ltd.). The system was tuned for optimum sensitivity using the standard material NIST SRM 612 with low oxide formation (ThO/Th < 0.4%) and minimal element fractionation (e.g., Th/U = 1). Analyses consisted of 20 s gas background measurement and 22 s sample ablation. Spots of 60 μm were drilled with a fluence of 3.8 J cm^{-2} and 10 Hz repetition rate, resulting in a crater depth of approximately 22 μm. Data reduction was carried out using Norsci LADR v0.6 with NIST SRM 612 as primary reference material and ^{43}Ca as internal standard. JCp-1*-NP pressed powder pellet was analyzed as quality control. A total of 12 spots were measured at different positions in each eggshell thin section and results were averaged together (*SI Appendix*, Table S3).

Dual Clumped Isotope Thermometry. Dual clumped isotope thermometry focuses on the simultaneous determination of Δ_{47} and Δ_{48} in CO_2 evolved from acid digestion of carbonates (36), where Δ_{47} and Δ_{48} represent the excess abundances of mass 47 and 48 isotopologues (R_{47} and R_{48}) relative to their stochastically expected abundances (R_{47}^* and R_{48}^*).

$$\Delta_{47} = \left(\frac{R_{47}}{R_{47}^*} - 1 \right) \times 1000, \quad \Delta_{48} = \left(\frac{R_{48}}{R_{48}^*} - 1 \right) \times 1000.$$

Dual clumped isotope thermometry tests whether the clumped isotopic composition of a given carbonate was exclusively controlled by temperature or additionally affected by kinetic effects (37, 38, 84). This represents a relevant step forward compared to the more traditional Δ_{47}-based thermometer (85) as it allows correction of eventual kinetic biases and accurate reconstruction of precipitation temperatures (38, 39).

Eggshell samples were pulverized using pestle and mortar, homogenized, and stored in a vacuum oven at 30 °C. For isotopic analysis, CO_2 was extracted and purified using the automated analytical setup described in the study by Fiebig et al. (36). To summarize, 10 ($\pm$ 0.2) mg carbonate material is reacted in 108 % H_3PO_4 at 90 °C for 30 min, and the produced CO_2 is then trapped and purified through a sequence of water traps and a gas chromatograph before being introduced into the dual inlet of a ThermoFisher 253plus gas source mass spectrometer. Each sample was measured in 5 to 10 replicates dependent upon the amount of material available. Each replicate analysis constitutes 13 acquisitions of 10 cycles (20 s integration time). The total integration time of 2,600 s at 16 V on m/z 44 corresponds to a shot noise limit of 7 and 23 ppm for Δ_{47} and Δ_{48}, respectively. In a first step, background-corrected, session-specific δ^{45}-δ^{49} values of replicates were obtained correcting raw m/z 47 to 49 intensities of each cycle for pressure baseline effects using Pysotope (39). Background-corrected δ^{45}-δ^{49} values, collected over five different analytical sessions, were finally projected to the Carbon

Dioxide Equilibrium Scale at 90 °C (CDES 90) using "D47crunch," a python library largely described in Daëron (86). The benefit of this particular correction script is it allows variance minimization within the single analytical session ("indep_session" method, drift correction enabled). This library also provides calculation of the long-term repeatability for both Δ_{47} and Δ_{48}. These values were then used to express the analytical error as 2SE (long-term repeatability × 1.96, divided by the square root of the number of replicates). It must be noted that no significant difference is found when Fiebig et al. (39) calibration data are reprocessed using "D47crunch" as demonstrated in the study by Davies et al. (87).

Disequilibrium values presented in the main text and Fig. 2 were calculated as:

$$\text{disequilibrium } \Delta_{47} = \Delta_{47(\text{measured})} - \Delta_{47(\text{equilibrium})}$$
$$\text{disequilibrium } \Delta_{48} = \Delta_{48(\text{measured})} - \Delta_{48(\text{equilibrium})}.$$

Expected equilibrium values were calculated based on measured ambient temperatures (reptiles) and known body temperatures (birds) listed in *SI Appendix*, Table S2 using the temperature dependence of Δ_{47} and Δ_{48} as determined by Fiebig et al. (39). Considering the absence of any significant departure from the equilibrium line in all the four *Troodon* eggshells, we used the Δ_{47}-based temperature to estimate the Δ_{48} disequilibrium offset shown in Fig. 4. The same applies to *T. hermanni*.

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information.

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