DINOSAUR PHYSIOLOGY

Comment on “Evidence for mesothermy in dinosaurs”

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Grady et al. (Reports, 13 June 2014, p. 1268) suggested that nonavian dinosaur metabolism was neither endothermic nor ectothermic but an intermediate physiology termed “mesothermic.” However, rates were improperly scaled and phylogenetic, physiological, and temporal categories of animals were conflated during analyses. Accounting for these issues suggests that nonavian dinosaurs were on average as endothermic as extant placental mammals.

For Mesozoic dinosaurs, Grady et al. (1) converted annual growth rates derived from skeletochronology to daily ones, which is problematic for two reasons. First, a minor source of error is that differences in the number and length of days per year in the distant past were not accounted for (5, 6). Second, the scaling of daily rates from annual ones is not straightforward, because most organisms do not grow continuously throughout the year, with growth restricted to favorable seasons (2, 4, 5). For animals that take many years to grow to adulthood, such as Mesozoic dinosaurs, daily growth rates calculated from annual ones are underestimates, because the conversion from years to days inappropriately assumes that the organism grew at a constant rate throughout the year (Fig. 1B). An analogous scaling issue has been noted in studies of sedimentary (7) and evolutionary rates (8). This scaling issue is inherent to the skeletochronological method regardless of the physiology of animals, growth rate was calculated using skeletochronology, wherein annually deposited lines of arrested growth (LAGs) within bones (3–5) (Fig. 1A) are used to estimate both mass and age of an individual throughout ontogeny (3–6).

Fig. 1. Improper conversion from annual to daily time scales leads to underestimation of the growth rates of extinct animals such as dinosaurs. (A) Dinosaurian bone histology (2) showing circumferential LAGs. (B) Hypothetical growth record derived from the LAGs shown in (A). The green line depicts daily growth rates as calculated by Grady et al. (1); the orange (active growth) and black (paused growth) segments represent a finer interpretation of the growth record. Gray and white bars represent alternating years. (C) Scaling effect on conversion from annual to daily growth is magnified at higher annual growth rates and when growth takes place over the course of a decreasingly small fraction of the year. Black circles indicate daily growth rate if growth were spread evenly over ~365 days; red circles indicate daily growth rate if growth were restricted to a ~6-month period. Brown and green curves apply to the sauropod Alamosaurus and the theropod Tyrannosaurus, respectively (6). (D) Body mass versus growth rate for vertebrates, modified from Grady et al. (1). Ranges for various groupings of species, following (1), are outlined and labeled. Two regression lines are shown: one for Mesozoic dinosaurs (y = 0.006x0.82; r² = 0.96) and one for placental mammals (their range denoted within the semitransparent blue shaded area; y = 0.056x0.64; r² = 0.91), following Grady et al. (1).
the organism, because many endotherms also pause their growth at different times of the year (4); the problem also applies to data in Grady et al. (1) derived from studies of extant animals for which the time between mass measurements includes slow- or zero-growth periods (Fig. 1C). Comparison of these growth rates is misleading if their denominators (growth periods) are not comparable in length.

Given the strongly seasonal paleoenvironments in which most known Mesozoic dinosaurs lived (9), a 3- to 9-month annual growth duration is likely. If the spaces between adjacent LAGs only represent 6 months, then daily growth rates presented for each Mesozoic dinosaur by Grady et al. (1) are underestimates by a factor of two. I repeated the Grady et al. (1) regression of growth rate on body mass, with the daily growth rates inferred for Mesozoic dinosaurs doubled to coarse-

ly account for the limited duration of growth throughout the year. This adjusted regression indicates that the Mesozoic dinosaur data are roughly centered within the distribution of data for placental mammals (Fig. 1D). However, it is not appropriate to create a separate regression line for Mesozoic dinosaurs, because their unit-"ing characteristic is not their biology or relatedness but their geologic age [in Grady et al. (1), both Mesozoic and later birds are excluded from the “Dinosaurs” category). In other words, the regression computed by Grady et al. (figure 1 in (1)) conflated clades with other categories of animals. A fairer comparison would be to compare clades only, which would mean including birds within Dinosauria, a category that would overlap the distribution of mammalian data (Fig. 1D).

Estimating the duration of growth within a year from bone tissue is a complex topic for future skeletonochronological research to address. Just as scaling down from annual to daily growth rates is not straightforward, scaling up of daily growth rates can be misleading. For example, scaling up of daily tissue apposition rates observed through fluorescent labeling studies would suggest that ostrich, mallard, collared dove, and common blackbird femora reached their full diameter in 41, 20, 16, and 8 days, respectively. These projected growth durations are substan-
tial underestimates for only the larger two species (10, 11), which highlights that the scaling issue raised herein biases measurements for larger animals more severely. Studies of evolutionary or sedimentary rates have addressed similar scaling issues by accounting for the interval at which a given rate was estimated (7, 8). Similar ap-

proaches could be applied to growth data, but growth in extinct animals such as nonavian dinosaurs first needs to be better studied at the spatiotemporal scales in which it occurs. Such research has begun with the quantification of histological features on increasingly finer scales (4, 5, 10, 12, 13).

Grady et al. (1) suggest that “the modern dichotomy of endothermic versus ectothermic is overly simplistic.” Indeed, any typology—including the proposed concept of mesothermy—imposed upon the continuum of organismal physiology bears the risk of oversimplifying life history to the degree that apparent patterns are not linked to the processes that they are hypothesized to represent.

REFERENCES AND NOTES

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