far back as latest Carboniferous[4]. Johnston ignores conclusions based on extensive studies of fossil reptile bones[5] which show that dinosaur bone resembles more that of large living endotherms than ectotherms. He argues that, because crocodiles are ectothermic and their teeth are similar to those of dinosaurs, then dinosaurs also must have been ectothermic. But similar teeth are also found in Cretaceous birds[6,7], implying either that they were ectothermic or that dental growth rings are not a sufficient indicator of overall physiology.

The precise connection between growth rings and thermal physiology is unknown, and it is likely that a complex set of phenomena is involved. Mammalian growth rings appear in constant as well as seasonal environments[8]; neither temperature nor moisture are proven causal factors. Endo/ectothermy is not a sharp dichotomy, but a continuous spectrum, as is homeo/poikilothermy[9]. Calcium stress may be due to seasonal, dietary, reproductive, structural, phylogenetic or other poorly understood influences; the pitfall of 'one-factor' ecology is that no one factor, internal or external, is likely to explain all observed metabolic responses. Mammals and birds have used various strategies to solve problems in energetics; the diversity of dinosaurs suggests that many physiological solutions may also have been available to them[10]. It seems imprudent to rule out other factors contributing to the growth of hard tissues merely because they cannot be accounted for.

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CONTRARY to Johnston's interpretation, the skeletal annuli he observed in dinosaur teeth[1] need not imply any seasonal temperature fluctuation but may simply be a result of seasonal variation in food resources created by seasonal rainfall patterns. Spinage[2] has shown that two distinct annual cementum lines are formed in the teeth of African buffalo (*Syncerus caffer*) from regions with bimodal precipitation whereas one exceptionally distinct annulation forms each year in buffalo from southern Tanzania where rainfall patterns are unimodally seasonal. Also, desert bighorn sheep (*Ovis canadensis*) possess annuli in both cementum and dentine resulting from a cessation of growth during dry summer months[3]. These observations of seasonal dental annuli formation in endotherms counter Johnston's arguments for ectothermy in dinosaurs.

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JOHNSTON[1] claims that 'growth zones' observable in dinosaur teeth give tooth age in years, and suggest that dinosaurs were crocodile-like ectotherms. Individual ages in many mammalian species can be determined by counting various types of growth rings, including those in dentine. But if the results are not checked against individuals of known age[2–4], serious errors can be made. One possibility is that annual growth lines are confused with the contour lines of Owen. Johnston says that there are "two main types of rings" in dinosaur teeth, with the implication that annual rings are easily distinguished. Studies on mammalian teeth suggest that true annual rings are apparently formed in the same way as, and are morphologically similar to, contour lines of Owen[2].

In the absence of studies on a living relative or other acceptable analogue, it is easy in growth ring studies for hypothesis to bias observations. We suspect that Peabody's paper[5] cited by Johnston gives an example of this. Peabody recognized as many as four annual growth zones in some teeth of the small Lower Permian reptile *Captorhinus*. Although he did not discuss tooth replacement, a common opinion among vertebrate palaeontologists at the time was that the teeth of Captorhinus were not replaced. It would have been reasonable to expect individual teeth to persist for 4 yr. However, it is now known that all the teeth of *Captorhinus* were being actively replaced[7]. It is unlikely that a single tooth in such a small animal would persist for 4 or more years; Peabody's 'annual growth zones' probably reflect a less than annual periodicity if they had a regular periodicity at all.

Because dinosaurs are extinct Johnston's 'annual growth zones' cannot be verified, and his counts can at best be established only as more or less reasonable by study of living animals. The crocodilians are the closest living toothed relatives of dinosaurs, but there is no substantial evidence as to how long their teeth last or whether they can be aged by counting growth zones. Although Edmund[8] found a life span of slightly more than 2 yr in *Alligator* teeth, his specimens were very small and do not provide a good parallel with dinosaurs. Neill[9] states that old alligators cease replacement and may become nearly toothless. Even if this is confirmed, it tells us nothing about the age of the remaining teeth or the number of growth zones they may contain. In any case Johnston's counts of eight annual rings in each of two tyrannosaur teeth seems rather high (though not impossible) in view of the fact that tyrannosaurs, as well as the other dinosaurs he cites, show active tooth replacement[6,10] which seems to have continued throughout life as we know of no evidence to the contrary.

Johnston notes that de Ricqlès' histological surveys[11,12] did not reveal seasonal growth rings in dinosaur bone. However, histology did not simply produce negative evidence. de Ricqlès argued cogently, on the basis of long-bone histology, that dinosaurs were probably relatively endothermic. Absence of cyclical growth lines in dinosaur periosteal bone was attributed to the rapid growth characteristic of endotherms. The growth zones observed in dinosaur teeth thus should not be considered in isolation; their interpretation must be consistent with a total histological picture that includes the rest of the skeleton.

Johnston's suggestion of crocodile-like endothermy in dinosaurs at first appears to contradict de Ricqlès, but the latter noted that animals may be neither fully endothermic nor fully ectothermic and that, although dinosaurs were relatively endothermic, they probably had their own peculiarities in thermal physiology. It is impossible to correlate environmental and/or endogenous factors with the formation of growth zones in dinosaur teeth. But even if Johnston is right in calling these growth rings seasonal, their existence simply suggests that de Ricqlès was right in supposing that dinosaurs were not completely comparable to large mammals in thermal physiology. It does not imply, in view of the total histological evidence that dinosaurs were crocodile-like ectotherms.

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