

1. Johnston, P. A. *Nature* **278**, 635–636 (1979).
2. Kleeval, G. A. & Kleinenberg, S. E. *Age Determination of Mammals from Annual Layers in Teeth and Bones* (in Russian) (translation by Israel Program for Scientific Translations, Jerusalem, 1969).
3. Morris, P. *Mam. Rev.* **2**, 69–104 (1972).
4. Morris, P. in *Development, Function and Evolution of Teeth* (eds Butler, P. M. & Joysey, K. A.) 483–494 (Academic, London, 1978).
5. Peabody, F. E. *J. Morph.* **108**, 11–62 (1961).
6. Edmund, A. G. *Contr. Life Sci. Div. R. Ont. Mus.* **52**, 1–190 (1960).
7. Bolt, J. R. & DeMar, R. E. *J. Paleont.* **49**, 814–832 (1975).
8. Edmund, A. G. *Contr. Life Sci. Div. R. Ont. Mus.* **56**, 1–42 (1962).
9. Neill, W. T. *The Last of the Ruling Reptiles* (Columbia University Press, New York, 1971).
10. Edmund, A. G. in *Biology of the Reptilia* **1**, Morph. A. (ed. Gans, C.) 117–200 (Academic, London and New York, 1969).
11. Ricqlès, A. de *Evol. Theory* **1**, 51–80 (1974).
12. Ricqlès, A. de in *Morphology and Biology of Reptiles* (eds Bellairs, A. d'A & Cox, C. B.) 123–150 (Linnean Society, London, 1976).

JOHNSTON REPLIES—Meinke *et al.* acknowledge that annual layers occur in bone of fossil (and living) ectotherms but deny that the similar rings which occur in the dentine of those animals are annual or even extrinsically induced by the change in seasons. Irrespective of anything else, however, this view is illogical: dentine is itself simply acellular bone. Furthermore, in Recent temperate and arctic terrestrial mammals<sup>1,2</sup> (marine mammals, cited by Meinke *et al.*, are ecologically inappropriate as analogues of terrestrial crocodiles and dinosaurs): (1) the most conspicuous dentine bands form simultaneously with annual layers in periosteal bone, and (2) dentine has been shown to be a sensitive indicator of annual, seasonally induced disruptions of growth. Meinke *et al.* give no evidence that the dentine in ectotherms (living or extinct) behaves differently.

Boyce, noting that severe seasonal contrasts can produce rings in the dentine of certain terrestrial mammals, overlooks my citation of the same phenomenon<sup>3</sup>; and Boyce provides no evidence that Alberta dinosaurs lived in seasonally xeric conditions comparable to those of desert bighorn sheep. Instead, palaeontological evidence<sup>4,5</sup> indicates that the western interior of North America was a humid, warm temperate to subtropical environment without extreme seasonal fluctuation of precipitation and temperature during Late Cretaceous time.

Bolt and Demar cite possible uncertainty in distinguishing the boundaries of annual layers in dentine (and bone) owing to the production of accessory bands (accentuated contour lines of Owen); however, these difficulties no more detract from the reality of seasonal disruptions in dentine deposition than does the occurrence of false annuli negate the phenomenon of true annuli in fish scales. Furthermore, annual layers in the calcified tissues of Recent terrestrial mammals (and by extrapolation, crocodiles and dinosaurs) can usually be distinguished: they are more pronounced and regularly spaced than are accessory bands<sup>1,2</sup>.

Meinke *et al.* err in claiming the impossibility of finding more than two annual rings within a crocodile tooth: the number of annual layers in crocodile dentine gives the age of the tooth (minimum age if the pulp cavity is occluded), not just its functional age. In one 100-yr-old crocodile<sup>6</sup>, each tooth probably has been replaced about 50 times—an average of about once every 2 yr. In the Nile crocodile, two or three replacing teeth can be lodged beneath a functional one, and as many as six replacing teeth have been recorded at a single locus<sup>6</sup>. Thus, in a mature individual, a tooth could easily reside in the jaw for 4 yr, two before eruption and two after (longer if more than one successional tooth occurs below a given functional tooth), resulting in the accumulation of four annual layers in the dentine.

The number of major bands in dinosaur teeth is consistent with probable replacement rates: a maxilla of *Antrodemus* sp. (Princeton University Museum No. 16554–9), for example, exhibits three generations of teeth<sup>7</sup>, and if the average tooth replacement interval in mature *Antrodemus* was 2 yr (not unreasonable by analogy with Recent crocodiles), each tooth must have been held for 6 yr (4 yr before eruption and two while functional), yielding six annual layers in the dentine. If the replacement interval ranged from 1 to 3 yr during the life of an individual, the total life of a given tooth could be from 3 to 9 yr depending on the age of the individual. Although absolute replacement rates are not known for dinosaurs, relative rates can sometimes be inferred: hadrosaur and ceratopsian teeth, which are stacked for evident rapid replacement in a specialized grinding mill, generally have fewer rings than do carnosaur teeth, the function of which is not dependent on occlusal wearing of crowns.

Bolt and DeMar's model<sup>8</sup> of tooth replacement in *Captorhinus* describes the pattern of replacement but says nothing of rate. Small size alone is not necessarily indicative of rapid replacement: *Sphenodon* (Rhynchocephalia) and certain acrodont lizards are *Captorhinus*-sized or smaller, yet the lateral teeth wear heavily with age and are probably not replaced at all in mature individuals<sup>9</sup>. There is no histological evidence to support Bolt and DeMar's model of rapid replacement (in fact, heavy wear on many specimens of *Captorhinus*<sup>8,10</sup> suggests relatively slow replacement) nor can the model account for the occurrence of the tallest teeth at or near the centre of the rows of teeth, a definitive feature of *Captorhinus* multiple-rowed dentitions<sup>11</sup> (R. C. Fox, personal communication). Consequently, Peabody's interpretation<sup>12</sup> of growth zones in *Captorhinus* teeth remains a reasonable one.

Mesozoic toothed birds do not show dinosaur or crocodile-like zones in their

teeth (*contra* Meinke *et al.*) (see Yale Peabody Museum specimens 1206, 1474, uncatalogued thin-sections, all teeth of *Hesperornis*, YPM 1728, teeth of *Ichthyornis*); possibly Meinke *et al.* observed ringed teeth in small mosasaur (Lepidosauria) jaws (having lacertilian rows of nutritive foramina), for dentigerous fragments of two such jaws are in the Yale toothed-bird collections (R. C. Fox, personal communication).

Meinke *et al.* attribute the undeniably close resemblance of dentinal rings in dinosaurs and crocodiles to phylogenetic propinquity. *Champsosaurus*, a Late Cretaceous–Eocene eosuchian (and undoubted ectotherm), displays dentinal rings like those in Upper Cretaceous dinosaurs and crocodiles. Would Meinke *et al.* explain this in terms of "phylogenetic propinquity" of archosaurs and eosuchi-ans, groups whose last common ancestry is no younger than Permian and perhaps Carboniferous<sup>13</sup> (almost as remote as for archosaurs and mammals)?

Phylogenetic 'explanations' only describe results of process, not process itself (at least for those who believe natural selection is the source of adaptive resemblance between organisms), and it is clearly self-contradictory that resemblances purported to stem from phylogenetic relationship would have completely different physiologic origins, as Meinke *et al.* would have us believe.

Finally, Meinke *et al.* argue that, owing to their diversity, dinosaurs might be expected to show a range of physiological thermoregulation. Perhaps, but if so diversity by itself will not carry the argument: after all, Recent reptiles are far more diverse taxonomically than are dinosaurs, yet all are ectothermic.

I thank J. Osborn, D. Wigglesworth, R. C. Fox and R. Barwick for helpful comments.

PAUL A. JOHNSTON

Department of Geology,  
The University of Alberta,  
Edmonton, Alberta,  
Canada T6G 2E9

1. Kleeval, G. A. & Kleinenberg, S. E. *Age Determination of Mammals from Annual Layers in Teeth and Bones* (in Russian) (translation by Israel Program for Scientific Translations, Jerusalem, 1969).
2. Morris, P. *Mam. Rev.* **2**, 69 (1972).
3. Johnston, P. A. *Nature* **278**, 635–636 (1979).
4. Dodson, P. *Palaeogeogr. Palaeoclim. Palaeoecol.* **10**, 10 (1971).
5. Estes, R. *Univ. Calif. Publ. Geol. Sci.* **49**, 1 (1964).
6. Poole, D. F. G. *Proc. zool. Soc. Lond.*, 136 (1961).
7. Edmund, A. G. *Contr. Life Sci. Div. R. Ont. Mus.* **52** (1960).
8. Bolt, J. & DeMar, R. *J. Paleont.* **49**, 814 (1975).
9. Edmund, G. in *Biology of the Reptilia* (eds Gans, C., Bellairs, A. & Parsons, T.) **1**, 117 (Academic, London, 1969).
10. Clark, J. & Carroll, R. *Bull. Mus. comp. Zool. Harv.* **144**, 353 (1973).
11. Fox, R. C. and Bowman, M. C. *Paleont. Contr. Univ. Kans.* **11** (1966).
12. Peabody, F. E. *J. Morph.* **108**, 11 (1961).
13. Ostrom, J. & Carroll, R. in *The Encyclopedia of Paleontology* (eds Fairbridge, R. & Jablonski, D.) 705 (Dowden, Hutchinson and Ross, Stroudsburg, 1979).