

- have resulted from expected increased flow velocities in response to a lowering of sea level. Upgradient of the Gulf Trough, most waters have adjusted radiocarbon ages greater than 10 ka, suggesting little recent (past 10 ka) recharge.
35. The recharge temperature refers to the temperature at the base of the unsaturated zone during ground-water recharge. It is assumed that water infiltrating the unsaturated zone maintains equilibrium with the unsaturated zone air, and as further recharge occurs, the infiltration water becomes isolated from further exchange with the unsaturated-zone air (4, 7, 47). Recharge temperatures were determined by gas chromatographic analyses of dissolved nitrogen and argon (4, 47) and have a precision of $\pm 1^\circ\text{C}$. Overall uncertainties in N_2/Ar recharge temperatures are near $\pm 2^\circ\text{C}$, considering uncertainties in amounts of excess air and denitrification.
 36. The average recharge temperature, determined from dissolved nitrogen and argon analyses, of 22 Holocene ground waters from southeast Georgia (37) is $15.2^\circ \pm 1.6^\circ\text{C}$, and that of 21 paleowaters is $9.9^\circ \pm 1.9^\circ\text{C}$. The mean annual temperature today is approximately 19°C (44). Recent calibration measurements completed after acceptance of this paper indicate that recharge temperatures determined by our nitrogen-argon gas chromatographic system should be warmer by approximately $3.1^\circ \pm 1.6^\circ\text{C}$. This correction places the

Holocene recharge temperatures near the expected mean annual temperature. Because the error applies to both Holocene and paleowaters, the average cooling of 5.3°C in paleorecharge temperatures is retained.

37. Most of the Holocene waters are from two recharge areas to the Upper Floridan aquifer in south-central Georgia (flow path III): (i) near Valdosta, Georgia (waters with low excess-air content caused by direct recharge from a river through sinkholes), and (ii) near Albany, Georgia (waters with 2 to 5 cm^3 of excess air per liter that are recharged by infiltration through a shallow unsaturated zone). Several other Holocene waters are from the recharge areas on flow paths I and II. All paleowaters are from flow paths I and II.
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Evidence of the Growth Plate and the Growth of Long Bones in Juvenile Dinosaurs

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Histological and ultrastructural evaluation of the ends of long bones of juvenile dinosaurs from the Upper Cretaceous Two Medicine Formation of Montana revealed the preservation of growth plates. Growth plates are discs of cartilage present near the ends of growing long bones that generate bone elongation. Comparison of the fossils with modern taxa demonstrated homology of the growth plate in birds and dinosaurs. The presence of an avian-type growth plate in dinosaurs adds a shared derived anatomical character corroborating inclusion of birds within the Dinosauria. Additionally, possession of a growth plate, which in birds is capable of producing rapid determinate long bone growth, implies that an avian developmental pattern may have been present in these dinosaurs.

In adolescent animals, growth plate cartilage, present near the ends of long bones, is responsible for producing bone growth (Fig. 1). The cells of the growth plate (chondrocytes) have a particular temporal and spatial arrangement and undergo a series of morphologic and other phenotypic changes in their brief life history. Germinal chondrocytes at the articular end of the growth plate enter the cell cycle and proliferate. After leaving the cell cycle, differentiated chondrocytes mature and hypertrophy. Growth plate chondrocytes produce and maintain a specialized extracellular matrix,

and each chondrocyte is thus enclosed in a lacuna. The chemical composition of the extracellular matrix is critical to chondrocytic development and proper function of the growth plate (1). At the metaphyseal end of the growth plate, endochondral ossification occurs. Here hypertrophic chondrocytes calcify their surrounding matrix and die at the junction of the cartilaginous growth plate with the bony metaphysis (chondro-osseous junction). With chondrocytic death, blood vessels, osteoclasts, and osteoblasts (bone-forming cells) invade the space formerly occupied by the chondrocytes. The osteoblasts then use the calcified cartilage matrix as a scaffold on which to produce new bone, thereby adding to the length of the bone shaft.

Growth plate morphology, such as growth plate height and chondrocytic volumes and shapes, varies among species, within a species at different ages, and even

within a bone in which the ends grow at different rates. The mechanisms by which these morphological differences are translated into differential rates of growth are beginning to be understood (2). Among living animals, the avian growth plate has a distinct organization, most notably in the shape of the chondro-osseous junction. This morphology may reflect a unique strategy for rapid bone elongation in which metaphyseal bone production is minimized.

Direct observation of the biology of extinct species is not possible, and therefore, our understanding of dinosaur growth is limited. While soft tissue, including cartilage, is rarely preserved in the fossil record, the calcified hypertrophic zone of the growth plate, adjacent to the newly forming bone, has greater potential to become fossilized. Because growth plate morphology can be related to rate of bone growth, comparison of the histologic appearance of the dinosaur growth plate with that of living animals may provide understanding of long bone growth processes in dinosaurs. We studied the microscopic morphology of growth plates at the ends of juvenile long bones of the dinosaur *Maiaasaura* (Ornithischia: Hadrosauridae), a bipedal, duck-billed dinosaur (3), and compared the microscopic structure with the growth plates of a bird (chicken), a mammal (dog), and an ectothermic reptile (monitor lizard). Birds and lizards have evolved from ancestors classified as diapsid reptiles, whereas mammalian ancestors are synapsid reptiles (4).

Maiaasaura was abundant in North America in the Late Cretaceous Period. The adults reached lengths of 9 m. The *Maiaasaura* specimens that we studied were recovered from the Two Medicine Forma-

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tion of Montana. The sediments of this formation were deposited by streams and shallow lakes between 84 and 72 million years ago (5). In general, juvenile dinosaur fossils are rare. However, they are abundant in the Two Medicine Formation in which dinosaur nesting sites have been recognized (6). It has been inferred, from analysis of these sites, that *Maiasaura* nested communally and probably provided parental care (7). The fossils are well preserved and suitable for microscopic study.

In general, the morphology of the avian growth plate shows differences from that of mammals and lizards when viewed in longitudinal section. The avian chondro-osseous junction describes an undulating line rather than the straight junction of mammal and lizard growth plates. In birds, invasion of the growth plate by metaphyseal vessels occurs at spatial intervals so that papillae of hypertrophic chondrocytes become included between the trabeculae of metaphyseal bone. In the growth plates of

mammals and lizards, the ossification front is essentially straight, because of simultaneous replacement of hypertrophic chondrocytes by bone in a transverse plane (Fig. 2).

Light microscopic examination of longitudinal sections of the ends of the fossilized juvenile *Maiasaura* long bones revealed the presence of structure we hypothesize to be the hypertrophic zone of the growth plate

(Fig. 3). Architecture typical of a growth plate interfacing with cancellous bone is evident, and our histological interpretation is that the calcified portion of the growth plate is preserved. In the juvenile *Maiasaura* specimens, the hypothesized zone of calcified cartilage appears as included papillae and islands of clustered hollow, ovoid structures between trabeculae of metaphyseal

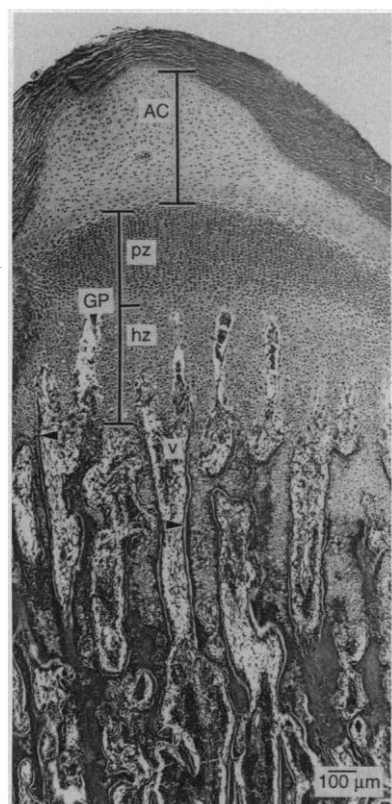


Fig. 1. Light micrograph of a longitudinal section of the growth plate in the proximal humerus of a 2-week-old chicken. Growth plate cartilage (GP) is located between articular cartilage (AC) and metaphyseal bone (arrow heads) of the elongating bone shaft. The growth plate contains a zone of proliferating chondrocytes (pz) and a zone of hypertrophic chondrocytes (hz). Blood vessels (v) from the metaphyseal bone invade the growth plate, bringing bone-forming cells which settle on calcified growth plate cartilage matrix.

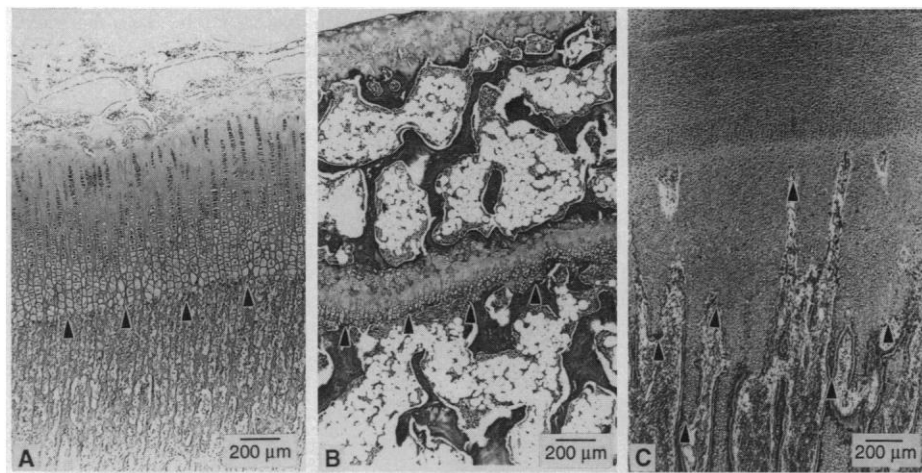


Fig. 2. Light micrographs of longitudinal sections of the growth plates of three living species: (A) mammal (dog), (B) ectothermic reptile (monitor lizard), and (C) bird (chick). Because of the slow, prolonged bone growth in lizards, mature bone is present above and below the growth plate; however, the organization of the growth plate, per se, is the same as in the mammal. In the mammal (A) and lizard (B), blood vessels invade the growth plate in a plane so that the junction between the growth plate and the bone, the chondro-osseous junction (arrowheads), is relatively straight. In the bird, the chondro-osseous junction undulates because metaphyseal vessels invade the growth plate at intervals, and growth plate cartilage becomes included within the newly formed bone. The obvious difference in heights between growth plates (A) and (B) is discounted because growth plate height within mammals at different ages differs by as much as the height difference between this dog and this lizard; however, at no time does the chondro-osseous junction appear undulating as in the bird.

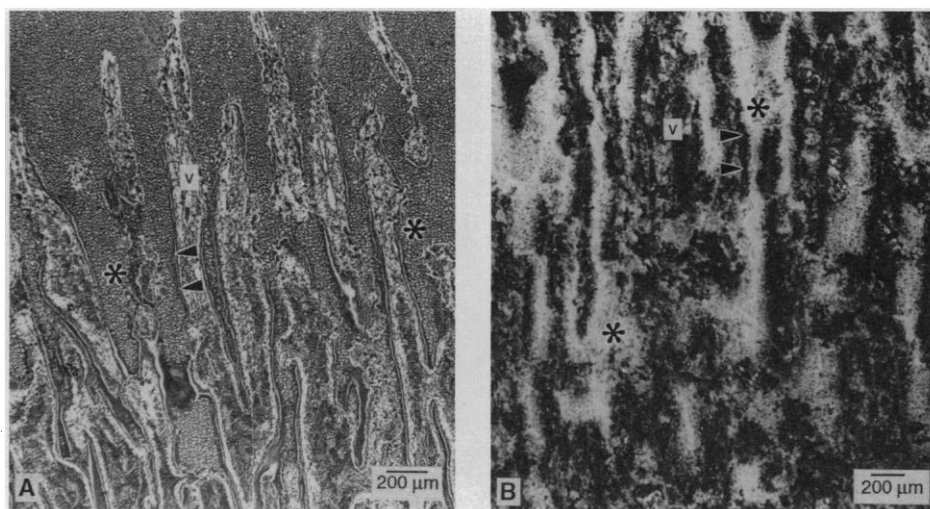


Fig. 3. Light micrographs of longitudinal sections of the chondro-osseous region from (A) chick and (B) dinosaur juvenile. In the chick, inclusions of hypertrophic chondrocytes (asterisks) are present between trabeculae of newly formed metaphyseal bone (arrow heads). In the dinosaur, hypertrophic chondrocytic lacunae (asterisks) are preserved between trabeculae in the newly formed bone (arrow heads). These lacunae are similar in size, shape, and density to the hypertrophic chondrocytes of the chick. Metaphyseal blood vessels (v) are filled with calcite in the dinosaur fossil.

bone. The distribution, spatial arrangement, and shape of these lacunae closely resemble the condition observed in birds. In addition, mammalian and lizard hypertrophic chondrocytes are quadrilateral, and these chondrocytes in both species have a columnar organization. In contrast, the hypertrophic chondrocytic lacunae of the dinosaur, like the hypertrophic chondrocytes of the bird, are oblate spheroids, and a columnar arrangement is not obvious.

We further tested our identification of the hypertrophic chondrocytic lacunae with the greater resolution afforded by scanning electron microscopy. We developed a method to etch calcite crystals differentially from the dinosaur bone to prepare them for viewing (8). With a scanning electron microscope, we observed the ultrastructure of the walls of the hypertrophic chondrocytic lacunae of modern species. The walls of the hypertrophic chondrocytic lacunae in the calcified part of the growth plate have

characteristic calcospherites (9). Calcospherites in the mammal and lizard are present only on the calcified walls of the lacunae, or those that are parallel to the direction of growth, whereas the transverse septa are thin and uncalcified. However, in the bird all of the lacunar walls are calcified and possess calcospherites.

In the dinosaur specimens, the same high degree of structural resolution can be seen as in the modern specimens. In the dinosaur, the walls of the lacunae have structures that appear to be identical to calcospherites, and these are present on all walls as in the bird (Fig. 4). Further evidence for preservation of the dinosaur growth plate is obtained from electron probe analysis. The Ca:P ratios determined for hypertrophic zone extracellular matrix are comparable in the dinosaur and bird (10). Calcite crystals, present between the bony structures of the fossil, are distinct in appearance and elemental composition

from the bone, indicating that the CaCO_3 in the ground water has not replaced the bone. Thus, we conclude that the original biomineral is preserved in these fossils, and therefore, that the microscopic structure observed represents biological structure, not artifacts of fossilization.

Comparison shows that the growth plates of the dinosaur and bird are most similar and plausibly are homologous. The alternative hypothesis, that this complex growth plate morphology evolved independently in dinosaurs and birds, seems less tenable.

Phylogenetic analysis places birds within the meat-eating dinosaurs, or theropods. This classification is based on anatomical similarities in the skeletons of the primitive bird, *Archaeopteryx*, and certain theropods (11, 12, 13). There are two major divisions of the Dinosauria: the Saurischia and the Ornithischia. Theropods are saurischian dinosaurs. In our study, we demonstrated that shared derived microscopic characters of the growth plate occur in a dinosaur and birds that are not present in mammals or lizards. Significantly, the dinosaur we examined is an ornithischian. It has been extensively argued that the Dinosauria (Saurischia plus Ornithischia) is a monophyletic group (11, 14). If this is the case, then the Saurischia and Ornithischia have a common ancestor, and all dinosaurs would possess the avian-type growth plate as a result of its presence in that common ancestor. Because the reptiles ancestral to mammals and to lizards had previously diverged from the ancestral dinosaur, lizards and mammals would not possess the dinosaur growth plate.

The presence of an avian-type growth plate in dinosaurs has several biological ramifications. This growth plate is capable of producing rapid determinate long bone growth in birds. For example, the proximal tibia of the 2-week-old mallard duckling elongates at a rate of over 1700 $\mu\text{m}/\text{day}$ (15) and the rate of longitudinal growth in the long bones of altricial species is even greater (16). It is plausible that this growth plate functioned similarly in dinosaurs. The histology of cortical bone of various dinosaurs is also indicative of rapid determinate growth (17). Rapid growth necessitates the high metabolism predicted if dinosaurs were indeed endothermic (12, 18). If dinosaurs attained giant stature in a relatively short period of development, this would provide the selective advantage of shortening the period in which the growth plates, which are structural weak points in bone, are present. Furthermore, there is evidence of the existence of parental care in various dinosaurs (7). Parenting is an extremely costly behavior and shortening its duration increases parental survivorship.

Both mammalian and avian growth

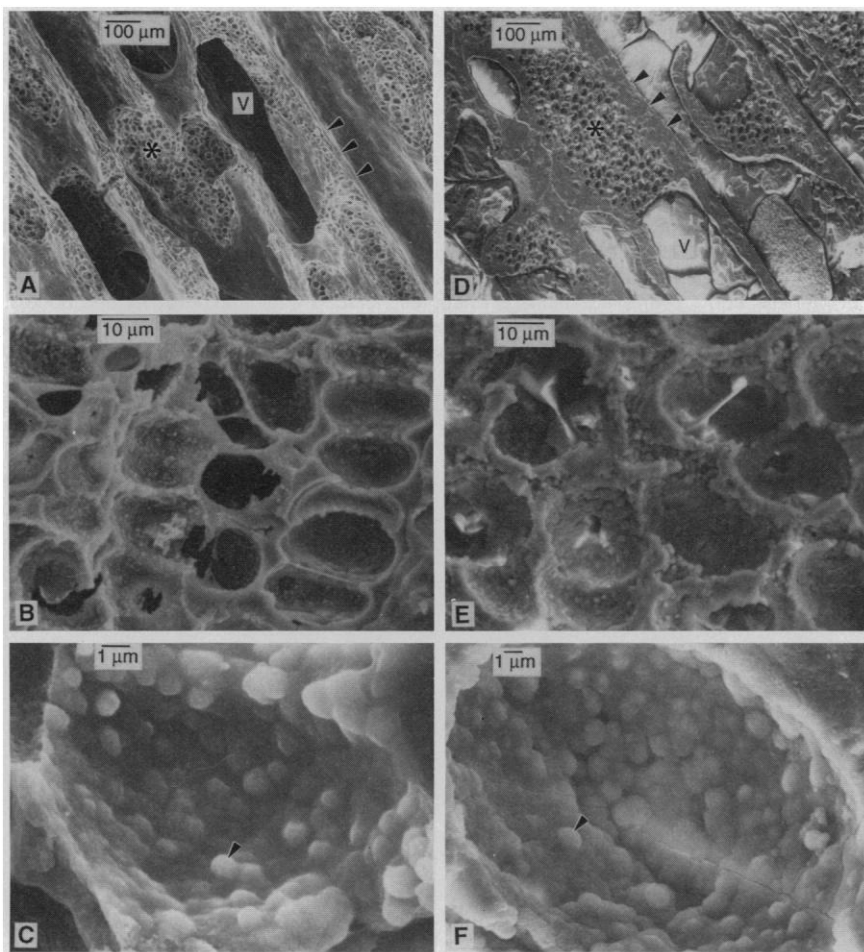


Fig. 4. Scanning electron micrographs of inclusions of hypertrophic chondrocytic lacunae in the chondro-osseous region of long bone ends of chick (A through C) and juvenile dinosaur (D through F). Hypertrophic chondrocytic lacunae (asterisk) occur as inclusions between metaphyseal bone (arrowheads) in the chick (A) and dinosaur (D). Metaphyseal blood vessels (v) are filled with calcite in the dinosaur. The shape and distribution of hypertrophic chondrocytic lacunae are similar in the bird (B) and dinosaur (E). Calcospherites (arrowhead) are present on all walls of the hypertrophic chondrocytic lacunae in birds (C) and dinosaurs (F).

plates are specialized for rapid long bone growth. Mammalian growth plates are capable of rapid bone elongation, in large part through longitudinally directed cellular swelling of the hypertrophic chondrocytes (19), whereas an increased population of proliferative chondrocytes appears to be significant in birds (15). Cellular swelling through water uptake allows great increase in cell volume without excessive energy expenditure. The avian plan of increased proliferation is energy demanding, but may be compensated by the coadaptation of reduced bone production. Although convergent evolution of rapid determinate growth in mammals and birds has been achieved by different cellular mechanisms, a high metabolic rate is required in both, and this energy-demanding adaptation seems to have been present in dinosaurs.

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Mantle Plume Helium in Submarine Basalts from the Galápagos Platform

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Helium-3/helium-4 ratios in submarine basalt glasses from the Galápagos Archipelago range up to 23 times the atmospheric ratio in the west and southwest. These results indicate the presence of a relatively undegassed mantle plume at the Galápagos hot spot and place Galápagos alongside Hawaii, Iceland, and Samoa as the only localities known to have such high helium-3/helium-4 ratios. Lower ratios across the rest of the Galápagos Archipelago reflect systematic variations in the degree of dilution of the plume by entrainment of depleted material from the asthenosphere. These spatial variations reveal the dynamics of the underlying mantle plume and its interaction with the nearby Galápagos Spreading Center.

Isotope and trace element studies have indicated the scale of mantle heterogeneity beneath ocean islands and have shown that different mantle regions are sampled by hot spot volcanism as the degree of partial melting and depth of melt extraction vary through time (1). Spatial variability can also be characterized by the study of lavas of similar age from different volcanoes that are simultaneously active in the same region. The Galápagos Archipelago, where coeval volcanism has occurred over distances of ~500 km, is an exceptional locality for such studies (2). The Sr-Nd-Pb isotopic variations in Galápagos lavas have been interpreted to indicate that asthenospheric mantle has been variably entrained into an upwelling mantle plume (2, 3). As the thermally buoyant plume rises, it bends from shear flow in the upper mantle as a result of overlying plate motion, and sur-

rounding mantle material is entrained as its viscosity decreases because of heating by the plume (4). In addition, hot spot ridge interaction has produced elevated La/Sm and ⁸⁷Sr/⁸⁶Sr ratios along the Galápagos Spreading Center to the north (5). However, He isotope ratios along the ridge are similar to those of normal mid-ocean ridge basalts (MORBs) (6), suggesting that the hot spot component reaching the ridge does not have a high ³He/⁴He ratio (7). In this report, we present and discuss new He isotope results for submarine basalt glasses from the Galápagos platform. The observed He isotope variations are sensitive to mixing between magmas or their mantle sources, to gas loss, and to crustal assimilation, providing additional insight as to the origin of the plume and its interaction with the shallow mantle and nearby spreading center.

We measured ³He/⁴He ratios as well as He and Ne concentrations in a suite of basalt glasses from seamounts around the Galápagos platform and in olivine phenocrysts from four subaerial samples (Fig. 1 and Table 1). Two subaerial samples are from Isla Floreana, and these have the most radiogenic Sr and Pb isotope compositions

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