

USE OF THE EXTANT PHYLOGENETIC BRACKET (EPB) CONCEPT IN RECONSTRUCTING THE DINOSAUR RESPIRATORY SYSTEM.

NORTON, James M., University of New England, 11 Hill's Beach Road, Biddeford, ME 04005, U.S.A.

The EPB concept was developed to provide a framework for inferring soft tissue structures in extinct animals and is applied here to a characterization of the dinosaur respiratory apparatus. The recognized EPB for dinosaurs consists of crocodylians and modern birds, and the respiratory systems of these animals appear to be quite different. Crocodylians have complex multicameral lungs fixed within the thorax, with main intrapulmonary bronchi that communicate with three rows of air chambers. The lungs are ventilated in a tidal pattern by changes in thoracic volume produced primarily by piston-like motions of the liver and abdominal organs. In contrast, the avian respiratory system is separated into rigid lungs for gas exchange and air sacs that serve as a bellows-like ventilatory apparatus providing relatively constant, unidirectional air flow through the gas exchange regions. The underlying structural affinity of these apparently dissimilar lung types is demonstrable through a comparative study of their embryology. The avian system represents an embryological fusion of crocodylian-type lateral chambers originating at different points along the intrapulmonary bronchus to form parabronchi. An accompanying expansion of other chambers forms the air sacs. In this EPB analysis, the bracket node (shared by crocodylians, dinosaurs, and birds) would therefore possess a multicameral, crocodylian-type lung. The outgroup node (shared by dinosaurs and birds) would possess a relatively rigid, fixed-volume parabronchial lung with associated air sacs, similar to the paleopulmo possessed by all modern birds. Support for this position comes from the observation that pneumatization of bone by air sacs is present in birds and is demonstrable in some fossil dinosaurs, but is not present in extant crocodylians. Modern birds, in addition to parabronchial lungs, have an air capillary system that greatly increases the gas exchange surface area. These very small diameter air capillaries are only possible in a rigid lung due to the high surface tensions present. In addition, they can be found only in an obligatorily oviparous animal that produces an egg with a calcareous shell. The air capillaries develop embryologically as fluid-filled tubes that sprout from the parabronchi. Because the lung is rigid, these air capillaries cannot be inflated and the fluid must be removed by reabsorption. The time required for fluid reabsorption is provided by a dissociation between the onset of air ventilation and the time of hatching. Following the initial opening of the shell, the avian embryo breathes air from an air pocket within the fixed-volume egg with gas exchange supplemented by the chorioallantoic membrane. When the fluid has finally been reabsorbed from the air capillaries, the embryo hatches. The modern avian lung would therefore have evolved in two stages: the development of the parabronchial architecture (dinosaurs and birds) and the subsequent development of air capillaries to improve gas exchange (birds only). The existence of air capillaries in the lungs of at least some and perhaps all dinosaur genera is precluded by fossil evidence that some dinosaurs may have been viviparous. The presence of parabronchial lungs in dinosaurs, even without any air capillaries, would have afforded these animals an energy-efficient, highly compliant ventilatory apparatus particularly suited to animals possessing relatively long necks per unit body mass (since respiratory dead space would have been confined to the trachea). Such parabronchial lungs would also provide a gas exchange system that could likely support metabolic rates and body temperatures intermediate between those of modern reptiles and birds. In support of this statement is the observation that modern passerine birds have additional respiratory gas exchange area in the form of the neopulmo, and maintain higher body temperatures than do non-passerine species. In the extant forms, therefore, increasing respiratory tract specialization correlates with increasing body temperature. Assuming that dinosaurs possessed air sacs and parabronchial lungs with no air capillaries, this EPB analysis would support the following sequence of relative body temperatures: passerines > non-passerines > dinosaurs > crocodylians. Given the absence of fossilized lungs, EPB analysis provides a reasonable reconstruction of a putative dinosaur respiratory system based on available fossil evidence and comparisons with extant groups, and provides a working hypothesis that could be tested by additional evidence related to dinosaur viviparity, bone pneumatization, and the characteristics of dinosaur eggshells.