Unidirectional flow in lizard lungs: a paradigm shift in our understanding of lung evolution in Diapsida

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Abstract

Conventional wisdom has held that unidirectional pulmonary airflow is unique to birds and is an adaption enabling high rates of gas exchange, essential for sustaining flight as well as an endothermic metabolism. Recent visualizations and measurements of flow in the lungs of monitor and iguanid lizards show a bird-like pattern of unidirectional flow in these lineages. These findings call for a paradigm shift in our understanding of lung evolution in diapsids. This pattern of flow is not unique to birds. It is much older than previously believed, and it may be advantageous to the low-energy lifestyles typical of ectothermic animals.

Keywords: Birds; Ectothermic animals; Lungs; Lung evolution; Unidirectional airflow

The bird lung has long fascinated scientists (Coiter, 1573). It is a very compact and complex organ with a great capacity for gas exchange, which is critical for sustaining flapping flight (Maina, 2000), an innovation that enabled birds to undergo an extensive, adaptive radiation. The topography of the conducting airways is strikingly different from that of mammals and gives rise to counterintuitive patterns of airflow. Whereas the conducting airways of mammals arborize with the branches terminating in gas exchange structures (the alveoli) that expand and contract to cause ventilation, most of the avian conducting airways form a circuit, much like the arteries, capillaries, and veins of the blood circulatory system, and air flows through this circuit in a consistent direction during both phases of ventilation, pulled into and pushed out of the body by volume changes in avascular air sacs that are connected to the conducting airways. The one-way flow of air is not caused by mechanical valves, but arises from poorly understood aerodynamic forces. Although numerous features have been purported to be critical to creating unidirectional flow, such as an enclosed bronchus that has grown deep into the lung, partitioning of the respiratory system into a gas exchange region and a portion that functions in ventilation, the presence of multiple chambers within the lung with perforations in their walls (Wolf, 1933), and the presence of abdominal air sacs, the true nature of the aerodynamic valves remains poorly understood. Nevertheless, unidirectional flow has been widely seen as an adaptation that supports high rates of metabolism, which are not only important for flight but also for an endothermic thermoregulatory strategy.

Recently, unidirectional intrapulmonary airflow has been documented in non-avian reptiles that do not fly, have a low-energy, ectothermic life history, and lack most or all of the pulmonary features purported to be key to the aerodynamic valves of birds (Farmer, 2010, Farmer and Sanders, 2010, Cieri et al., 2014, Schachner et al., 2014, Farmer, 2015a, b). These discoveries raise questions about the phylogenetic distribution of unidirectional airflow, its date of origin, the functional underpinnings and selective drivers for the flow, as well as the anatomical features that create aerodynamic valves. Its presence in birds, crocodilians, monitor and iguanid lizards suggests it is ancestral for diapsids, indicating a minimum date for its origin in the Permian Period. However, more data are needed on patterns of flow in the tuatara and other lepidosaurs to determine if it is truly widespread in this lineage. Furthermore, data on patterns of intrapulmonary flow in chelonians and amphibians will be important to our understanding of both the phylogenetic distribution and evolutionary history of this character.

Computational fluid dynamics models can help unravel the mystery of the aerodynamic valves that create unidirectional flow (Cieri et al., 2014). Green iguanas have large paired lungs that sit in the thoracoabdominal cavity, the apices extending into the neck to the 4th cervical vertebra and the bases extending nearly the length of the trunk (Fig. 1A). The internal lung topography is deceptively simple, with the dorsal portion of the primary bronchus terminating at the hilus, while the ventral portion flattens and widens to form part of an oblique septum that partitions the lung into a cranial chamber and a larger caudal chamber (Fig. 1B and C). A single ostium connects these chambers: intercameral perforations are lacking. However, even in these simple lungs there is

unidirectional flow along portions of the walls in both chambers that arises from high-speed jets that emanate from the primary bronchus at the hilus and the intercameral ostium during inspiration (Fig. 1E).

Unidirectional flow is not an adaptation for flight or endothermy, although it may be an exaptation that provided the ancestors of birds with a foundation from which their high-performance lungs evolved (Farmer, 2015a). Several hypotheses for the functional significance of unidirectional flow in ectotherms have been proposed. Because unidirectional flow occurs during apnea in American alligators, it may play a role in harnessing the heart as a pump for air, thereby reducing stratification of gases that can slow diffusion and also improve movement of gases from anatomical dead spaces into gas exchange parenchyma (Farmer, 2010). It has also been proposed to facilitate wash-out of lung gases, to reduce the cost of breathing, the rates of evaporative water loss, the rates of heat loss that are due to the enthalpy of vaporization, and to improve crypsis (Farmer, 2015a). Studies that enhance our understanding of the functional significance of this flow in ectotherms are sorely needed.

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Figure Caption

Fig. 1. Pulmonary anatomy and airflow in green iguana (*Iguana iguana*). (A) Left lateral view of green iguana showing parasagittal section in region of the hilus of the left lung. Arrow points to septum separating cranial and caudal chambers. (B) Dorsal and (C) ventral views of the right lung in coronal plane showing hilus (arrow) and ostium (arrow) to the caudal chamber. (D) Medial view of computational fluid dynamics (CFD) mesh of right lung. Lines mark coronal and axial sections projected in (E) and (F). (E) Inspiration, (F) expiration. Warm (red) and cool (blue) colors indicate flow craniad and caudad, respectively. Intensity indicates speed. Visualization of flow matched the CFD model. Figure after Cieri et al., 2014. Abbreviations: C, cervical vertebra; T, thoracolumbar vertebra; t, trachea.