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How birds breathe: Did evolution finally get it right?

Flight and the efficiency of the respiratory system

Powered (active) flight is a defining lifestyle trait of birds. Showing the exacting evolutionary requirements for flight, powered flight has only ever developed in insects, the extinct pterodactyls, birds and bats (Fig. 1). Energetically, the form of locomotion is extremely demanding. A flying budgerigar, e.g., increases its oxygen consumption thirteen times the value at rest. The respiratory system of birds is exceptionally structurally complex and efficient. These properties stem from various structural- and functional adaptations. They comprise: a) large volume of inhaled air; b) sizable hearts which pump large volumes of blood to the lungs and then to the rest of the body; c) short pulmonary circulatory time, i.e., the time blood pumped by the heart to the lung takes to return after it is oxygenated, permitting efficient delivery of oxygen to the tissues; d) in particularly the high altitude flyers, high hemoglobin affinity for oxygen which helps maintain its supply to the brain especially when there is little of it; e) separation of the respiratory system into a gas exchanger (lung) and a ventilator (air sacs); f) presence of novel gas-exchange designs such as crosscurrent system (CCS), countercurrent-like system (CCLS) and the multicapillary serial arterialization system (MCSAS) and; g) noteworthy pulmonary structural adaptations.

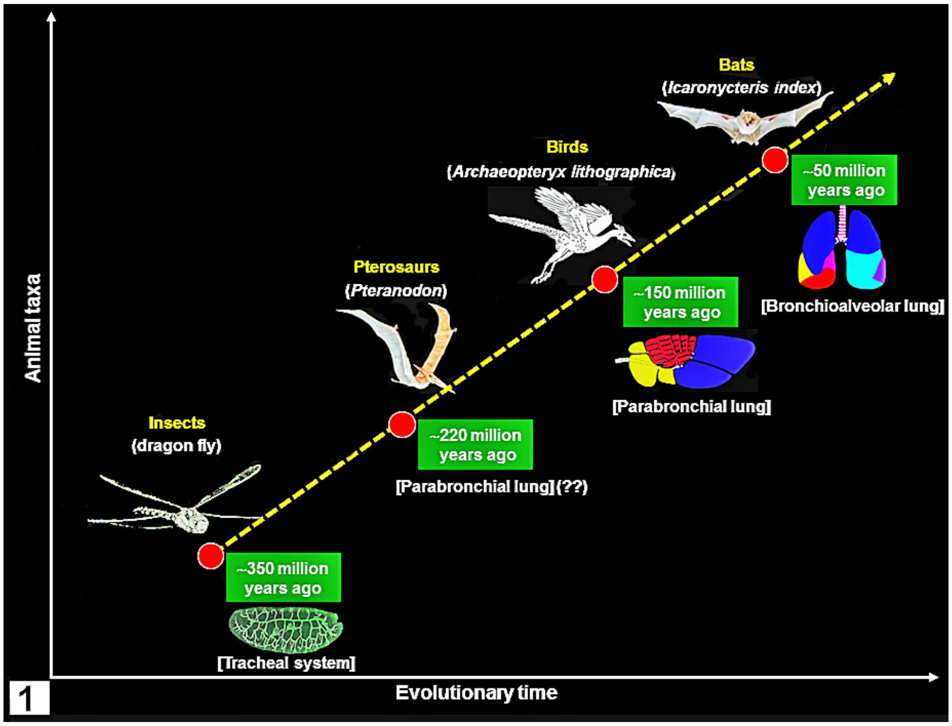

Fig. 1. In the animal kingdom, powered (active) flight has only ever evolved in insects, the now extinct pterodactyls, birds and bats – chronologically in that order. Insects evolved a tracheal system, bats retained the bronchioalveolar (mammalian) lung and the respiratory system of the pterodactyls is reported to have been bird-like (two question marks). Although the avian respiratory system is not a prerequisite for powered flight, among the air breathing vertebrates, birds have a remarkably efficient gas exchanger. The oldest bird is Archaeopteryx lithographica while the oldest bat is Icaronycteris index.

Structure of the respiratory system
The bird's lungs are small and compact (2A, B – inserts). The primary-, the secondary- and the tertiary bronchi (parabronchi) form complex hoop-like arrangement of airways (Fig. 2B, C – inserts). The air capillaries (ACs) and the blood capillaries (BCs), the respiratory units, occur in the gas exchange tissue (Fig. 2D) where the ACs range in diameter from 3 to 20 µm.

Function of the respiratory system of birds
The direction of the flow of air in the lumen of a parabronchus (Fig. 2D – insert) relative to the inward flow of the deoxygenated blood are essentially perpendicular: the arrangement forms a CCS; in the exchange tissue, blood and air flow in opposite directions, forming a CCLS and; in the exchange tissue of a parabronchus, the ACs and the BCs are arranged one-after-another, forming a MCSAS in which gas exchange occurs by an additive process.

The bird lung is ventilated continuously in a back-to-front direction by coordinated bellows-like actions of the air sacs (Fig. 2). Because the lung is continuously supplied with air, it can be argued that birds breathe nonstop. For the air to pass through the respiratory system, birds have to inspire twice and expire twice. The sequence of air flow is as follows: a) during the first inspiratory cycle, air flows from outside to the posterior air sacs (Fig. 2A); b) on the first expiratory cycle, air moves into the lung (Fig. 2B); c) on the second inspiratory cycle, the air in the lung travels to the anterior air sacs (Fig. 2C) and; d) on the second expiratory cycle, air is ejected to the outside (Fig. 2D).

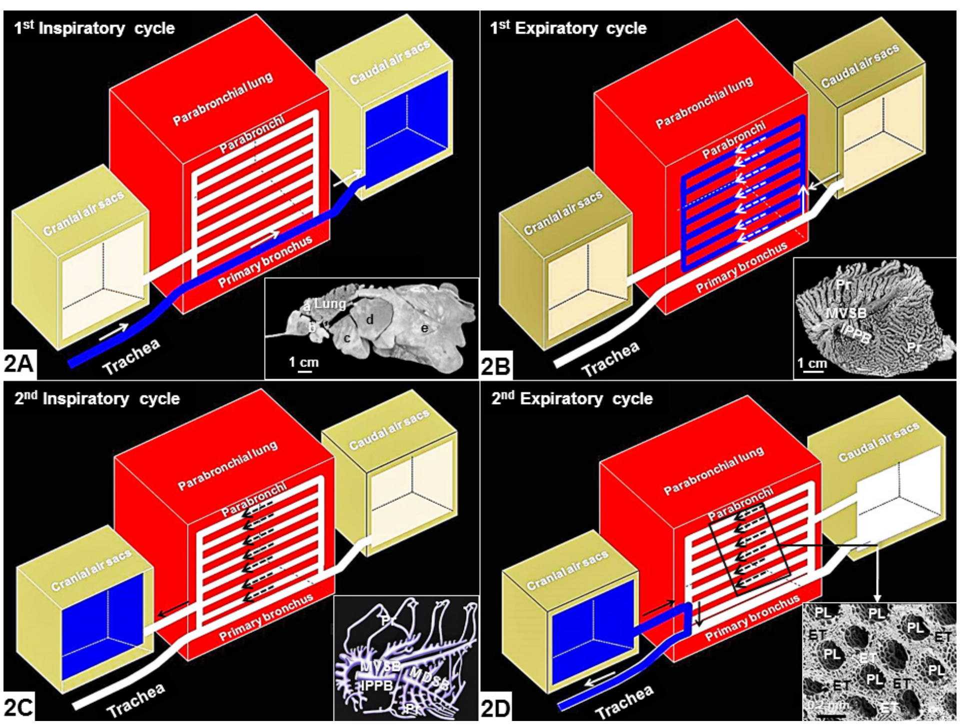

Fig. 2. Pathway followed by the inhaled air in the avian respiratory system shown by tracking a volume of air which is coloured blue. The succession is as follows: during the first inspiratory cycle (Fig. 2A), the air flows through the trachea, the primary bronchus to enter the posterior air sacs; in the first expiratory cycle, the air is

expelled out to the lung (Fig. 2B); during the second inspiratory cycle (Fig. 2C), the air in the lung moves into the anterior air sacs and; in the second expiratory cycle (Fig. 2D), the air in the anterior air sacs is expelled to the outside. The parallel dashed arrows in figures 2B-D show that the parabronchi of the lung are continuously and unidirectionally ventilated with air in a back-to-front direction. Inserts: Fig. 2A – Latex cast of the respiratory system of the domestic fowl showing a lung interposed between anterior air sacs [which comprise the cervical air sac (a), the interclavicular air sac (b) and the anterior thoracic air sac (c)] and posterior air sacs [which consist of posterior thoracic air sacs (d) and abdominal air sacs (e)]. Fig. 2B – Latex cast the lung of the domestic fowl showing the complexity of the airways: IPPB, intrapulmonary primary bronchus; MVSB, medioventral secondary bronchus; Pr, parabronchi. Fig. 2C – Diagram of the lung of the domestic fowl drawn as if transparent to show the complexity of the airways: IPPB, intrapulmonary primary bronchus; MVSB, medioventral secondary bronchus; Pr, parabronchi; MDSB, mediodorsal secondary bronchi. Fig. 2D – Scanning electron micrographs of the lung of the domestic fowl showing parabronchi which consist of lumen (PL) which is surrounded by exchange tissue (ET).

Morphometry of the avian lung

The respiratory system of birds forms as much as one-third of the volume of that of the body. With ~80% of it located in the BCs, the volume of blood in the bird lung forms as much as 36% of the lung volume. The respiratory surface area in a bird lung is ~15% greater than that of the lung of a mammal of equivalent body mass. The thickness of the blood-gas barrier in the lungs of small energetic birds is ~0.1 microns.

John N. Maina
Department of Zoology, University of Johannesburg, Auckland Park Campus 2006, Kingsway, Johannesburg, South Africa

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