

Pulmonary Transformations of Vertebrates **3**

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Abstract

The structure of the lung subserves its function, which is primarily gas exchange, and selection for expanded capacities for gas exchange is self-evident in the great diversity of pulmonary morphologies observed in different vertebrate lineages. However, expansion of aerobic capacities does not explain all of this diversity, leaving the functional underpinnings of some of the most fascinating transformations of the vertebrate lung unknown. One of these transformations is the evolution of highly branched conducting airways, particularly those of birds and mammals. Birds have an extraordinarily complex circuit of airways through which air flows in the same direction during both inspiration and expiration, unidirectional flow. Mammals also have an elaborate system of conducting airways; however, the tubes arborize rather than form a circuit, and airflow is tidal along the branches of the bronchial tree. The discovery of unidirectional airflow in crocodylians and lizards indicates that several inveterate hypotheses for the selective drivers of this trait cannot be correct. Neither endothermy

nor athleticism drove the evolution of unidirectional flow. These discoveries open an uncharted area for research into selective underpinning of unidirectional airflow.

Keywords

Unidirectional flow • Bronchial tree • Respiration • Evolution • Vertebrate • Lung • Bird • Mammal • Reptile

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3.1 Introduction

False facts are highly injurious to the progress of science, for they often endure long; but false views, if supported by some evidence, do little harm, for everyone takes a salutary pleasure in proving their falseness: and when this is done, one path towards

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error is closed and the road to truth is often at the same time opened. (Darwin 1871)

Many of the great transformations in the vertebrate story have been revealed through the study of the fossil record and by functional and developmental analyses of living vertebrates. Unraveling how the trunk, the head and neck, and appendages such as fins, wings, and limbs changed, as walking tetrapods evolved from swimming fish and flying birds evolved from running dinosaurs, has been possible using these approaches. Unlike the skeletal system, many of the major transformations of the vertebrate lung remain shrouded in mystery because it leaves little trace in the fossil record. There is general agreement that the vertebrate lung is an ancient organ, but there is little consensus on just how old it is, how and why it originated, or the importance of various selective factors driving its transformations as vertebrates radiated. Yet comparisons of lung structure in extant lineages reveal that this organ has undergone extraordinary modifications. The central function of the lung is gas exchange between air and blood, and so one might expect little structural diversity that is not directly related to differences in the capacity of various lineages for gas exchange, yet the lung is one of the most diverse organs of vertebrates, and this diversity is not necessarily correlated with differences in aerobic capacity. For example, the volume of the lungs with respect to body weight varies tremendously. In European chameleons, the lung is approximately 125 ml for 100 g body weight, occupying an enormous portion (about 54%) of the body, whereas in small mammals (mouse, rat, and rabbit), the lung volume is 6.4 ml for 100 g body weight and occupies just 6.3% of the body (Perry and Duncker 1978). Some vertebrates have completely lost this organ. The ancestors of plethodontid salamanders had lungs, but this lineage subsequently came to rely instead on gas exchange across the skin and buccopharyngeal region (Whitford and Hutchison 1965). Reduction or loss of one lung has evolved repeatedly in many, but not all, limbless tetrapods (Farmer 2011 and references therein; Van Wallach 1998). In many snakes, Gymnophiona, and most limbless lizards, there

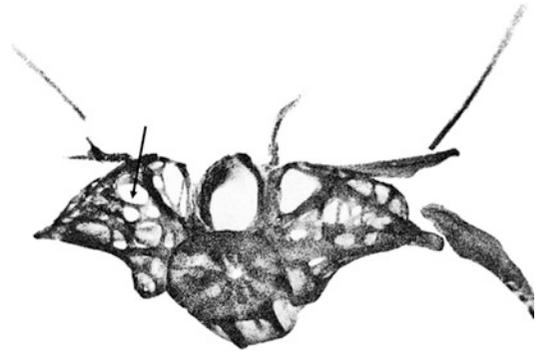


Fig. 3.1 Vertebra from the butterfly fish, *Pantodon buchholzi*, showing extensive pneumatization. Arrow points to a pneumatic space (from Nysten 1962)

is a reduction in the left lung, but in amphisbaenids there is a smaller right lung than left (Butler 1895; Van Wallach 1998). In some animals, the lung has taken the opposite path from the reduction seen in limbless tetrapods and has expanded beyond the thoracoabdominal cavity to enter the bones of the axial and even the appendicular skeleton. One of the most striking examples of this phenomenon, known as pneumatization, is seen in the butterfly fish (*Pantodon buchholzi*) (Nysten 1962) (Fig. 3.1), but it is also common in birds.

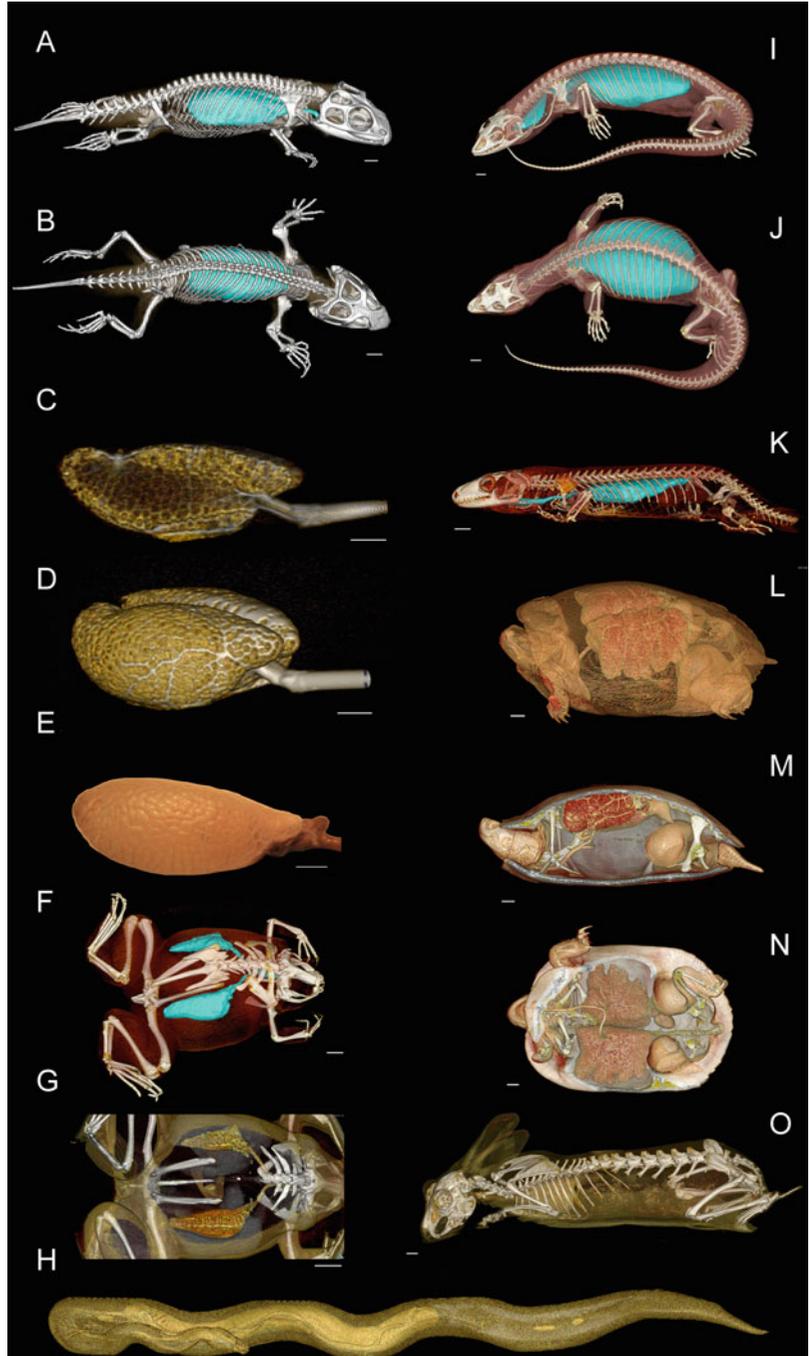
The biomechanics of the musculoskeletal systems that ventilate the lung also differ. For example, a buccal pump is used to push air into the lungs of fishes and amphibians, while amniotes use costal inspiration (Brainerd and Owerkowicz 2006). However, a similar positive pressure gular pump supplements costal ventilation in many lizards (Brainerd and Owerkowicz 2006). Crocodylians supplement costal ventilation by employing their gastralia (Farmer and Carrier 2000) and their diaphragmatic muscle-liver complex (Gans and Clark 1976), birds use dorsoventral movements of the sternum (Brackenbury 1987; Duncker 1971), and mammals supplement costal ventilation with the diaphragm.

The internal organization of the lung varies as much between lineages as the external architecture (Duncker 1978; Milani 1894, 1897; Perry 1983). The distribution of tissues where gas exchange occurs is relatively uniform in

mammals and many amphibians but highly concentrated, generally in a dorsocranial region, in other animals, such as birds and snakes, while the remainder of their respiratory system is relatively devoid of blood vessels (Maina 2006; Maina et al. 1989, 1999). The topography of the

conducting airways is also highly variable. In some lineages, such as amphibians and the tuatara, the primary bronchus terminates at the lung hilum (Fig. 3.2), and there is neither an internal network of tubes nor significant septation forming distinct chambers; the lung parenchyma

Fig. 3.2 Computed tomography data of lungs in tetrapods. (a–e) Tuatara. (a) Lateral and (b) dorsal views showing large, inflated lungs (blue); (c) lateral view of lung with parasagittal cut; (d) dorsocranial view of both lungs; (e) photograph in lateral view. (f–g) African clawed frog. (f) Dorsal view; (g) dorsal view with coronal cut to show the lung lumen. (h) dorsal view of a ball python. (i–j) Savannah monitor. (i) Dorsolateral and (j) dorsal views. (k) Bearded dragon in lateral view. (l–n) Red-eared slider. (l) Dorsolateral view; (m) lateral with parasagittal cut; (n) ventral view. (o) Lateral view of a rabbit. Scans were made on live unanesthetized (frog, turtle, bearded dragon, python) and anesthetized (rabbit) animals as well as specimens with artificially inflated lungs (tuatara, monitor). Scale bar = 1 cm



simply arises directly from the visceral pleura in wide, polygonal structures. In stark contrast, in birds and mammals there is an extensive conducting network.

Such large differences in pulmonary architecture raise cardinal questions about the evolution of this organ. Can this diversity be explained by functional factors other than gas exchange? If so, what are they? Did key environmental factors, such as changing levels of atmospheric oxygen and carbon dioxide over time, give rise to this diversity? Have the forces associated with the mechanics of breathing influenced the internal design of the lungs? Are there unique aspects to the development of the lung that generate a greater range of morphologies than are found in other organs and that underpin the exceptional diversity of this organ? Thus, the lung presents a very exciting opportunity to an evolutionary biologist aiming to understand the unfolding of this diversity, from the ancient fishes that first evolved lungs as a supplement to respiration with gills to the highly sophisticated lungs of extant birds and mammals.

3.2 When Did the Vertebrate Lung Evolve?

Biologists of the 1800s used the lung as a character that distinguished fish from amphibians. Accordingly, when the lungfish were discovered, they were initially classified as amphibians. For example, in an early description of the Australian lungfish, Gerard Krefft wrote to the Zoological Society of London (Krefft 1870) describing a “gigantic Amphibian allied to the Genus *Lepidosiren*.” It is now clear that these animals should be classified as fishes and that most of the basal living bony fishes have a lung, even if the organ is no longer used for air breathing. For example, adult coelacanths have a vestigial lung, but a sizable lung, with bony plates as covering, is found in early embryos (Cupello et al. 2015). Similar plates can be detected in the fossil remains of many coelacanths (Cupello et al. 2015), leaving a hard-part correlate for the presence of lungs. Among the ray-finned fishes (Actinopterygii), lungs are found in the most

primitive family, the Polypteridae (reedfish, bichirs), as well as in the Neopterygii (gar, bowfin). It was suggested by Sagemehl (Sagemehl 1885) that the single, dorsal gas bladder that is common in teleosts evolved gradually from paired, ventral lungs. However, differences in development have been proposed to indicate that lungs and gas bladders are not homologous organs (Hsia et al. 2013). More recently, patterns of expression of cassettes of genes in the gas bladder of zebrafish and in lungs (Cass et al. 2013), as well as the presence of vestigial pulmonary arteries in *Acipenser* and *Polyodon*, two primitive fishes that do not breathe air (Longo et al. 2013), shore up the homologies of these organs and corroborate the scenario that lungs were present at least as early as the first bony fishes (Liem 1989), and their descendants either inherited a lung or descended from lineages in which the lung underwent a transition to a gas bladder.

Thus, early fishes evolved an organ that will later be critical to one of the greatest transformations of vertebrates, the transition from an aquatic lifestyle to a terrestrial one, at least 100 million years before this transition took place (Boucot and Janis 1983). The fact that lungs are not an adaptation for a terrestrial existence, but initially served some other function, means that they are a remarkable example of an exaptation. Furthermore, their origin in this distant past is perplexing because the early bony fishes were marine (Boucot and Janis 1983), and an inveterate view of the selective pressure driving lung evolution is aquatic hypoxia, which is more commonly encountered in freshwater habitats, such as the Amazon River basin, than in saltwater ecosystems, which are stirred by tides and waves (Kramer et al. 1978). Thus, their ancient origin raises questions of the initial selective pressure for the origin of lungs in marine environments. Other aspects of the traditional paradigm are also in need of scrutiny. For example, although the African and South American lungfishes were once believed to be good analogues for understanding the evolution of aerial respiration, it has been argued that these are not good models for the first fishes that evolved lungs because their gill filaments are so

reduced that they are obligate air breathers (Farmer 1997 and references therein). These fish drown if not allowed to breathe air! This cannot have been the initial condition for the first fishes that evolved lungs. Better analogues are the Australian lungfish, the Polypteridae, and the Neopterygii. In all of these groups, activity is a strong stimulus to breathe air, even when the fish are swimming in well-oxygenated water and could, presumably, choose to obtain the requisite oxygen with the gills (Farmer 1997). The answer may lie not in the level of oxygen available in the water as much as the level of oxygen available to the heart. The ventricles of most fishes have little or no coronary circulation and obtain oxygen from blood that is contained within the lumen of the heart. The level of oxygen in this blood is increased when the fish breathe with their lungs. The lungs, therefore, may have been favored as a mechanism to expand aerobic capacities and may have been particularly important in increasing the power of the heart (Farmer 1997).

3.3 Transformations in the Vertebrate Lung

The transition to a terrestrial lifestyle created new selective pressures on the respiratory system. In the clade that became most highly specialized for terrestriality, the amniotes, the lung is the primary organ for gas exchange and gills, skin, and other organs contribute minimally or not at all. There are a few exceptions, such as the use of cloacal bursae for aquatic respiration by some turtles (Mathie and Franklin 2006), but the majority of amniotes rely on the lungs to exchange both carbon dioxide and oxygen between blood and gases contained within the lungs. An expanded capacity for gas exchange is needed for terrestrial locomotion because the metabolic cost of transport is considerably greater for walking tetrapods compared to swimming fish. That is, for an animal to move a gram of mass a given distance, the cost is higher in terrestrial than in aquatic vertebrates. Furthermore, for an animal to be able to sustain this extra cost, it must provide the energy through aerobic metabolic pathways.

Another important selective factor driving the design of the lungs is that the power required for locomotion, that is, the energetic cost for a given unit of time, is a function of locomotor mode. For example, flapping flight has a greater power requirement than either terrestrial or aquatic locomotion. Thus, selection on the lungs for expanded capacity will be greatest for these flying vertebrates (Maina 2000). Because pulmonary gas exchange occurs exclusively by diffusion, and rates of diffusion are proportional to the surface area through which the gases diffuse and inversely proportional to the distance over which diffusion takes place, it is possible to analyze morphometrically the capacity of the lung for gas exchange, the anatomical diffusion factor, which is the ratio of the surface area for diffusion divided by the harmonic mean thickness of the blood-gas barrier. Assessment of anatomical diffusion factor reveals that mode of locomotion coevolves with lung capacity (Maina 1998, 2000).

As gas-exchange surface area within the lung increased, an effective mechanism was needed to bring gases into contact with the gas-exchange parenchyma. This presumably led to the evolution of the extensive network of conducting bronchi of mammals and birds. A less extensive system of airways has evolved in crocodylians, chelonians, and some lizards. The topography of these networks influences patterns of airflow. It is therefore important to the efficacy of gas exchange, as well as in how inhaled particulate matter is deposited, and in the metabolic cost of breathing. The effects of these networks on the flow of lung gases have been studied largely in the mammalian and avian respiratory systems, both empirically and using either physical or computational models, but are poorly understood in other lineages.

3.4 The Conducting Airways of the Bronchoalveolar Lung

The amniote trachea is a fibromuscular tube supported by cartilaginous rings. In amniotes with two lungs, the trachea bifurcates to form two primary bronchi that carry air to and from each lung. In mammals, the tubes continue to

arborize within the lungs, with the shape of the larger intrapulmonary bronchi being preserved by cartilaginous rings and plates. The cartilage gradually disappears as the tubes become smaller, and by the time the tubes are about 1 mm in diameter, they are no longer supported by cartilage and are termed bronchioles (Weibel 1963, 1984). Bronchioles continue to arborize until they terminate in the gas-exchange units, the alveoli, which are heavily invested with blood capillaries—in humans there are approximately 1000 pulmonary capillaries for each alveolus—and this massive investment of blood capillaries creates an enormous gas-exchange surface area. A tendency for the alveoli and bronchioles to collapse in the absence of the cartilaginous support that is present in the more proximal airways is countered by elastic tissues in the walls, or septa, of the alveoli. A honeycombed topography of the alveoli enables the septa to mechanically interact in such a way to help keep the alveoli open. Although there is some variation in the branching patterns of the conducting airways of different mammalian lineages (Fig. 3.3) (Montiero and Smith 2014), the structure of the lungs is sufficiently similar that a bronchoalveolar lung is generally believed to have been present in the common ancestor of extant mammals, providing a minimum date for the origin of the organ in the Triassic period (reviewed in Farmer 2015a).

The diameters, taper, and branching patterns of the airways play an important role in the flow of lung gases, for example, influencing whether there is laminar or turbulent flow, as well as the resistance to airflow (Weibel 1963; West 1995). Laminar flow through a tube consists of a series of concentric, cylindrical layers of flow, with the layer nearest the wall moving most slowly, due to frictional forces with the wall, and the central cylinders most rapidly. With laminar flow, the resistance is determined by the viscosity of the fluid, the length of the tube, and is inversely proportional to the radius of the tube to the fourth power, if the walls of the tube are smooth, in the well-known Poiseuille's law. The resistance is also dependent on the pressure difference driving flow and inversely related to the velocity of the

flow. If the flow is turbulent, where unsteady vortices appear chaotically and interact with each other, the resistance to flow is proportional to the difference in pressure driving the flow, divided by the velocity squared. The resistance is more heavily influenced by the density of the fluid, rather than by the viscosity. Turbulent flow tends to occur with high velocities, high gas density, and large tube radii in a relationship known as the Reynolds (Re) number. Flow changes from laminar to turbulent when the Reynolds number exceeds 2000:

$$\text{Re} = (\rho \times \text{Ve} \times D) / \eta$$

where η = viscosity, ρ = density, Ve = linear velocity, and D = airway diameter.

In humans, airflow in the trachea and the larger airways is turbulent, but in the small-diameter airways, it is laminar. Thus, the Reynolds number is important in determining the resistance to flow in individual airways. Furthermore, the resistance throughout the airways depends on the topography, with resistance of tubes arranged in series being additive, but for tubes arranged in parallel, the reciprocal of the total resistance is the sum of the reciprocals of the resistance of each tube. Thus, many small-diameter tubes, when arranged in parallel, create a low total resistance in spite of Poiseuille's law, because flow in them tends to have a low Reynolds number and is laminar. For these reasons, the total resistance to flow in the smallest airways of the bronchoalveolar lung is very low, with the largest component of airway resistance occurring in the medium-sized bronchi (Weibel 1963, 1984). In mammals, airway resistance changes depending on the state of the lung, decreasing with increasing lung volume.

During idealized, normal ventilation, air leaves the lung by the same path it entered, tidal airflow. However, the patterns of flow are complicated, and under some conditions, biases can arise. Pendelluft ("swinging air"), or interregional airflow that arises from inhomogeneous inflation or deflation of the lungs, can result in significant exchange in volume at local bifurcations (Greenblatt et al. 2014). Pendelluft may be a relatively important factor influencing

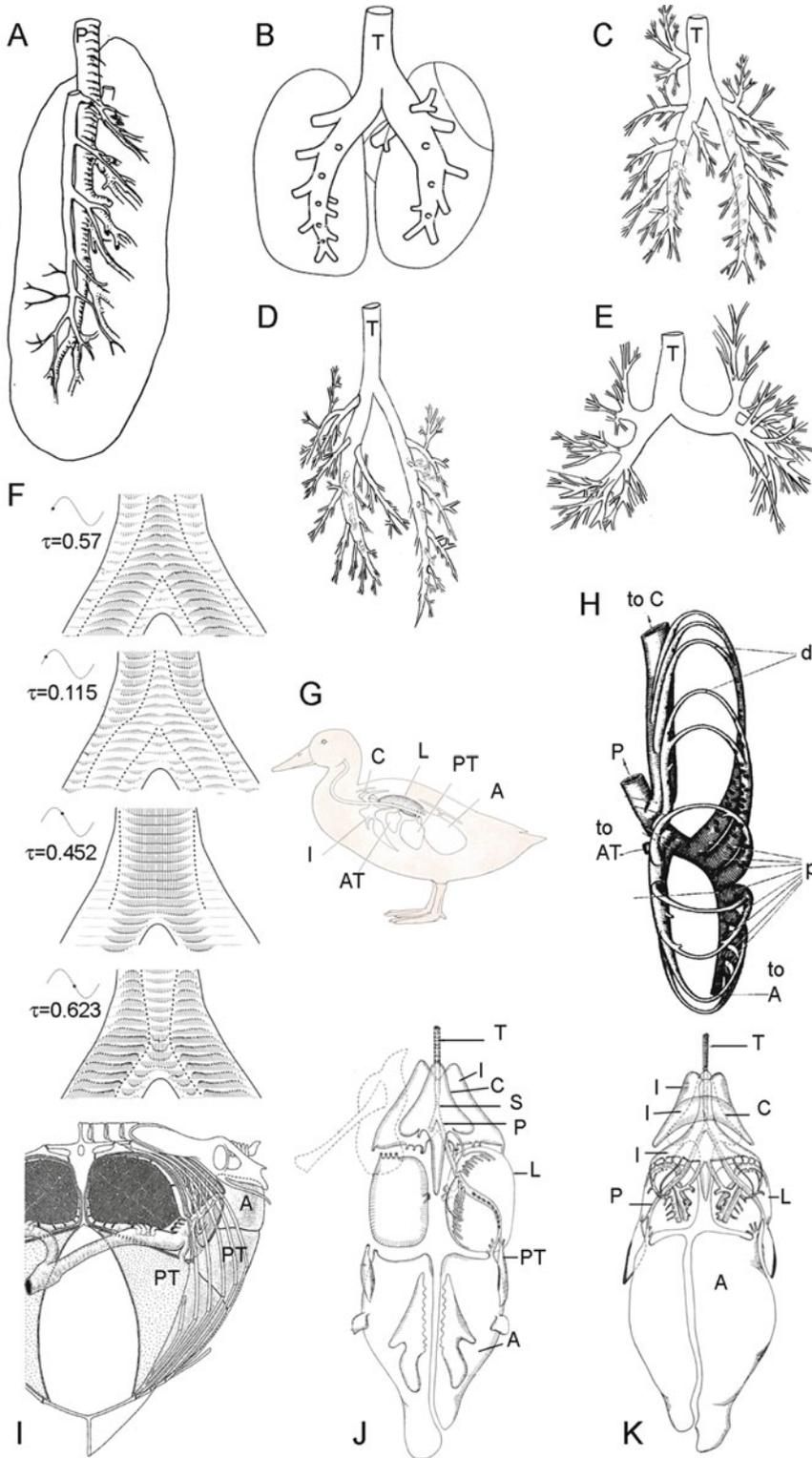


Fig. 3.3 Conducting airways and patterns of airflow in mammals and birds. Ventral view of mammalian bronchial tree: (a) the left lung of a dugong (after Pick 1907); (b) echidna (after Perry et al. 2000); and (c) pig, (d) rat,

and (e) human (all after Montiero and Smith 2014). (f) Patterns of airflow with high-frequency ventilation during four phases of inspiration (positive trace) and expiration. Note the direction of flow differs in the center of the

airflow in nonmammalian lungs but has been little studied. Another poorly studied phenomenon that determines flow is the relationship between frequency and tidal volume. High frequency but low tidal volume ventilation can create biases of flow (Fig. 3.3) (Heraty et al. 2008) and is sufficiently effective at gas exchange to enable adequate ventilations in humans with tidal volumes that are smaller than the anatomical dead space volume. The interaction between tidal volume and respiratory frequency is poorly studied in nonmammalian respiratory systems.

3.5 The Conducting Airways of the Avian Lung

Birds have undergone a fascinating and extensive adaptive radiation, much of it underpinned by their ability to fly, which enabled birds to interact with their environment in a new way and opened ecological opportunities. Powered flight is an energetically demanding form of locomotion and therefore requires a high capacity for gas exchange (Maina 2000). Thus, the respiratory and cardiovascular systems, as well as other components of the oxygen cascade, changed in tandem to enable the requisite high rates of gas exchange with the environment. In addition, birds evolved an endothermic thermoregulatory strategy, whereby they produce sufficient internal heat to regulate body temperature. Endotherms have greater rates of gas exchange at rest than do ectothermic animals. Consequently, the avian respiratory system is renowned for its great capacity for gas exchange (Maina 2000).

Descriptions of the avian respiratory system date back hundreds of years to the work of Coiter (1573). Since then, numerous scientists have

endeavored to understand its unique and intriguing structure (Maina 2002). Akester described it as “. . . the most complicated respiratory system that has ever evolved. . .” (Akester 1960). It is distinct from that of mammals in several ways. First, the avian respiratory system is highly heterogeneous, consisting of ventilatory structures and a gas-exchange region (Maina 1989). The air sacs are specialized to move air in and out of the body, while the lungs are specialized for gas exchange (Fig. 3.3). These structures lie in separate body compartments: the lungs in the *cavum pulmonale* and the air sacs in the *cavum subpulmonale*, with the exception of the abdominal air sacs that lie in the abdominal cavity. The horizontal septum forms the floor of the *cavum pulmonale*, while the oblique septum and the pericardium separate the air sacs from the rest of the viscera (Duncker 1971). There is a set of sacs in the cranial part of the bird and a second set in the caudal part. During inspiration, the air sacs are pulled open to bring air into the body, and the air sacs are compressed to expel air from the bird on expiration. Ostia in the horizontal septum enable the air sacs to connect to the rest of the respiratory system within the *cavum pulmonale*. Here, the primary bronchus enters the ventromedial aspect of the lung and continues to course dorsally, laterally, and caudally in a drawn-out S-shaped curve (Fig. 3.3). The abdominal air sacs arise from the distal ends of the intrapulmonary bronchi. A set of secondary bronchi, known as ventrobronchi, branch near the point of entry of the bronchus into the lung (the hilum), in a bottlebrush manner. More distally there is generally a region of the intrapulmonary bronchus that is free of secondary branches, known as the mesobronchus, after which arise more secondary airways, known as laterobronchi

Fig. 3.3 (continued) airways compared to near the walls (after Heraty et al. 2008). (g) Schematic of duck illustrating position of the air sacs (after Schmidt-Neilsen 1971); (h) dorsal view of the conducting airways in the right lung of a goose (after Brackenbury 1971); (i) cranial view of conducting airways, air sacs, and lungs of an idealized bird (after Duncker 1971); (j) dorsal and (k)

ventral views of conducting airways, lungs, and air sacs of a chicken (after Akester 1960). *Air sacs* = A abdominal, AT anterior thoracic, C cervical, I interclavicular, PT posterior thoracic, P primary bronchus, d dorsobronchi, L lung, p parabronchi, and T trachea

and dorsobronchi (Fig. 3.3). The second tier of airways divides further to form smaller-diameter tubules, the parabronchi, which anastomose. Air capillaries radiate off the parabronchial lumina and are the site of gas exchange (Duncker 1971). Thus, the conducting airways form a circuit, analogous to the arteries, capillaries, and veins of the blood circulation, and like the flow of blood, air travels in a consistent direction through most of these airways during both phases of ventilation, unidirectional airflow.

Early studies and speculations about patterns of airflow in the avian lung attributed the fact that the flow was unidirectional to activity of physical valves (Bethe 1925; Wolf 1933); however, a lack of evidence for either sphincters or valve leaflets and the fact that the valve remains effective in dead animals eventually led to the conclusion that some sort of aerodynamic valve gives rise to unidirectional flow (Dotterweich 1936; Hazelhoff 1951) (reviewed in Butler et al. 1988). Although glass models demonstrated that topography alone can create unidirectional flow (Dotterweich 1936; Hazelhoff 1951), compared to these models, the topography of the avian conducting airways is complex, and questions remain regarding how the avian anatomy gives rise to one-way flow.

Other aspects of the avian respiratory system remain enigmatic. How, when, and why did the bird lung evolve? Did non-avian dinosaurs and pterosaurs have an avian-like respiratory system? Studies on the sister taxon of birds, the crocodylians, are providing insight into aspects of the respiratory system in avian forerunners.

3.6 Airflow in the Crocodylian Lung

In the Crocodile ...and Alligator the bronchus enters the lung near its center, and passes somewhat obliquely into the lung until it reaches the junction of the lower and middle third; here it breaks up into eight or fifteen tubular passages. These tubular passages are studded with a great many air-sacs. ... In these animals the lung for the first time gives a structure as it is found in

Mammals. There are many air-sacs, which in turn communicate with a common cavity, or atrium, all of which communicate with a single terminal bronchus. A single lobule of the mammalian lung is simply enlarged to form the lung of the Crocodile; the lung of the former is only a conglomerate of that of the latter. (Miller 1893) p. 171

Each bronchus is continued directly backwards into a wide canal, which dilates into an oval sac-like cavity at the posterior end of the lung, representing the mesobronchium with the posterior air-sac in birds. In the dorsal and mesial wall of the mesobronchium there are five or six apertures, which lead into as many canals, representing the entobronchia in birds. These pass, the anterior two almost directly forwards, and the others more or less obliquely, to the dorsal margin; and they lie quite superficially on the mesial face of the lung. The first is very much larger than the others, and ends in a dilatation at the anterior end of the lung. It is united with the second by transverse branches. Along the ventral margin of the lung there are four saclike chambers, which communicate, in the case of the two anterior, with the entobronchia, and, in the case of the two posterior, with the mesobronchium. Finally, there are two very large canals, external to these, which communicate with the mesobronchium by large apertures in its dorsal wall, and give off branches to the outer face of the lung, representing the ectobronchial system of birds. The orifices with which the surfaces of all these canals, except the anterior half of the mesobronchium, are thickly set, lead into depressions, which are often so deep as to become cylindrical passages, simulating the parabronchia of birds. Thus, notwithstanding all the points of difference, there is a fundamental resemblance between the respiratory organs of Birds and 'those of' Crocodiles pointing to some common form (doubtless exemplified by some of the extinct Dinosauria), of which both are modifications. p. 569 (Huxley 1882)

These scientists could not have arrived at more different conclusions regarding the structure of the crocodylian lung. Is it like an enlarged mammalian lobule or is it more like the lungs of birds? It is certainly distinct from that of birds in lacking air sacs. However, it is birdlike in that the conducting bronchi do not form a bronchial tree, but anastomose to form a circuit. In much of this network, airflow is unidirectional, flowing caudad in the airway that arises from the most proximal ostium of the primary bronchus (Fig. 3.4)

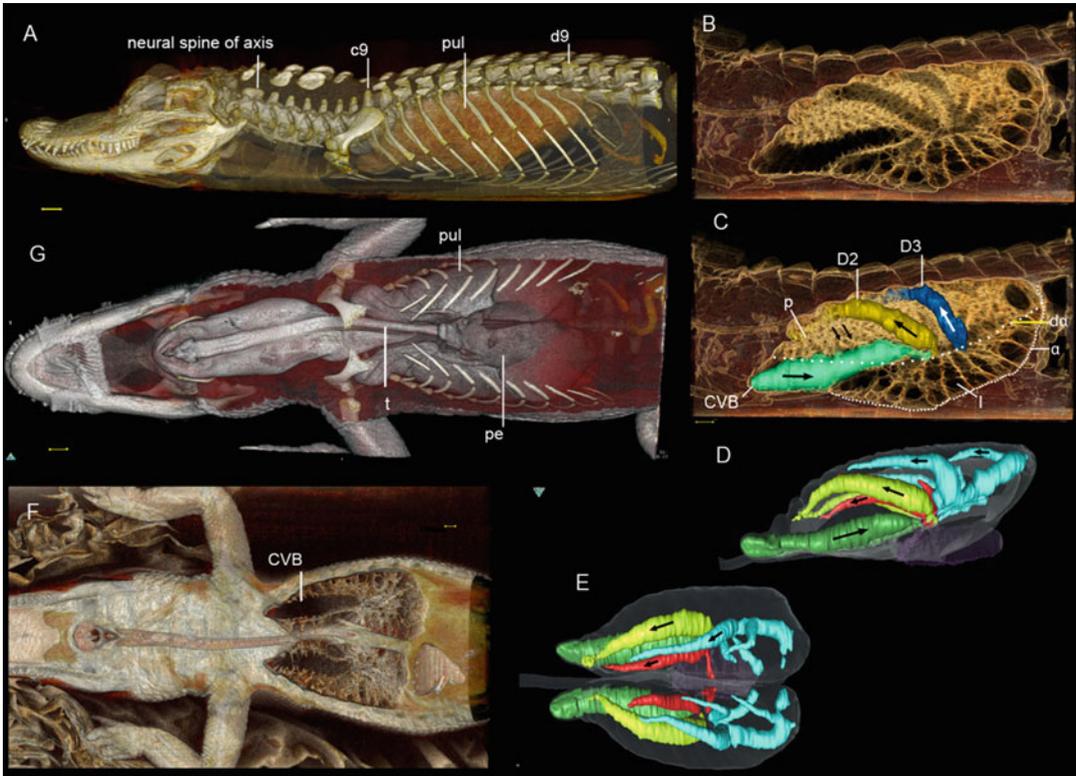


Fig. 3.4 Crocodilian anatomy and airflow. Computed tomography of American alligator in lateral (a–d) and ventral (e–g) view. c–d show voxels of the major airways in color. Air flows craniad in the blue, red, and yellow airways and caudad in the green airway, the cervical ventrobronchus (CVB). pul, lung; pe, pericardium. l,

avascular locules hypothesized to be homologous to the avian air sacs; alpha, region hypothesized to be homologous to the oblique septum; da, region hypothesized to be homologous to the horizontal septum (after Farmer 2015b). scale bar, 1 cm

and flowing craniad in the other airways (Farmer 2010; Farmer and Sanders 2010). Closer inspection shows other features that are extremely bird-like. For example, the gas-exchange tissue is concentrated in the dorsal regions of the lungs, the ventral and caudal portions containing locules with few blood vessels (Fig. 3.4). It has been hypothesized that these locules are homologs of the avian air sacs (Farmer 2015b). Furthermore, the ostia for most of these locules lie on the floor of the intrapulmonary bronchus, in a location analogous to the horizontal septum of birds, which contain the ostia to the air sacs.

There are a number of implications for the discovery of unidirectional flow in crocodilians.

First, because crocodilians and birds are crown-group archosaurs, unidirectional flow was probably present in pseudosuchians, pterosaurs, and non-avian dinosaurs. Second, avian style air sacs are not requisite for unidirectional flow since the simpler structures of crocodilians are sufficient to act as bellows. What, then, is the primary function of avian air sacs? These structures vary considerably between species, and investigations are wanted to shed light on the functional underpinnings of this variation. Third, the bones of crocodilians are not pneumatized. Furthermore, as pointed out previously, animals without air sacs show pneumaticity (Fig. 3.1). Therefore pneumaticity is an

imperfect hard-part correlate for the presence of air sacs. Fourth, the presence of unidirectional flow in a semiaquatic, ectothermic, sit-and-wait predator suggests that it is not an adaptation for endothermy or for flight. Thus, alternative explanations should be sought for the functional benefits of unidirectional flow. Fifth, since unidirectional flow did not arise to support the high metabolic demands of flight or endothermy, it is possible unidirectional flow may be more widespread and could occur in other ectotherms, such as lizards, turtles, amphibians, and lung breathing fish.

3.7 Airflow in the Lepidosaur Lung

At least two species of lepidosaurs, with strikingly different lungs, have unidirectional airflow: the green iguana (Cieri et al. 2014) and the savannah monitor (Schachner et al. 2014). In both species, gases flow from caudal toward cranial during inspiration and expiration in large regions of the lungs. Iguana lungs are paired organs that occupy a large part of the body cavity when fully inflated (Fig. 3.5). The cranial end of the dorsocranial chamber underlies cervical vertebra 4 and overlies the heart extending to thoracic vertebra number 5 (T5). The cranial end of the ventrocaudal chamber abuts the heart, and the caudal end extends to approximately T10. A horizontally (coronally) oriented septum partitions the lung into a dorsocranial chamber and a ventrocaudal chamber. The intrapulmonary bronchus enters the lung ventromedially and, at the hilum, opens dorsally such that the ventral portion, still containing partial rings of cartilage, forms part of the floor of the horizontal septum. An ostium in the distal portion of this bronchus is the sole connection between the two chambers. The chambers are cavernous structures with a few partial septa and small niches along the walls and along the horizontal septum (Fig. 3.5). In both of the chambers, there is caudal-to-cranial flow during both phases of ventilation throughout much of the volume of the

chambers. The mechanisms driving this unidirectional flow are unresolved. Convective momentum, whereby high-speed fluid streams are created when air is pulled through the primary bronchus during inspiration, may play a dominant role. These jets of air, one in the cranial chamber and one in the caudal chamber, widen as they enter the cavernous chambers, and as they move along, they entrain air on all sides of the stream. This process, known as the Coanda effect, decreases the pressure in between the jet and the walls of the lung, a very unstable situation. Eddies arising from the partitions in the walls or from the niches that are common along the horizontal septum and certain regions of the lung (Fig. 3.5) may serve to deflect the stream, where it can then lock onto a wall and keep flowing. If these internal structures serve such a function, one would expect them to be reasonably well conserved between lungs of different individuals, a testable hypothesis. Furthermore, the hypothesis that the Coanda effect plays a role in directing and creating unidirectional flow needs testing.

3.8 Future Directions

A number of areas are in need of more work. More studies are needed on the phylogenetic distribution, fluid dynamics mechanisms, effects on gas exchange, and functional significance of the patterns of airflow. Specifically, to be able to map changes through time using phylogenetic bracketing, data on patterns of airflow in amphibians, chelonians, as well as additional measurements on lepidosaurs with diverse lung morphologies are sorely needed. Insight into mechanisms for these patterns of flow will come from additional structure-function studies, as well as computational fluid dynamics models. Finally, it will be important to identify and to test key hypotheses for the effects on blood gases and on the functional significance of these patterns of flow.

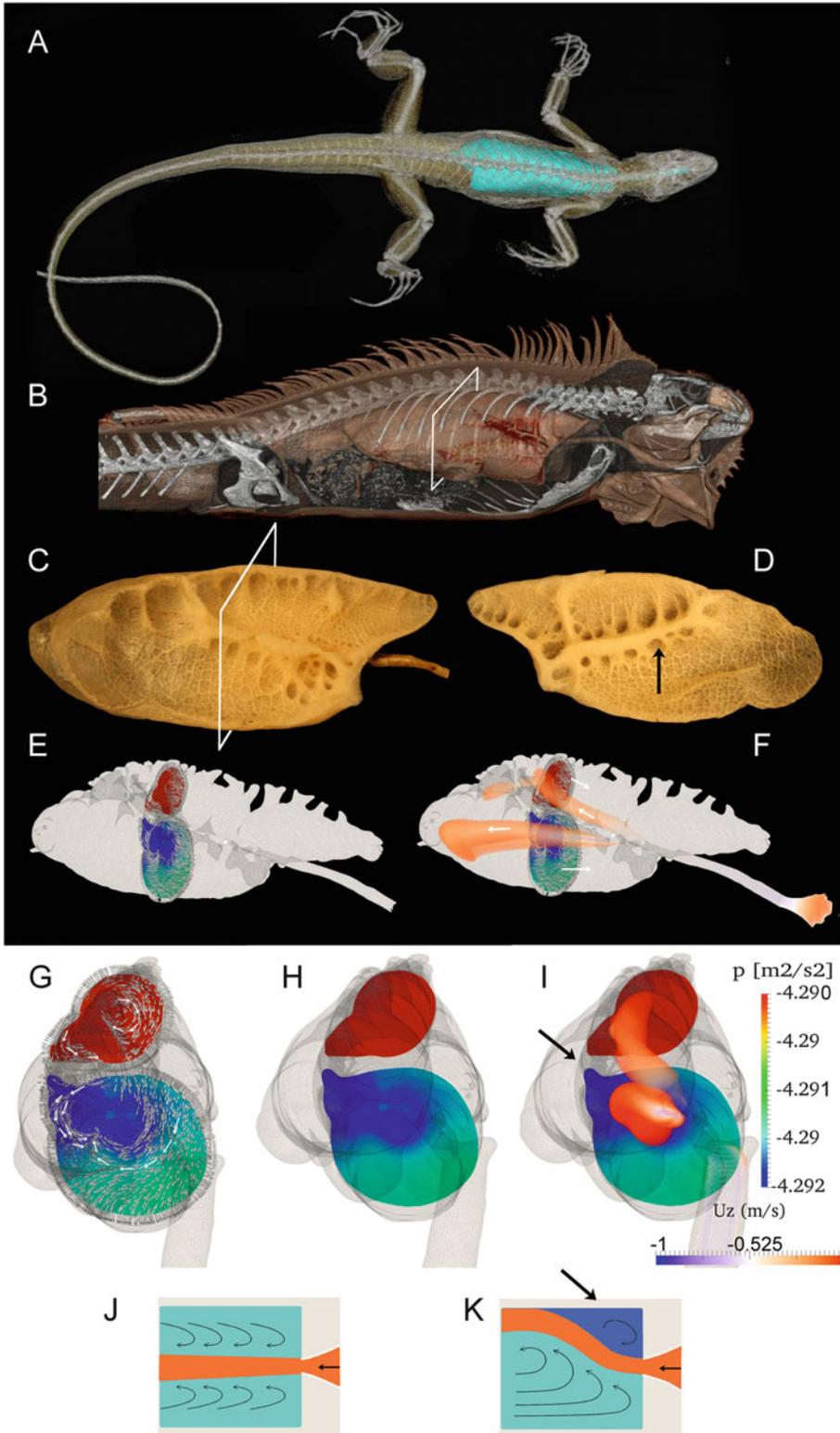


Fig. 3.5 Anatomy and patterns of airflow in iguana lungs. (a) Computed tomography data of a green iguana (*Iguana iguana*) in dorsal view with pulmonary voxels

colored turquoise. (b) Lateral view of iguana showing trachea and right lung. *White square* shows region of the lung where pressure is illustrated in the computational

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Fig. 3.5 (continued) model (e–i). (c) Dried iguana lung that has been cut in the parasagittal plane in lateral view. (d) Lateral wall of dried lung rotated 180° from plane of cut about the vertical axis. *Black arrow* shows region of the ventral chamber where pressure was modeled during inspiration (e–i) and where small niches are present on both sides of the septum separating the craniodorsal chamber from the caudoventral chamber. (e) Lateral view of mesh generated from computed tomography data of iguana lung showing axial slice of pressure over gas density during inspiration (*scale bar* in part I). Model is from Cieri et al. (2014). *Small silver arrows* indicate direction of airflow in the slice. (f) Same as in (e) but with the inspiratory jet visualized (*velocity scale* as in part I). *White arrows* have been superimposed to indicate direction of flow for ease of visualization. (g) Cranial view of axial pressure over gas density during inspiration, with *small silver arrows* indicating direction of airflow and *white arrows* superimposed for ease of visualizing airflow. Note the low-pressure zone associated with the

niches on the lateral walls of the horizontal septum. (h) Same as in (g) but with the arrows removed for ease of visualization of the zones of pressure. (i) Same as in (h) but with the inspiratory streams in both the dorsocranial and ventrocaudal chambers visualized, showing the cranial to caudal path of the streams (*orange jet*). (j) Illustration of the Coanda effect for a high-speed stream of air flowing into a wide container. The stream entrains air from both sides and becomes broader, carrying more air away from the ostium (inlet of nozzle) in the center of the chamber. This causes a drop in pressure in the zones between the stream and the walls, which in turn results in flow along the walls in the direction of the ostium. This is an unstable situation. A disturbance in the flow or the shape of the container can cause the equalizing flow returning along the walls to push the stream toward one wall, where it will lock onto the wall as it continues to flow (after Angrist 1964). In the iguana lung during inspiration, flow in most of the caudal chamber is craniad, with direction of flow of the high-speed stream caudad

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