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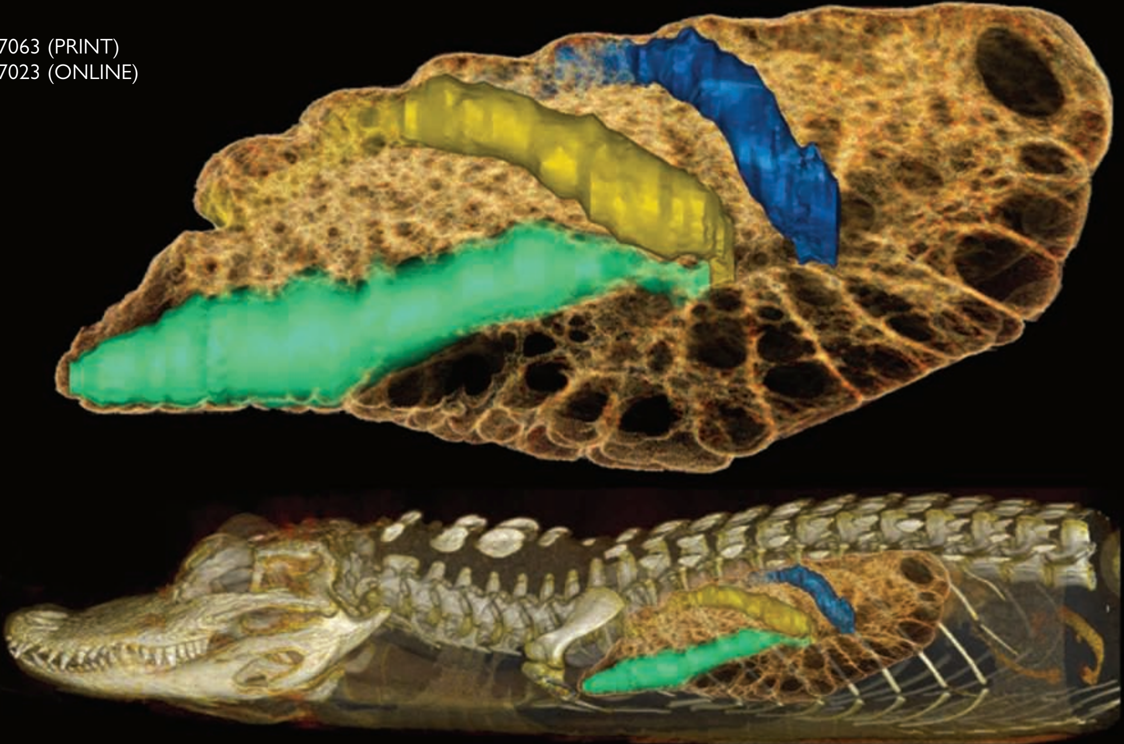

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Cover image: Top panel: Lateral view of a parasagittal section of computed tomography (CT) data of the lung of an American alligator (*Alligator mississippiensis*) with three of the conducting airways rendered in color. During both inspiration and expiration, airflow in the green bronchus is caudad, toward the right of the image, and craniad in the yellow and blue airways. Middle panel: lateral view of CT data of alligator showing position of the lungs in the thoracic cavity. Bottom panel: An adult alligator in South Carolina is photographed in the high walk. See the article, "Similarity of Crocodilian and Avian Lungs Indicates Unidirectional Flow Is Ancestral for Archosaurs" by C.G. Farmer for more information. Photo by Phil Wilkinson.

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SYMPOSIUM

Similarity of Crocodilian and Avian Lungs Indicates Unidirectional Flow Is Ancestral for Archosaurs

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From the symposium "Integrated Biology of the Crocodilia" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2015 at West Palm Beach, Florida.

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Synopsis Patterns of airflow and pulmonary anatomy were studied in the American alligator (*Alligator mississippiensis*), the black caiman (*Melanosuchus niger*), the spectacled caiman (*Caiman crocodilus*), the dwarf crocodile (*Osteolaemus tetraspis*), the saltwater crocodile (*Crocodylus porosus*), the Nile crocodile (*Crocodylus niloticus*), and Morelet's crocodile (*Crocodylus moreletii*). In addition, anatomy was studied in the Orinoco crocodile (*Crocodylus intermedius*). Airflow was measured using heated thermistor flow meters and visualized by endoscopy during insufflation of aerosolized propolene glycol and glycerol. Computed tomography and gross dissection were used to visualize the anatomy. In all species studied a bird-like pattern of unidirectional flow was present, in which air flowed caudad in the cervical ventral bronchus and its branches during both lung inflation and deflation and craniad in dorsobronchi and their branches. Tubular pathways connected the secondary bronchi to each other and allowed air to flow from the dorsobronchi into the ventrobronchi. No evidence for anatomical valves was found, suggesting that aerodynamic valves cause the unidirectional flow. *In vivo* data from the American alligator showed that unidirectional flow is present during periods of breath-holding (apnea) and is powered by the beating heart, suggesting that this pattern of flow harnesses the heart as a pump for air. Unidirectional flow may also facilitate washout of stale gases from the lung, reducing the cost of breathing, respiratory evaporative water loss, heat loss through the heat of vaporization, and facilitating crypsis. The similarity in structure and function of the bird lung with pulmonary anatomy of this broad range of crocodilian species indicates that a similar morphology and pattern of unidirectional flow were present in the lungs of the common ancestor of crocodilians and birds. These data suggest a paradigm shift is needed in our understanding of the evolution of this character. Although conventional wisdom is that unidirectional flow is important for the high activity and basal metabolic rates for which birds are renowned, the widespread occurrence of this pattern of flow in crocodilians indicates otherwise. Furthermore, these results show that air sacs are not requisite for unidirectional flow, and therefore raise questions about the function of avian air sacs.

Introduction

Thomas Huxley, with his usual sagacity, pointed out the importance of the similarity of the respiratory systems of crocodilians and birds when he wrote,

> Thus, not withstanding 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 (Huxley 1882).

More than a hundred years after Huxley's work, a deeper understanding of the striking similarity between these lungs became evident with the discovery that crocodilians share with birds a rather remarkable pattern of unidirectional airflow, in which gases move throughout most of the conducting airways in the same direction during both inhalation and exhalation due to the presence of aerodynamic valves (Farmer 2010; Farmer and Sanders 2010). The importance of this discovery lies not only in expanding our understanding of the fundamental resemblance of these respiratory systems, adding to the preponderance of evidence that allies these clades, but also in the broader context of demonstrating again the fallacy of the argument of irreducible complexity, for which the avian lung has been held up as an example (Denton 1985).

The avian respiratory system is certainly complex (Duncker 1971; Maina 2000): Akester (1960) stated that it is, "..the most complicated respiratory system that has ever evolved". This complexity appears to have led to a number of erroneous views. Most notable is the error of linking patterns of skeletal pneumaticity to patterns of airflow and efficiency of gas exchange. King (1957), in his study of patterns of pneumaticity of the domestic chicken, noted that these patterns vary widely from one individual to the next, and even between different sides of the body of the same individual, and that a lack of comprehension of this variability has led to invalid generalizations about pneumaticity. King (1957) argued that it is paramount to understand this variability in order to ascertain the limits of generalizations. Indeed, he stated, "It is a remarkable fact that after three centuries of research all the great questions of the functional anatomy of the avian respiratory tract still remain unanswered" and attributed the slow progress to a failure to recognize fundamental variations in structure and function in different avian species. Further evidence against linking patterns of pneumaticity to patterns of airflow and efficiency of gas exchange is discussed elsewhere (Farmer 2006). Another problem that has plagued understanding of these respiratory systems is that numerous authors use anatomy alone to extrapolate information about physiology, when what is needed are empirical, physiological data to draw conclusions based on evidence. For example, numerous publications state that the anatomy of crocodilians is consistent with crosscurrent gas exchange and therefore this mechanism of gas exchange was probably present in dinosaurs too (see discussion of this topic by Perry and Sander (2004) and references therein). However, crosscurrent gas exchange cannot be determined by studies of the anatomy. Measurements on blood and lung gases are requisite to elucidate the mechanism of gas exchange in these lungs. A third area of confusion is the role of the air sacs in the aerodynamic valves. In a brilliant and technically extraordinary study, Brackenbury (1989) bilaterally occluded the abdominal air sacs, as well as the cranial and caudal thoracic air sacs, and found no effect on the aerodynamic valve in resting or in exercising chickens. However, other workers conclude, "abdominal air sacs . . . are crucial for unidirectional flow in the paleopulmo of birds" (Perry and Sander 2004) even though the abdominal sacs in some birds, such as the kiwi, are so reduced in size their existence has been debated (Huxley 1882).

The avian respiratory system consists of a network of conducting airways that anastomose to form a circuit: this architecture lies in stark contrast to the more familiar blindly ending bronchial tree of mammals. The avian airways connect to avascular air sacs, which effect ventilation. The functional underpinnings of this design are not understood in spite of a long history of study, which is reviewed by Duncker (1971) dating back to work by the Dutch anatomist and physician, Volcher Coiter (1573), and by Allen (1951) for avian studies dating back to Aristotle (Coiter 1573; Allen 1951). Initially, studies and speculations about patterns of airflow through this circuit attributed the unidirectional flow to physical valves, either passive leaflets such as those found in the heart or the veins, or active sphincters (Brandes 1924; Bethe 1925; Portier 1928; Dotterweich 1930, 1936; Wolf 1933; Vos 1934). However, Hazelhof (1951) demonstrated that this flow can arise from the topography of the airways and that mechanical valves are not requisite, nor have they been found (Hazelhoff 1951). Hazelhoff's experiments and ideas have been refined and validated by a number of investigations (Brackenbury 1971, 1972, 1979; Bret and Schmidt-Nielsen 1972; Scheid and Piiper 1972, 1989; Scheid et al. 1972; Banzett et al. 1987, 1991; Butler et al. 1988; Kuethe 1988; Wang et al. 1992; Brown et al. 1995; Maina and Africa 2000). Butler et al. (1988) suggested four possible mechanisms governing gas flow in birds: (1) elastic pressures associated with the changes in volume of the air sacs, (2) resistive pressures arising from gas friction, (3) unsteady inertial pressures arising from the acceleration and deceleration of airway gas during the inspiratory–expiratory cycle, (4) dynamic pressures arising from convective momentum of gas. Gases of differing densities and velocity were used to gain insight into the importance of convective inertia, especially for the inspiratory valve (Wang et al. 1988; Brown et al. 1995). These studies showed that convective momentum, which is a function of the density of the gas multiplied by the square of its linear speed, is key to the inspiratory valve (Wang et al. 1988). The mechanical underpinnings of the expiratory valve are less well understood. Furthermore, the importance of certain anatomical features for the functioning of both the inspiratory and expiratory valves is still unclear.

Duncker (1971) reviewed and discussed features of the anatomy that may play essential roles in the aerodynamic valves. He listed:

(1) The point of origin of the ventrobronchi, with rigidly extended openings directed cranially, so

that these airways form an acute angle with the intrapulmonary bronchus. These bronchi dilate remarkably in width.

(2) The origin of the dorsobronchi in the region of the primary bronchus that arches with the concave side mesial. The initial portions of the dorsobronchi are narrow and their diameters can be regulated. The dorsobronchi also form acute angles with the primary bronchus.

(3) The origin of the laterobronchi opposite to the anterior dorsobronchi, their initial angle also forming an acute angle with the intrapulmonary bronchus.

(4) Connection of the posterior air sacs to the primary laterobronchus.

Other features that have been suggested to play a role in the aerodynamic valves include a narrowing of the primary bronchus proximal to the opening of the ventrobronchi, the segment accelerans (Wang et al. 1992), and an expansion of the width of the intrapulmonary bronchus prior to the openings of the dorsobronchi. Finally, as previously mentioned, the air sacs have been purported to play a role in the valve (see Perry and Sander 2004).

The discovery of the same pattern of airflow in crocodilians with similar anatomical features as birds provides an opportunity to identify common, conserved features that may be important to the aerodynamic valves. Although this study focuses on documenting patterns of airflow in crocodilians, I have also attempted to identify common anatomical characters of crocodilians and birds to help throw into sharp relief the features that may be fundamentally important for the aerodynamic valves from those that are unimportant. I have relied heavily on Duncker's (1971) monograph for generalizations about avian anatomy. These comparisons are meant to stimulate and help direct further empirical research, which will perhaps expand our understanding of the aerodynamic valves both of birds and of crocodilians, as well as elucidate selective drivers for these patterns of flow. In the summary, I speculate on several testable hypotheses for these selective drivers.

Materials and methods

In vivo experiments

In vivo procedures were approved by the University of Utah Animal Care and Use Committee and were carried out on the American alligators. I measured intrapulmonary airflow by implanting a dual thermistor flow meter (HEC 132 C, Hector Engineering, Ellettsville, IN, USA). I visualized airflow using an endoscope with a diameter of 0.9 mm (Model number HSF 009 1000 NVK, Hawkeye Pro Microflex Borescope, Gradient Lens Corporation) and with a field of view of 55 degrees. I held the scope in one location while animals insufflated an aerosolized mixture of propylene glycol and glycerol (Froggy's Fog—Swamp Juice, Froggys Fog, LLC) and I recorded videos using a Luxxor Video Camera System (LXX-VBSM) that was interfaced to a computer with a USB 2.0 Image Capture Interface (VC-USB2). I recorded the videos with Debut Video Capture software at a rate of frame capture of 29.97 frames per second and determined the direction of airflow visually. I recorded airflow at the nares with a pneumotachograph (Hans Rudolph Inc.). I amplified this signal with an AC/DC strain gauge amplifier (P122, Grass Instruments, Warwick, RI, USA) and converted all analog signals to digital (Biopac Systems, Goleta, CA, USA) at a sampling rate of 60 Hz and recorded these signals on a computer using AcqKnowledge software (Biopac Systems). I measured the electrocardiogram using cutaneous leads, sampling at 200 Hz and filtering and amplifying the signals (P122, Grass Instruments).

Ex vivo experiments

I measured airflow in separate experiments in excised lungs by implanting a dual thermistor flow meter (HEC 132 C, Hector Engineering) or by visualization of aerosolized propylene glycol and glycerol as described in the *in vivo* methods. I intubated the trachea and ventilated the lung with a syringe. I measured tracheal flow with a pneumotachograph (Hans Rudolph Inc.) as described in the *in vivo* methods. Sample sizes varied depending on species. The largest sample sizes were obtained for the American alligator ($N = 11$), the saltwater crocodile ($N = 10$), and the spectacled caiman ($N = 5$), and so conclusions are weighted toward these species. Sample size was 3 or less for the remaining species. Information on mass was not available for all the individuals because of variation in the way they were obtained. For example, in many of the animals only torsos were available, having been donated by abattoirs. Where this information is known it is reported.

Anatomy

To visualize the anatomy I used both gross dissections and computed tomography. I reconstructed these CT data into images with OsiriX (v.5.8.2 64-bit).

Results and discussion

Much of the anatomy of the lungs of alligators and crocodiles has been described previously (Huxley 1882; Perry 1989, 1990; Farmer and Sanders 2010; Sanders and Farmer 2012; Schachner et al. 2013). The focus here is investigating whether or not unidirectional flow is common throughout the crocodilians and highlighting features that have not been described previously in detail, or features that are common to all the crocodilians I have studied to date and which can be compared with similar features in birds. I also noted differences that corroborate or cast doubt on the role of aspects of avian anatomy in the aerodynamic valve.

In many crocodiles (e.g., *Crocodilus niloticus*, *Crocodylus porosus*, *Crocodylus palustris*, *Crocodylus intermedius*), this study (Huchzermeyer 2003; Grigg and Kirshner 2015); and some birds (Clench 1978; Fitch 1999), the trachea and primary bronchi do not travel a straight course to the lungs, but form loops in larger individuals (Fig. 1). In birds this loop is thought to play a role in sound production (Fitch 1999). Its function in crocodilians is unknown. In contrast, the trachea of alligators, spectacled caiman, black caiman, and the dwarf crocodile run in a straight course to the carina and the primary bronchi also course directly toward their respective lungs (this study; also Grigg and Kirshner 2015). Sound production in alligators occurs in the larynx (Riede et al. 2011, 2015) but a role for the trachea has not been ruled out. Unidirectional flow occurred independently of the presence or absence of a looping trachea.

The position of the lungs within the thoracic cavity was consistent across all species examined. The dorsal mesentery, a median vertical sheet of tissue, forms a septum in the thoracic cavity and cranial abdominal cavity. The alimentary canal runs through the middle of the sheet while the lungs and two halves of the liver lay to either side. The lungs occupy the right and left sides of the cranial region of the thoracic cavity, the pleural cavity, the apex extending to the eighth or ninth cervical vertebra and the base extending in its dorsal portion to approximately the ninth thoracic vertebra (Fig. 1A–C) (Mushonga and Horowitz 1996). Here the lung attaches to the liver through the pulmohepatic ligament, which forms part of the wall (mainly lateral) of a recess between the liver and the lung, the hepatopulmonary bursa (Fig. 1) (Butler and Parker 1889; Mushonga and Horowitz 1996). These bursae communicate through a narrow passage with the pleural cavities. The hepatopulmonary ligament passes into a membranous tract that merges with the caudal lung and the mediastinal tissue. It has been proposed that this serous tissue is homologous with the avian oblique septum (Huxley 1870; Butler and Parker 1889; Pool 1909), which fuses with the dorsal pericardium and together with the dorsal portion of the sternum separates the avian body into a cavum respiratorium, containing the lungs and all air sacs except the abdominal air sac, and caudoventrally into a cavum cardioabdominale, containing the heart, liver, alimentary tract, and abdominal air sacs. In birds, the cavum respiratorium is subdivided by the horizontal septum (avian diaphragm), the lungs, and intrapulmonary bronchi lying dorsal to the horizontal septum in the cavum pulmonale, and all the air sacs except the abdominal air sacs lying ventral to the horizontal septum in the cavum subpulmonale (Duncker 1971). In birds the oblique and horizontal septa are formed when portions of the lung invade the pulmonary folds and divide them, the ventral portion of the fold giving rise to the oblique septum and the dorsal portion giving rise to the horizontal septum (Pool 1909; Duncker 1971). In crocodilians a similar topography exists with the gas-exchange parenchyma lying dorsal to the ventral aspects of the intrapulmonary bronchus and the saccular regions of the lung lying dorsal to the representative of the oblique septum (Fig. 1C) but ventral to the intrapulmonary bronchus, in the topographical position of the avian horizontal septum. Figure 1 illustrates the topographical location in the body cavity of the avian horizontal and oblique septa, superimposed on the lateral image of an American alligator.

In crocodilians the parietal pleura attaches dorsally to the longus colli muscles, the bodies of the last cervical and the thoracic vertebral bodies, and to the intercostal muscles and ribs. Deep sulci are formed in the lungs by the ninth cervical ribs and, to a lesser degree, the subsequent thoracic ribs. Ventromedially the lung attaches directly to the mediastinal pleura and ventrally to the esophagus. The pleural space, where the visceral and parietal pleura are readily separated, completely surrounds the apical region of the lung to the root of the lung, demarcated by the hilus, but is found only dorsally and laterally caudal to the hilus (Fig. 1). The primary bronchus and pulmonary vessels enter the ventromedial aspect of the lung approximately half way between the apex and the dorsal portion of the base (Fig. 1). At the hilus, the pulmonary artery is cranial and the pulmonary vein caudal to the bronchus. The medioventral surface of the lung caudal to the hilus does not float freely in the pleural cavity but adheres

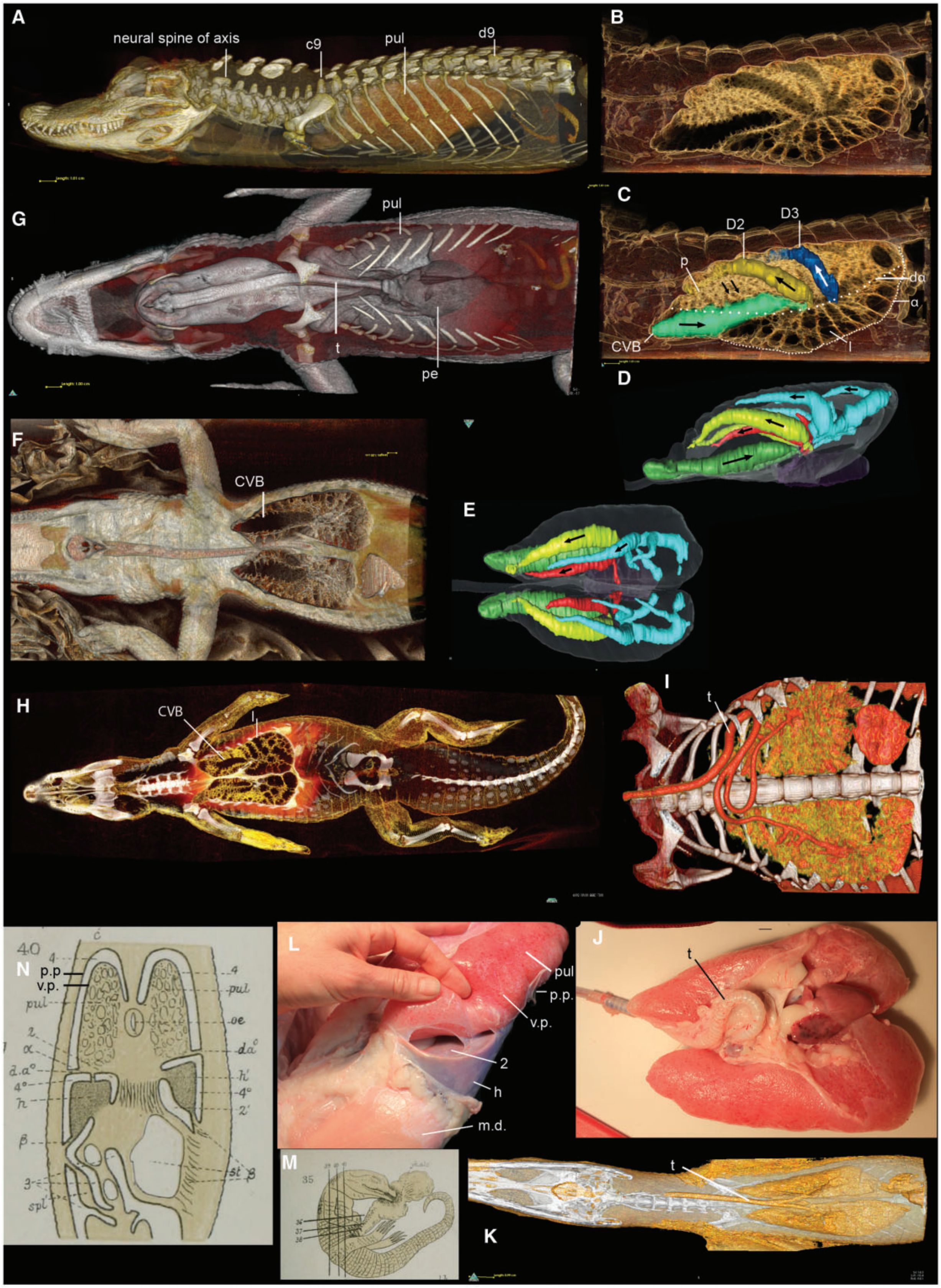

Fig. 1 Anatomy and patterns of airflow in crocodilians. American alligator (**A–G**) in lateral view (A–D), dorsal view (E–F), and ventral view (G). The apex of the lung can be seen underling cervical vertebrae 8 and 9 while the dorsal part of the base of the lung extends to thoracic vertebra 9. View of transection in the parasagittal plane without (B) and with (C) colored voxels illustrating the airways.

(continued)

to the underlying structures of the pericardial sac, portions of the liver, left and right aorta, and esophagus, except where there are bursae, as noted above and by Mushonga and Horowitz (1996).

The intrapulmonary bronchus retains cartilaginous support in its most proximal portion, but this is lost as the bronchus courses laterally, caudally, and dorsally. In alligators, the bronchus increases in diameter along this path until it approaches the level of vertebral centra at which point it curves medially and gradually decreases in diameter as it continues to the dorsal base of the lung (Fig. 1). The first secondary bronchus to arise from the primary bronchus does so from its lateral aspect very near the midline of the lung in the sagittal plane (Fig. 1). The opening to this bronchus is a conical, cartilaginous structure that contains smaller ostia in its walls. The conical portion of the CVB opens into a secondary bronchus that is poorly vascularized and widens remarkably as it courses craniad. It is the largest of the secondary airways, and extends to lie alongside the cervical vertebra. This bronchus has been termed the cervical ventral bronchus (CVB) (Farmer and Sanders 2010; Sanders and Farmer 2012) and postulated to be homologous to the avian embryonic mesial moiety of the first ventrobronchus that develops into the cervical air sac and to the first avian ventrobronchus. Measurements of flow have been made in this bronchus in all species and the flow is always caudad (Fig. 1). The volume of this bronchus indicates it is serving both a storage function and as a major conducting airway. It is the same airway termed D1 by Broman (1940). The ostia of the conical portion of the CVB connect to several other poorly vascularized bronchi that run in tandem along the CVB, although not as far craniad.

On the dorsal aspect of the intrapulmonary primary bronchus, very near the ostium to the CVB, a large and long bronchus arises that courses dorsally and then cranially (M1 of Broman 1940, and red bronchus of Fig. 1), coursing medially and parallel to the CVB (Fig. 1). There is very little distance between the ostium of M1 and the CVB and yet the flow runs craniad in M1, as it does in the remaining dorsobronchi (Fig. 1). M1 has clear connections to medioventral locules (chambers) that overlie the heart. These locules occupy the location of the interclavicular and thoracic air sacs of birds. There is no fusion of the locules at the midline, as there is with the avian interclavicular sacs. The intimate connection of these chambers to the heart implicates them in generating the cardiogenic unidirectional airflow measured during apnea (Farmer 2010) (Fig. 2). As the heart beats it may mechanically agitate these locules, which are firmly attached to the pericardium, producing airflow. However, cardiogenic flow may also arise from the pulsations of the blood vessels within the lungs. Further experiments are needed to sort out the mechanisms underlying cardiogenic, unidirectional flow.

Small parabronchi connect the ventrobronchus and its branches to the network of dorsobronchi, conducting air through the majority of gas-exchange parenchyma (Fig. 1). The minimum diameters of these connections are approximately 1 mm, which falls within the size range of the diameters for the avian parabronchi (Duncker 1971).

Besides the region of the lung that overlies the heart, the caudoventral aspect of the lung is also composed of poorly vascularized locules (Fig. 1). The diameters of the ostia to these chambers tend to be much smaller than those leading to the dorsobronchi and they lie opposite the ostia to the dorsobronchi, perhaps serving to direct flow into the dorsobronchi during exhalation. Based on their topographical position in the body and the patterns of flow in these locules, which is primarily tidal, they

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Fig. 1 Continued

Dashed lines (C) illustrate purported homologs of the oblique septum (small dots) and the topological position corresponding to the avian diaphragm = horizontal septum (large dots). Arrows indicate direction of airflow. Ventral view (G) illustrates the intimate location of the pericardium with the lungs. (**H**) Dorsal view of spectacled caiman showing the position in the body and the CVB and caudoventral locules. (**I**) Ventral view of adult female Orinoco crocodile showing looping trachea and primary bronchi. (**J–L**) Saltwater crocodile. (J) Ventral view of juvenile shows looping trachea whereas the trachea is straight in a hatchling (K). (L) Dorsolateral view of juvenile showing the parietal pleura (reflected back), the visceral pleura, and the pulmohepatic bursa, the roof of which has been suggested to be homologous to the avian oblique septum. (**M**, **N**) Unhatched crocodilian. (M) The plane of section (40) shown in N. (N) A number of features illustrated in (C) and (L), including parietal and visceral pleura, pleural cavity (cavum pulmonale), pulmohepatic ligament (homolog of avian oblique septum), pulmohepatic recess = hepatopulmonary bursa. CVB, cervical ventrobronchus; c, cervical vertebra; d, dorsal vertebra; D2, dorsobronchi 2; D3, dorsobronchi 3; da, representative (homolog) of avian diaphragm = horizontal septum; h, right lobe of the liver; h′, left lobe of the liver lobe; l, laterobronchi = caudoventral locules; m.d., diaphragmaticus muscle; oe, esophagus; p, parabronchi and gas-exchange parenchyma; pe, pericardium; p.p., parietal pleura; pul, lung; spl′, fatty "spleen", st., stomach cavity; t, trachea; α, pulmohepatic ligament = homolog of avian oblique septum; β, omental septum (ventral portion of posthepatic septum); 2, right pulmohepatic recess = hepatopulmonary bursa; 2′, left pulmohepatic recess; 3, peritoneal cavity; 4, pleural cavity; 4°, pulmohepatic portion of body-cavity; M, N after, Butler and Parker (1889); D, E after, Farmer and Sanders (2010).

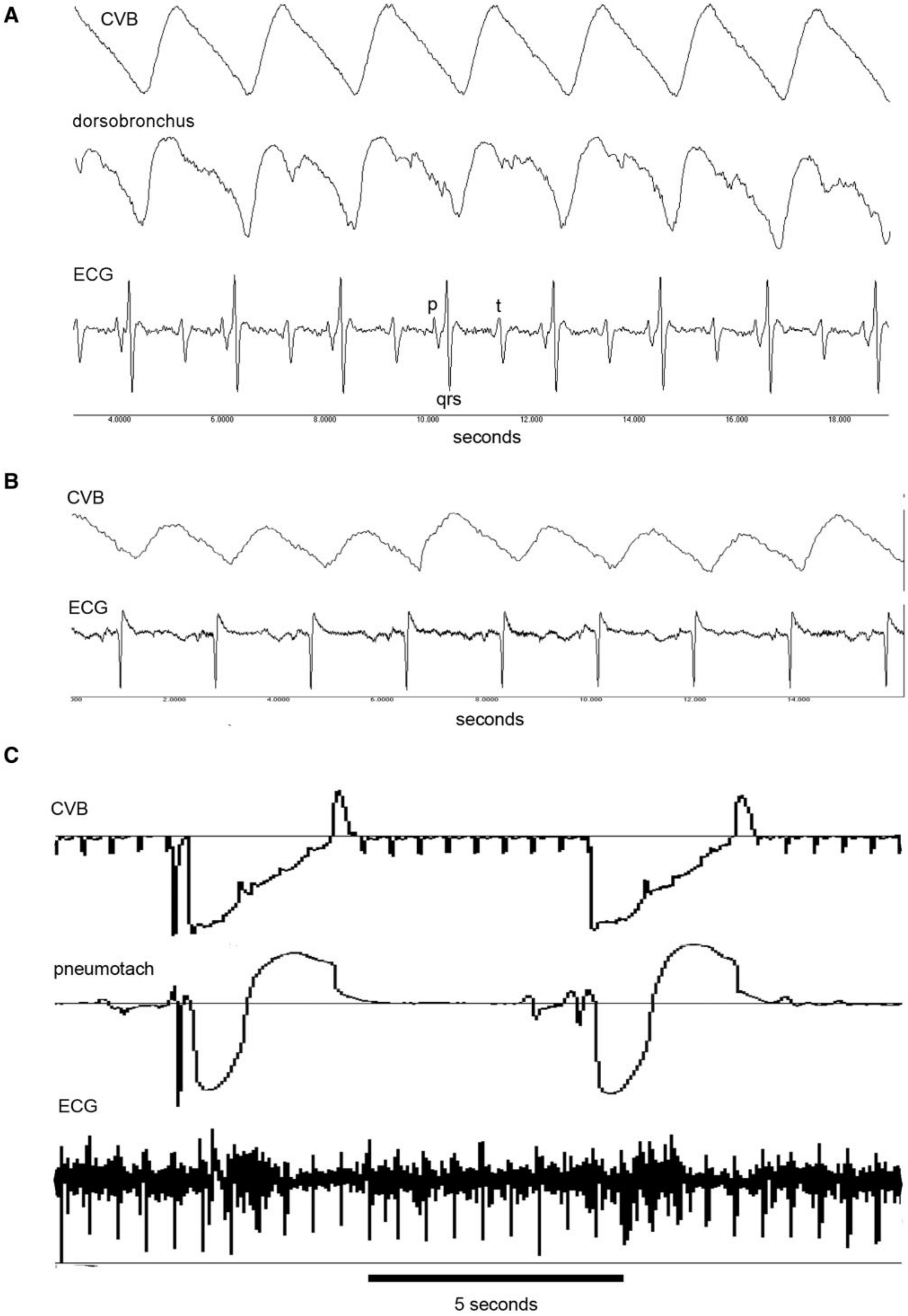

Fig. 2 Cardiogenic unidirectional flow. (**A–C**) Electrocardiograms and flow traces collected from the cervical ventrobronchus and a dorsobronchus for three different animals. (A) and (B) were collected during a period of apnea. No breathing is shown. The trace shown in (C) was collected shortly after the animal ran on a treadmill and includes a recording of airflow at the nares recorded with a pneumotachograph.

appear to be homologous to the avian laterobronchi and air sacs.

Summary

In this study unidirectional flow was measured during ventilation in excised lungs in all species studied, with flow in the CVB running caudad and flow in the dorsobronchi running craniad (Fig. 1). In addition, unidirectional flow was measured *in vivo* in American alligators. This unidirectional flow continued during periods of apnea, powered by the beating heart (Fig. 2).

Birds and crocodilians share a number of pulmonary features that are strikingly similar, suggesting that a similar topography was present in their common ancestor. These features include the separation of the thoracoabdominal cavity by an oblique septum into a cavum respiratorium and a cavum cardioabdominale. The cavum respiratorium is further subdivided into a region bounded ventrally by the oblique septum and dorsally by the ventral floor of the intrapulmonary bronchus. This region is reminiscent of the avian cavum subpulmonale and contains avascular locules reminiscent of the avian air sacs. The region containing the intrapulmonary bronchus and the dorsobronchi and parabronchi lies dorsal, in the pleural cavity, the cavum pulmonale. Another striking similarity is the acute angle formed between the intrapulmonary bronchus and the ventrobronchi, with rigidly extended openings into the ventrobronchi, which dilate remarkably. This topography seems well conserved and may be important to the aerodynamic valve.

However, several observations of the anatomy of crocodilians also suggest that we do not fully understand the aerodynamic valves in either crocodilians or birds. Duncker (1971) reviewed and discussed features of the anatomy of birds' lungs that may play roles in the aerodynamic valves (see the above discussion). However, many of these characters are not present in crocodilians. For example, avian style air sacs and a segment accelerans are not present in crocodilians. Duncker (1971) proposed that the origin of the dorsobronchi in the region of the primary bronchus where it arches in a convex manner near the lateral body wall is important. However, the first dorsobronchus of crocodilians arises very near the ostium to the CVB, well before the intrapulmonary bronchus begins its curve toward medial in the midline, suggesting that the topographical position of the dorsobronchi in birds at the medial bend of the intrapulmonary bronchus may not play a role in the valve. However, the relationship between the ostia of the dorsobronchi and the avascular locules in crocodilians and the avian dorsobronchial ostia to the air sacs is very consistent, and supports a role of this topography in the expiratory valves. Finally, in both clades the intrapulmonary bronchus dilates considerably in its caudal course, also suggesting an aerodynamic function. The sensitivity of the aerodynamic valves to these features may be revealed by computational studies of fluid dynamics. These differences may mean that the same mechanisms do not underpin the aerodynamic valves of crocodilians and birds. The differences certainly underscore the need for additional research into this fascinating area of biology.

The looping pattern of flow seen in birds and crocodilians shares so many remarkable features that the parsimonious explanation for this similarity is shared inheritance as originally proposed by Huxley (1882). This discovery begs the question of the functional significance for this pattern of flow. It has recently been postulated (Farmer 2015) that the unidirectional pattern of flow is serving to efficiently flush gases from the lung, thereby reducing the number of breaths required compared with the exponential wash out seen in mammals. For example, in humans a tidal volume of about 0.5 L is mixed with a residual lung volume of about 3 L with each breath, diluting the freshly inspired air (West et al. 2007). In contrast, with unidirectional flow a bolus of air moves from one compartment of the lung to the next, reducing the mixing of stale and freshly inspired air. Thus, unidirectional flow could reduce rates of ventilation for a given rate of gas exchange, thereby reducing the work of breathing, reducing respiratory water loss, conserving heat, and improving crypsis. It has also been postulated that cardiogenic, unidirectional flows facilitate gas exchange during apnea (Farmer 2010).

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