

# INSPIRATORY AERODYNAMIC VALVING IN THE AVIAN LUNG: FUNCTIONAL MORPHOLOGY OF THE EXTRAPULMONARY PRIMARY BRONCHUS

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## Summary

The form, geometry and epithelial morphology of the extrapulmonary primary bronchi (EPPB) of the domestic fowl (*Gallus gallus* var. *domesticus*) and the rock dove (*Columba livia*) were studied microscopically and by three-dimensional computer reconstruction to determine the structural features that may be involved in the rectification of the inspired air past the openings of the medioventral secondary bronchi (MVSB), i.e. the inspiratory aerodynamic valving (IAV). In both species, the EPPB were intercalated between the clavicular and the cranial thoracic air-sacs. A notable difference between the morphology of the EPPB in *G. g. domesticus* and *C. livia* was that, in the former, the EPPB were constricted at the origin of the MVSB, while a dilatation occurred at the same site in the latter. In both species, a highly vascularized, dorsally located hemispherical epithelial swelling was observed cranial to the origin of the MVSB. The MVSB were narrow at their origin and variably angled relative to the longitudinal axis of the EPPB. Conspicuous epithelial tracts and folds were observed on the luminal aspect of the EPPB in both *C. livia* and *G. g. domesticus*. From their

marked development and their orientation relative to the angled MVSB, these properties may influence the flow of the air in the EPPB. It was concluded that features such as syringeal constriction, an intimate topographic relationship between the EPPB and the cranial air-sacs, prominent epithelial tracts and folds, an epithelial swelling ahead of the origin of the first MVSB (corresponding to the 'segmentum accelerans'), and narrowing and angulation of the MVSB at their origin, may together contribute to IAV to a variable extent. In as much as the mechanism of pulmonary ventilation and mode of airflow in the parabronchial lung are basically similar in all birds, the morphological differences observed between *G. g. domesticus* and *C. livia* suggest that either the mechanism of production of IAV or its functional efficiency may be different, at least in these two species of birds.

Key words: birds, lung, bronchus, epithelial swelling, segmentum accelerans, domestic fowl, *Gallus gallus domesticus*, rock dove, *Columba livia*.

## Introduction

The lung/air-sac system of birds is structurally the most complex (e.g. King, 1966; Duncker, 1972) and functionally the most efficient (e.g. Scheid, 1979) gas exchanger that has evolved in the air-breathing vertebrates (Maina, 1998). The flow of the inspired air through the extrapulmonary primary bronchi (EPPB) directly into the caudally located mediiodorsal secondary bronchi (MDSB) and partly into the posterior (caudal thoracic and abdominal) air-sacs, completely bypassing the openings of the large cranial medioventral secondary bronchi (MVSB), a process termed 'inspiratory aerodynamic valving' (IAV) by Banzett et al. (1987, 1991) and Wang et al. (1988), is little understood. [Extrapulmonary primary bronchus is the term used to refer to the section of the primary bronchus between the bifurcation of the trachea and pulmonary hilus while the intrapulmonary primary bronchus (mesobronchus) is the section between the pulmonary hilus and the ostium of the

abdominal air-sac. The former is termed *bronchi primarii, partes extrapulmonales* and the latter *bronchi primarius, pars intrapulmonalis* (King, 1979)]. Through an exceptional structural design (e.g. Maina, 1998), the process of IAV enables the gas exchange tissue (parabronchial) of an internalized, tidally ventilated respiratory organ to be continuously and unidirectionally ventilated with air in a caudocranial direction (e.g. Scheid et al., 1972; Powell et al., 1981).

The generation of a unidirectional airflow through the parabronchi in a bidirectionally ventilated organ could be explained by the existence of anatomical valves that open and close in phase with the breathing cycle. Indeed, succumbing to such appealing conceptual reasoning, certain early authors such as Brandes (1924), Bethe (1925) and Dotterweich (1930, 1933) regarded the airflow in a bird's lung to be produced by alternating mechanical opening and closing of several valves.

Fig. 1. Dorsal view of a latex cast of the lung/air-sac system of the domestic fowl (*Gallus gallus* var. *domesticus*). Arrows indicate the lungs. t, trachea; cv, cervical air-sac; cl, clavicular air-sac; cr, cranial thoracic air-sac; ca, caudal thoracic air-sac; a, abdominal air-sac. Scale bar, 1 cm.

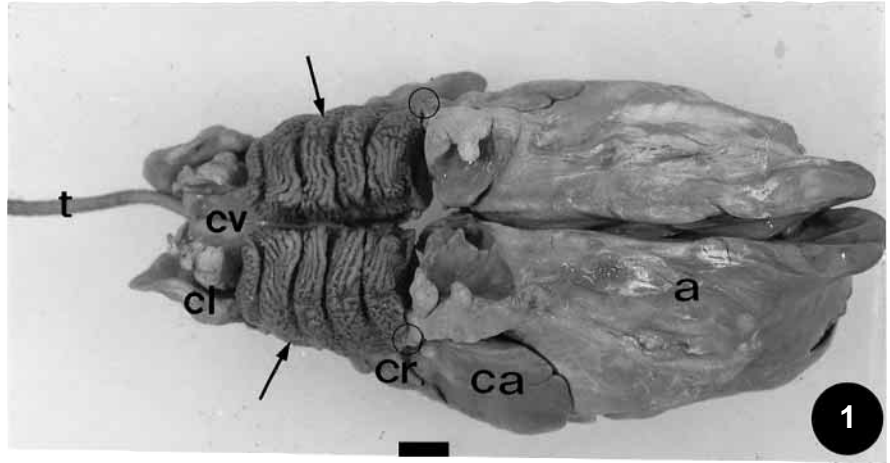
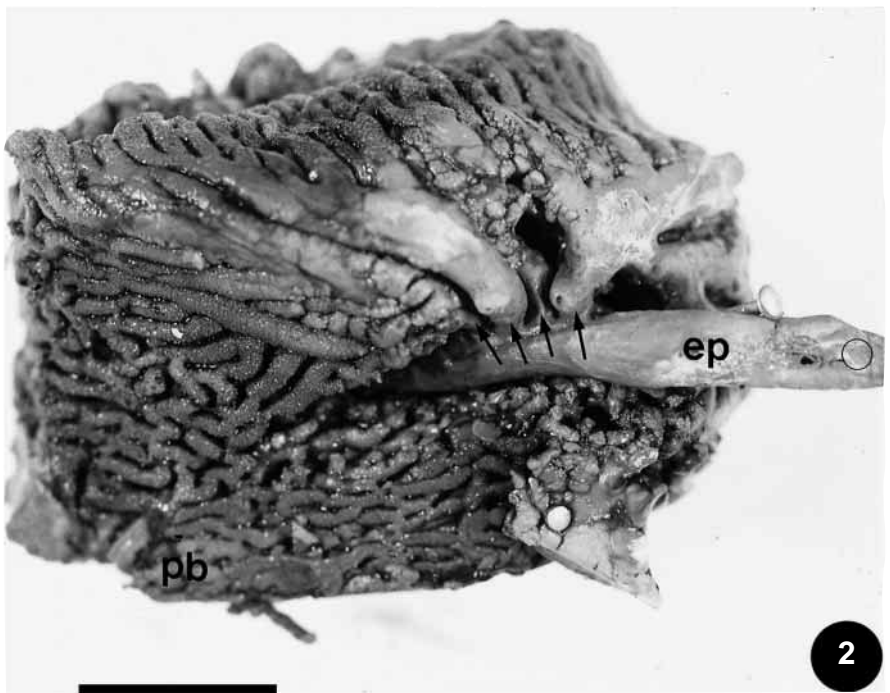


Fig. 2. Medial view of a latex cast of the lung of the domestic fowl (*Gallus gallus* var. *domesticus*) showing the extrapulmonary primary bronchus (ep) and the angulated medioventral secondary bronchi (arrows). pb, parabronchi; the circle shows the syrinx. Scale bar, 1 cm.



Vos (1935) envisaged the existence of at least one valve in each lung. Reassessing the anecdotal assertions and failing to find unequivocal proof of their existence, Dotterweich (1936) introduced the concept of 'fluid valve' and deduced that the shunting of air past the MVS in the avian lung could be explained totally on the basis of aerodynamic forces. Until very recently (e.g. Banzett et al., 1987, 1991; Butler et al., 1988; Kuethe, 1988; Wang et al., 1988), this explanation was embraced unquestionably without thorough and rigorous theoretical analysis, experimental testing and evaluation and morphological substantiation.

The primary objectives in the present study were: (i) to study comparatively the size, geometry and epithelial morphology of the EPPB in the domestic fowl (*Gallus gallus* var. *domesticus*) and the rock dove (*Columba livia*) to establish the morphological features that may be directly or indirectly

involved in the rectification of the inspired air past the openings of the MVS in two species of different body sizes and metabolic capacities, and (ii) to determine whether a 'segmentum accelerans', a constriction of the EPPB deduced to be present by Wang et al. (1992) from radiographic measurements of the airflow in the lung of the goose *Anser anser*, is present in *G. g. domesticus* and *C. livia*.

#### Materials and methods

Six mature specimens of the domestic fowl (*Gallus gallus* var. *domesticus* L.) and six of the rock dove (*Columba livia* L.) were used in this investigation.

#### Latex casting

Two specimens of *G. g. domesticus* and two of *C. livia* were

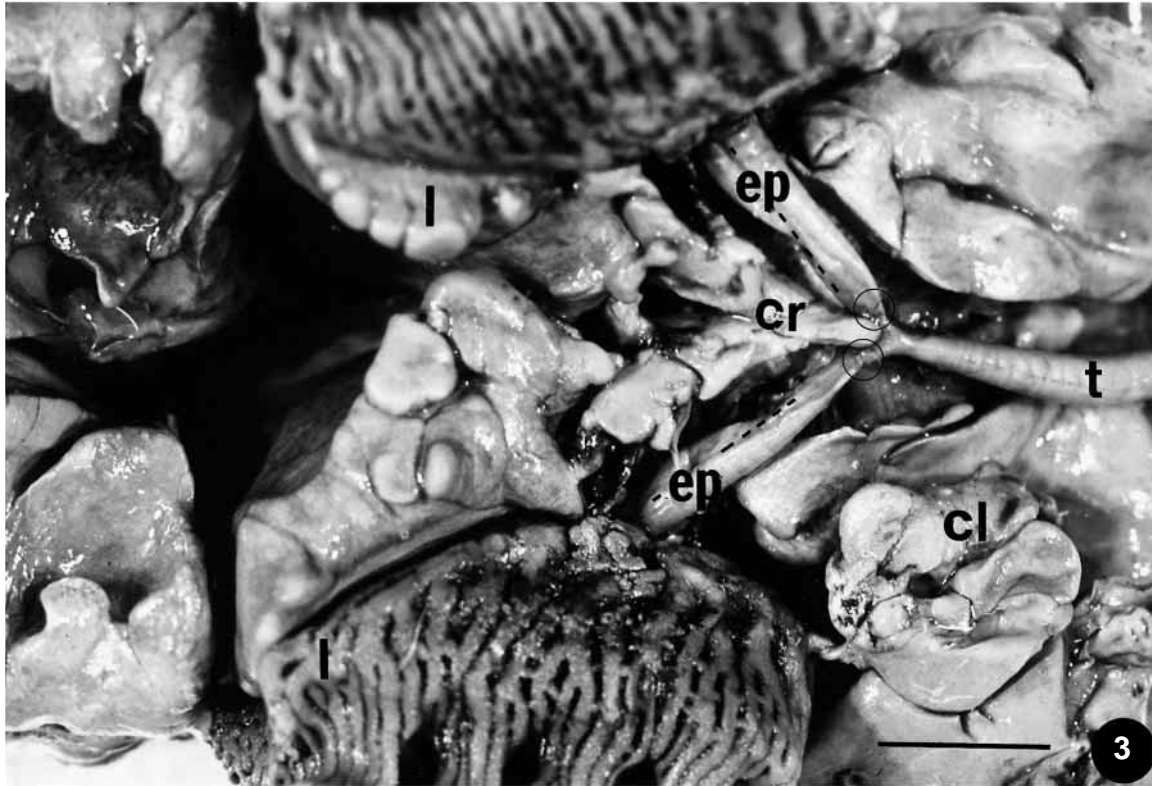


Fig. 3. Ventral view of a latex cast of the air-sacs and lungs of the domestic fowl (*Gallus gallus* var. *domesticus*) showing the lungs (l), the trachea (t), the extrapulmonary primary bronchi (ep) and the clavicular (cl) and cranial thoracic (cr) air-sacs. The circles indicate the location of the syrinx; the dashed line shows the ventral location of the space between the C-shaped cartilages of the extrapulmonary primary bronchus. Scale bar, 1 cm.

killed by injection of 2~ml of sodium pentobarbitone ( $200 \text{ mg cm}^{-3}$ ) into the branchial vein. The trachea was exposed and transected, and a two-way cannula was inserted and ligated to keep it in place. To ensure satisfactory filling of the lung/air-sac system with the fixative, the residual air was aspirated using a 50 ml syringe. A stock solution of latex rubber (Latex White, ZCP-652-OIOR, Griffin & George Ltd, UK) was mechanically injected through the second channel. When the coelomic cavity tensed slightly, the injection was stopped and the trachea ligated ahead of the cannula. Subsequently, the entire body was immersed in 75% hydrochloric acid. After 5 days, the macerated tissue was physically removed to expose the cast, and the bodies were re-immersed in freshly prepared acid, if necessary. After the final clearance, the cast was washed and placed in distilled water.

#### Light microscopy

Two specimens of *G. g. domesticus* and two of *C. livia* were killed through intravenous injection with sodium pentobarbitone as described above and the trachea cannulated. The lung/air-sac system was fixed by intratracheal instillation with 2.3% glutaraldehyde buffered in sodium cacodylate (pH 7.4; osmolarity  $350 \text{ mosmol l}^{-1}$ ) at a pressure head of 3.3 kPa. To enhance the penetration of the fixative, the coelomic cavity was continuously massaged to express the

residual air. When the fixative stopped flowing, the trachea was ligated, and the fixative was left *in situ* for 24 h. Subsequently, two paramedian incisions (on opposite sides of the sternum) were made through the pectoral muscles and the sternum, and the coracoids were disarticulated. The heart and the liver were exposed and removed, and the lungs (still attached to the trachea and the EPPB) were carefully removed from the costal attachment. Later, the EPPB were isolated by cutting them between the tracheal bifurcation and the hilus of the lung.

In one specimen, the EPPB were decalcified in EDTA, changed several times daily over a period of 3 weeks, while in the other the pieces were left in fixative. Both the decalcified and the undecalcified EPPB were processed for light microscopy using standard laboratory techniques and embedded in paraffin wax. Serial transverse sections were cut at a thickness of  $10 \mu\text{mol l}^{-1}$ , mounted on glass slides, and stained with Haematoxylin and Eosin. Both sets of sections were studied to assess the histomorphology and configuration of the epithelial lining. The decalcified sections, which were of superior quality, were used for three-dimensional reconstruction.

#### Transmission electron microscopy

The EPPB of the fixed lungs of one specimen of *G. g. domesticus* and one of *C. livia* were processed for electron

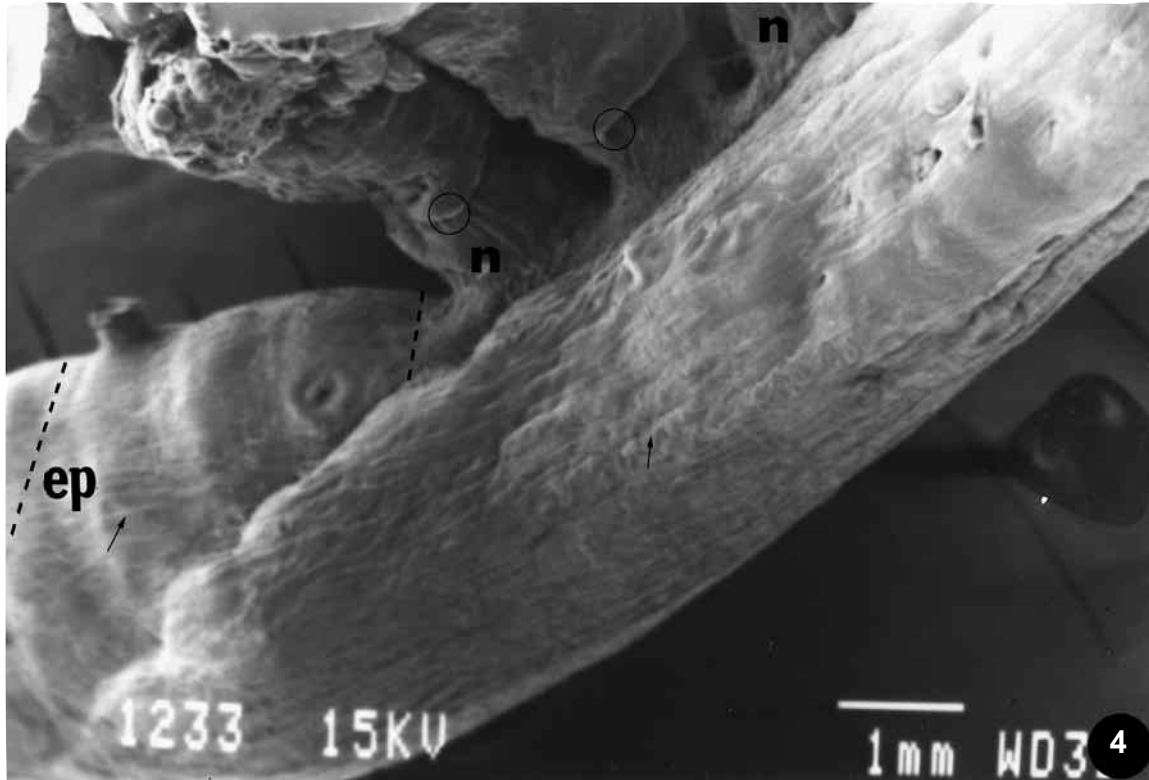


Fig. 4. Close up of the origin of the medioventral secondary bronchi (n) from the extrapulmonary primary bronchus (ep) of the domestic fowl (*Gallus gallus* var. *domesticus*). Note the angulation and the constriction (circles) of the medioventral secondary bronchi close to their origin. The arrows show the impressions left by the epithelial folds. The region between the dashed lines (on the caudodorsal aspect of the extrapulmonary primary bronchus cranial to the first medioventral secondary bronchus) is occupied by a hemispherical epithelial swelling. Scale bar, 1 mm.

microscopy. The tissue was dehydrated in ascending concentrations of ethanol and in acetone, block-stained in a 5% solution of uranyl acetate, and infiltrated and embedded in epoxy resin (Epon 812<sup>®</sup>). Semithin sections were cut and stained with Toluidine Blue for examination and orientation. Ultrathin sections were cut, harvested on carbon-coated 200-wire-mesh copper grids, stained with 2.5% lead citrate, and examined in a Jeol 800A transmission electron microscope at 80 kV.

#### Scanning electron microscopy

The lung/air-sac systems in one specimen of *G. g. domesticus* and one of *C. livia* were fixed by intratracheal instillation with 2.3% glutaraldehyde. The EPPB were removed and immersed in fixative for 2 weeks. Subsequently, they were cut longitudinally into two equal halves to enable the luminal aspect of the epithelial lining to be viewed. The pieces were dehydrated in five changes of absolute alcohol over a period of 2 weeks, critical-point-dried in liquid carbon dioxide, mounted on aluminium stubs, and sputter-coated with gold-palladium complex before viewing on a Jeol (JSM 840) scanning electron microscope at an accelerating voltage of 15 kV.

#### Three-dimensional reconstruction

60 equidistantly spaced sections from a total of 900 sections

in *C. livia* and 120 sections from a total of 1800 in *G. g. domesticus* were traced using a *camera lucida* at a magnification of 30 for the trachea and 50 for the EPPB in *C. livia* and 30 for the EPPB in *G. g. domesticus*. The tracings were aligned, three triangulated coordinates fixed, and the outlines entered into a Kontron Videoplan Imaging System (Kontron Elektronik GmbH, Munich, Germany). The epithelium, cartilage and adventitial coverings were assigned different colour codes. The three-dimensional reconstruction software had a rotation and transection capability. Depending on the adequacy of the initial reconstruction, sections/tracings were added as necessary. In *C. livia*, serial sections of a piece of trachea, which was visibly, and from the latex cast preparation conspicuously, cylindrical, were reconstructed to serve as a control.

#### Results

The respiratory system of birds consists of a lung/air-sac system (Fig. 1). The lungs are small and compact (Figs 1, 2). They are firmly attached to the ribs that leave deep costal impressions (Fig. 1). The trachea bifurcates into the left and right extrapulmonary primary bronchi (Fig. 3), each of which enters the lungs at the hilus on the medial aspect. The EPPB

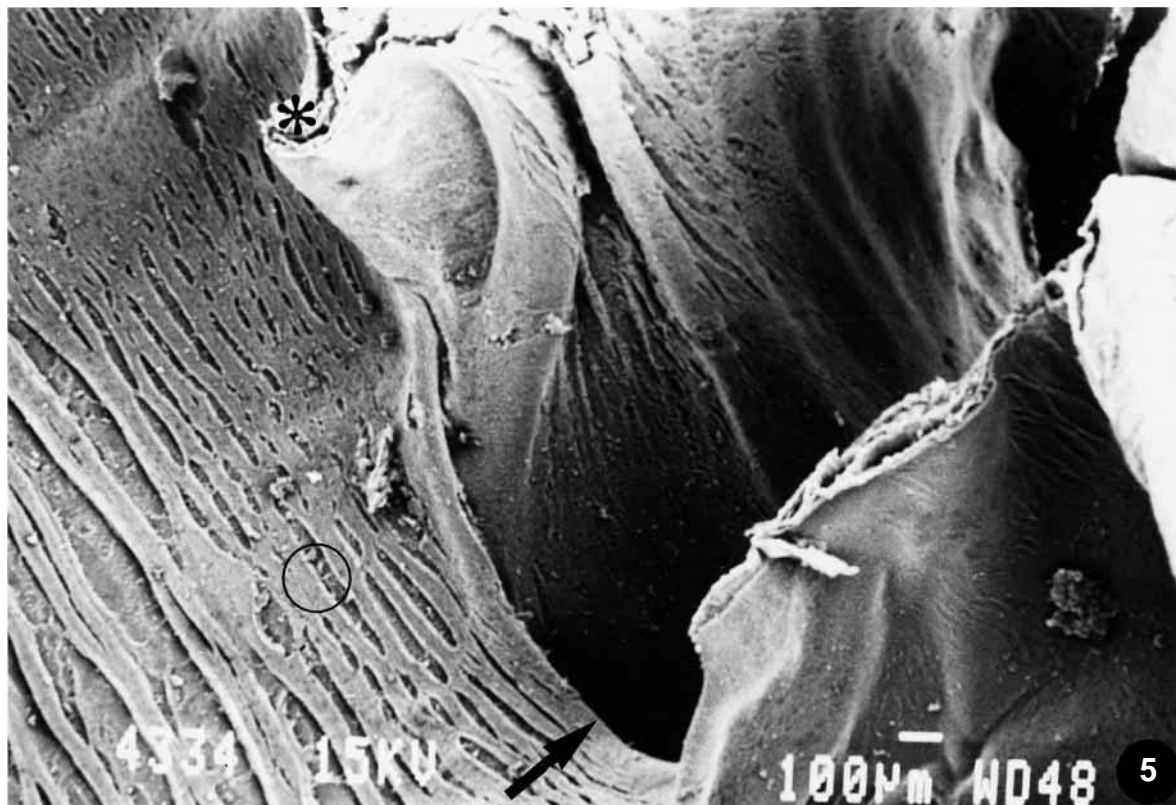


Fig. 5. View of the first medioventral secondary bronchus (arrow) arising from the extrapulmonary primary bronchus of the rock dove, *Columba livia*. The circle shows an area of conspicuous epithelial tracts. The asterisk indicates the terminal part of the epithelial swelling that extends cranial to the first medioventral secondary bronchus. Scale bar, 100  $\mu$ m.

are intercalated between the clavicular and the cranial thoracic air-sacs (Fig. 3). Four MVSB arise from the primary bronchus (Figs 2, 4).

In *G. g. domesticus*, the length of the EPPB was 12 mm; the diameter increased from 2 mm at the syringeal end to 4 mm at the middle, and decreased to 2.3 mm towards the hilus. In *C. livia*, the corresponding values were 7, 1.2, 2 and 1.7 mm, respectively. The syringeal slit was oriented dorsoventrally (Fig. 3). Along the EPPB, the slit lies in line with the origin of the MVSB (Fig. 2). In *G. g. domesticus*, the MVSB were inclined (Figs 2, 4, 5) at angles of 110°, 100°, 90° and 60° (measured in a clockwise direction relative to the EPPB) from the first to the fourth, respectively: the corresponding values in *C. livia* were 100°, 105°, 85° and 45°. A prominent constriction of the EPPB was observed at the origin of the MVSB in *G. g. domesticus* (Figs 2, 4): in *C. livia*, a dilatation occurred at the same site. In the EPPB of *G. g. domesticus*, a hemispherical epithelial swelling was observed (Figs 6, 7, 8): in *C. livia*, a similar but less conspicuous swelling was observed on the dorsal aspect of the EPPB, just before the origin of the first MVSB.

Conspicuous epithelial folds and tracts were observed in the EPPB of *C. livia* and *G. g. domesticus* (Figs 5, 8). In both species, the EPPB (including the epithelial swelling) was lined by a ciliated columnar epithelium with scattered goblet cells and subepithelial tubuloacinar glands (Fig. 9). The epithelial

swelling was highly vascularized (Figs 7, 9). Abundant connective tissue elements like collagen, elastic and smooth muscle tissue were observed in the subepithelial space (Fig. 9). The blood vessels in the epithelial swelling had relatively thick walls for their diameters, and occasional valvular structures that protruded into their lumen were found.

In both *G. g. domesticus* and *C. livia*, while the trachea was cylindrical and the tracheal cartilages were complete (Figs 10A,B), the EPPB had incomplete (C-shaped) cartilages (Figs 10C,D). The interconnection between the ends of the cartilages was ventrally located (Figs 3, 10C,D): a band of connective tissue closed the gap. In both species, the opening of the EPPB was narrow at the syringeal end, moderately dilated at the middle, and narrow immediately cranial to the origin of the first MVSB.

### Discussion

In fluid flow mechanics, internalized flow displays closely coupled interactions with the geometry of the confining space. Thus the design of the respiratory airways should in some way reflect the airflow patterns. Little is known, however, about the actual correlation between the physics of the airflow (i.e. airflow velocity, airflow regimen and local airflow patterns) and the geometry and size of the airways in the bird lung. Furthermore, since the ostia (the connections to the air-sacs)



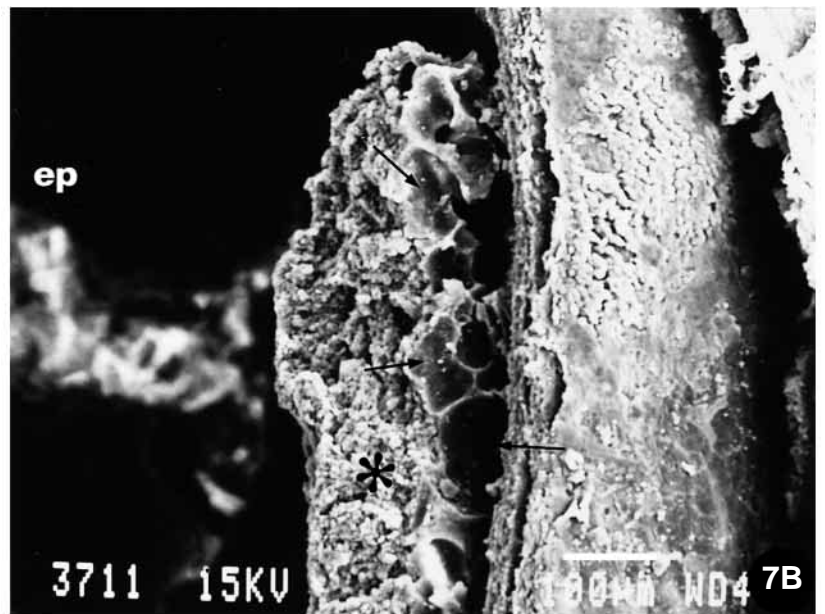
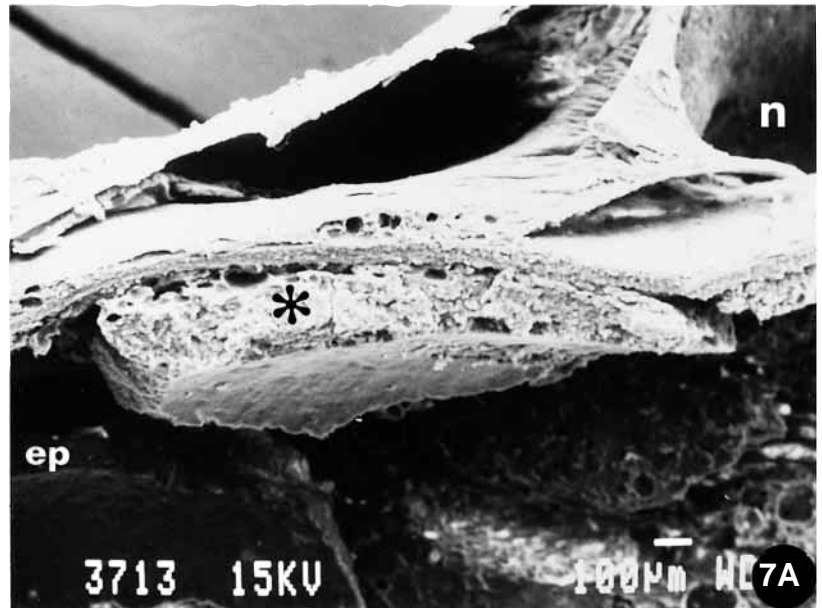
Fig. 6. Side view of the extrapulmonary primary bronchus (ep) of the domestic fowl (*Gallus gallus* var. *domesticus*) showing an epithelial swelling (circled) just before the origin of the first medioventral secondary bronchus (n). Scale bar, 1 mm

occur at both ends, various pathways for airflow exist in the avian lung: the actual route taken by the inspired air in a breathing cycle thus cannot possibly be predicted by mere physical examination. Although heuristically useful, conceptual models are qualitatively and quantitatively gross oversimplifications of a highly complex dynamic structural system.

By propelling the inspired air directly to the caudal end of the lung, the parabronchial lung is ventilated continuously and unidirectionally in a caudocranial direction. Mechanical valves have not been found in the avian lung, even in those sites where they would functionally be expected to occur, e.g. at the openings of the MVSB (for IAV) and at the mesobronchus-MDSB junction in the case of expiratory aerodynamic valving (e.g. King and Payne, 1960; King, 1966; Duncker, 1971; Scheid et al., 1972; Jones et al., 1981). Because the unidirectional airflow persists in paralyzed pump-ventilated and fixed (dead) avian lungs (Scheid and Piiper, 1972), some structure-specific aerodynamic mechanisms are highly implicated in the rectification of the airflow in the pathways of the avian lung.

The mechanism of IAV in the avian respiratory system has been a matter of intense debate, controversy and imaginative speculation. Through studies of gas density, flow velocity and pressure differences on structural models, Banzett et al. (1987, 1991), Butler et al. (1988) and Wang et al. (1988) theorized that

a constriction of the EPPB occurred anterior to the openings of the MVSB. They envisaged that the narrowing accelerated the inspired air, creating a forward convective momentum that propelled it straight into the intrapulmonary primary bronchus (mesobronchus). From radiographic measurements of the diameter of the primary bronchus (after insufflation of the airways with powdered tantalum) in the goose *Anser anser*, Wang et al. (1992) reported a constriction at a site anterior to the origin of the MVSB and called it the 'segmentum accelerans'. Much earlier, on a glass model, Hazelhoff (1943) had speculated that a constriction at a similar site would have had a similar effect on performance. More recently, using an equal-diameter T-junction model, Wang et al. (1988) and Butler et al. (1988) experimentally determined that a constriction ahead of the MVSB had a significant rectifying effect on the airflow past their openings. Brackenbury (1972) hypothesized that inertial forces generated cranial to the first MVSB might contribute to IAV. However, no morphological evidence was offered to authenticate this premise. Of the approximately 9000 known extant species of bird (e.g. Gruson 1976), morphological (e.g. shape and geometry) and morphometric (e.g. length and diametrical dimensions) data on the EPPB and the MVSB, the structural features that must prominently contribute to IAV, are scarce and even controversial (e.g. King, 1966; McLelland, 1989). Only the domestic fowl (*Gallus gallus* var. *domesticus*), the pigeon (*Columba livia*), the domestic duck (*Anas*



Figs 7. (A,B) Close up views of the epithelial swelling (asterisk) on the caudodorsal aspect of the extrapulmonary primary bronchus (ep) in the domestic fowl (*Gallus gallus* var. *domesticus*). n, first medioventral secondary bronchus; arrows indicate vascular spaces. Scale bars, 100  $\mu$ m.

*platyrhynchos*) and the goose (*Anser anser*) have been studied to any meaningful extent (Payne and King, 1959; Akester, 1960; King, 1966; Duncker, 1971, 1974; King and Molony, 1971; Butler et al., 1988; McLelland, 1989; López et al., 1992; Wang et al., 1992).

In *G. g. domesticus*, Akester (1960) and King and Molony (1971) reported that immediately caudal to the syrinx, the cross-sectional area of each primary bronchus was 15 mm<sup>2</sup> and the combined cross-sectional area of the two bronchi exceeded that at the caudal end of the trachea (12.5 mm<sup>2</sup>). King and Molony (1971) further observed that the largest cross-sectional area occurred approximately midway between the syrinx and the pulmonary hilus, the value gradually decreasing caudally to measure approximately 20 mm<sup>2</sup> opposite the first MVSB, 17 mm<sup>2</sup> between the fourth MVSB and the first MDSB,

10 mm<sup>2</sup> at the third MDSB, and 2.5 mm<sup>2</sup> close to the entrance to the abdominal air-sac. In the goose *Anser anser*, the mean diameter of the EPPB was 7.4 mm and that at the constriction, i.e. immediately before the first MVSB, was 3.8 mm (Banzett et al., 1991). Our measurements on *G. g. domesticus* correspond with those of Akester (1960) on the same species, compare with those on the goose *Anser anser* (Banzett et al., 1991) and conform with the cross-sectional area measurements of King and Molony (1971) on *G. g. domesticus*.

Among others, Hazelhoff (1943), King (1966) and Brackenbury (1972) speculated that narrowing of the EPPB close to the origin of the MVSB, angulation of the MVSB relative to the long axis of the EPPB, constriction of the MVSB at their origin and syringeal narrowing may contribute to IAV. Scheid et al. (1972) pointed out that the direction-dependent

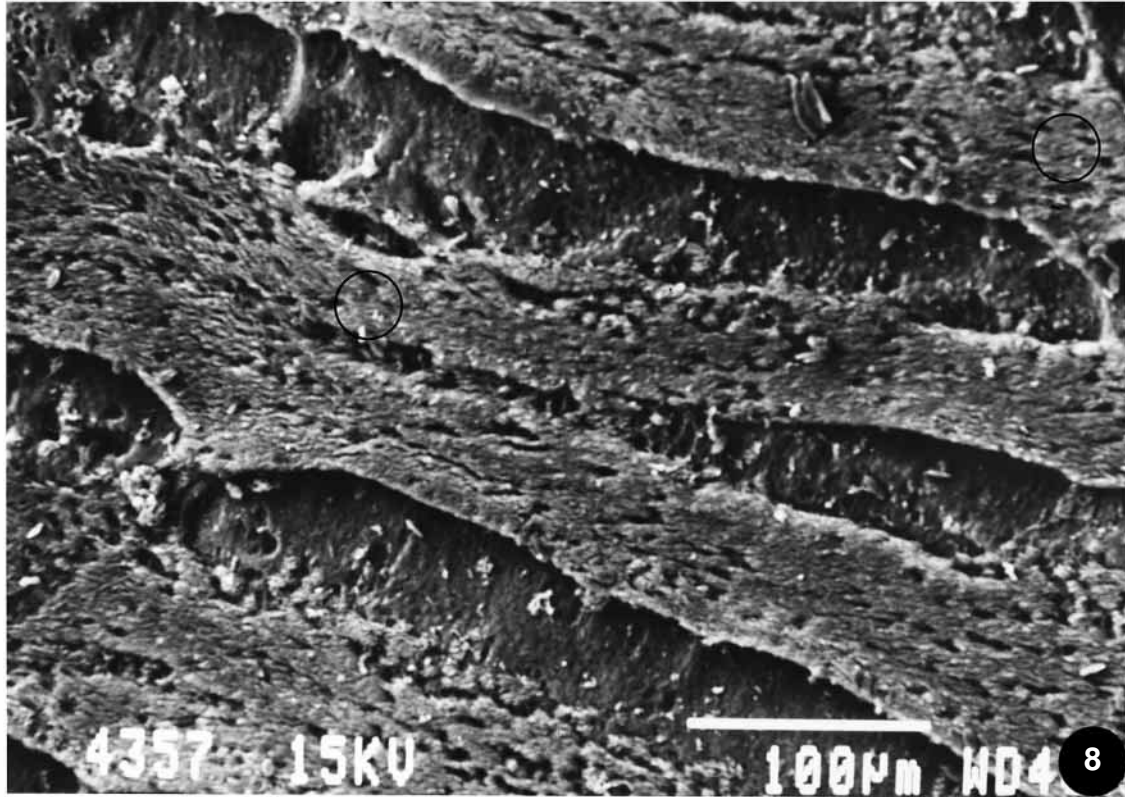


Fig. 8. Epithelial tracts (circled) on the extrapulmonary primary bronchus of the rock dove, *Columba livia*. Scale bar, 100  $\mu\text{m}$ .

resistance of tubes having abrupt diametrical changes might be important factors in IAV. Molony et al. (1976) considered that the  $\text{CO}_2$ -dependent flow resistance at the orifices of the MVSB might contribute to IAV. In a complete departure from these considerations, using an equal-diameter T-junction physical model, Wang et al. (1988) and Butler et al. (1988) determined that changing the angles of the MVSB had absolutely no effect on inspiratory valve performance and that narrowing their orifices had very little effect on its function.

Although such findings may accurately reflect the true state in a simplified (fixed) model, different conditions may prevail in the complex, dynamic living system. Interestingly, unidirectional airflow (i.e. rectification of the inspired air past the MVSB) persists in paralysed pump-ventilated and 'dead' avian lungs (e.g. Scheid and Piiper, 1972). Theoretically, if a physical model is accurately representative of the structure of the avian lung, the two, i.e. the dead lung and the physical model, should experimentally perform essentially the same. The presence of a rectifying capacity in a dead (fixed) avian lung may be explained by the fact that, in this state, the epithelial swelling (which could be the segmentum accelerans) relaxes, assuming a thickened (swollen) form. This was evident in our preparations (Fig. 7). The distension of the epithelial swelling may explain the reported rectification of the airflow in the pathways of passive avian lungs. The difference between airflow rectification in 'dead' and 'living' lungs should, however, be that in the latter, changes in the degree of

rectification with shifts in airflow velocity and  $\text{CO}_2$  concentration in the inspired air are possible. Wang et al. (1992) observed that the segmentum accelerans changed under such circumstances, e.g. it was very thin or inconspicuous during ventilatory hyperpnea but thick and distended during breathing at rest. Our observation that in a 'dead' state the epithelium is swollen suggests that the distended condition is the resting (passive) form of the structure. Subsidence of the epithelial swelling should therefore be the active process when energy is expended to modulate airflow velocity.

In both *G. g. domesticus* and *C. livia*, a hemispherical epithelial swelling that narrowed the lumen of the EPPB was observed cranial to the origin of the MVSB. The swelling corresponded with that of a constriction reported by Wang et al. (1992) in the lung of the goose *Anser anser* that, from its conceived function, was called a 'segmentum accelerans'. The presence of a physical constriction (epithelial swelling/segmentum accelerans) in both *G. g. domesticus* and *C. livia* renders further support to the observation made by Banzett et al. (1987, 1991), Butler et al. (1988) and Wang et al. (1988) that narrowing of the EPPB anterior to the origin of the MVSB may be central to the process of IAV. Through Bernoulli's effect, such a constriction should accelerate the flow of inspired air past the openings of the MVSB, causing a pressure drop along the downstream axis of the primary bronchus. A relevant and interesting question that has been ignored or overlooked by the investigators is why during IAV



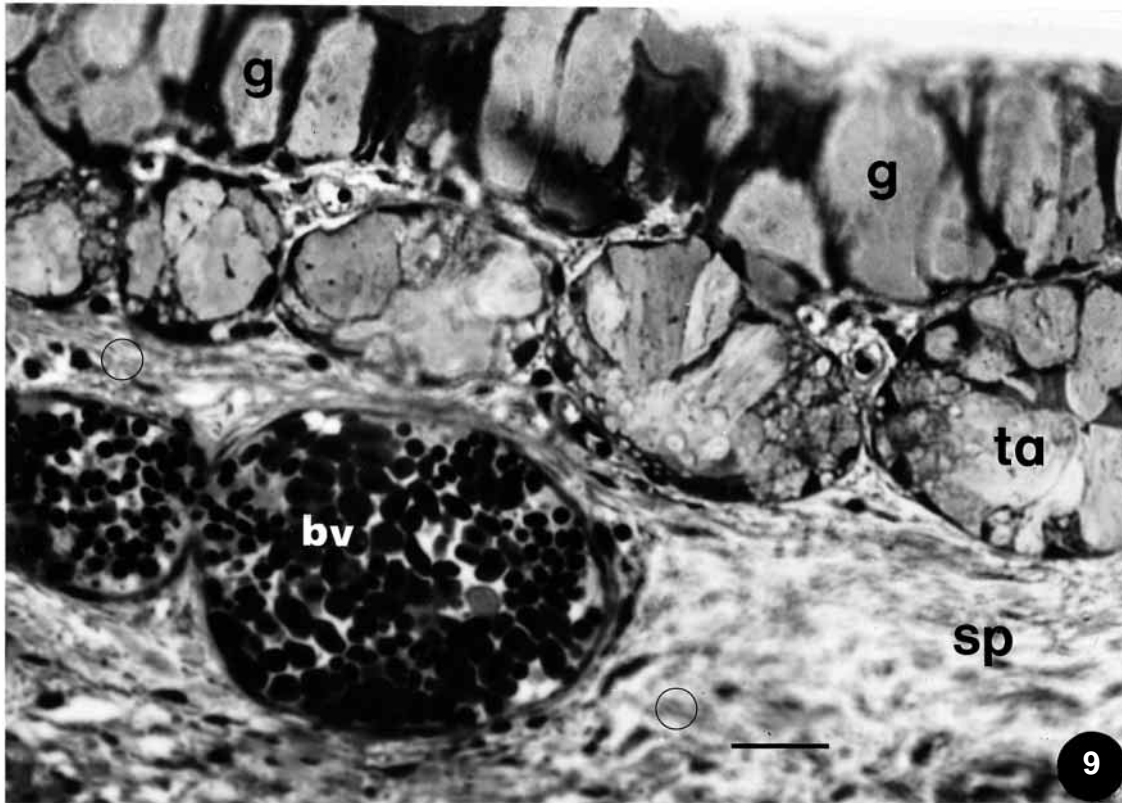


Fig. 9. Histological view of the tissue at the region of the epithelial swelling in the extrapulmonary primary bronchus of the domestic fowl (*Gallus gallus* var. *domesticus*). The region is lined by an epithelium with columnar goblet cells (g). In the submucosa and the lamina propria, tubuloacinar glands (ta) and numerous blood vessels (bv) occur. Connective tissue elements that include elastic tissue (circled) are found in the subepithelial space (sp), closely surrounding the blood vessels. Scale bar, 4  $\mu$ m.

air is not extracted from the cranial air-sacs through the openings of the MVSB in a Venturi effect. We presume that the orientation, constriction and twisting of the MVSB at their origin (Figs 2, 4), features that Banzett et al. (1987, 1991), Butler et al. (1988), and Wang et al. (1988) considered 'not to play important roles' in IAV, may thwart withdrawal of air from the cranial air-sacs, a process that would create an internal airflow loop that would cause 'dilution' of the inspired air, rendering the gas-exchange process much less efficient. Scheid and Piiper (1989) observed that the orifices of the MVSB constituted perfect functional valves that were closed during inspiration. Moreover, it is plausible that the distension of the cranial air-sacs (to take up the vitiated air in the parabronchial system) during the inspiratory airflow phase may also prevent the extraction of air from them. Together, structural and functional features and processes may prevent the removal of air from the cranial air-sacs.

Banzett et al. (1987) and Wang et al. (1988) showed that IAV in the avian lung is dependent on gas velocity and density and that the mechanism may be more efficient at high flow velocities, a condition that occurs in exercise and during hypoxic-hyperpnea. It is reasonable to speculate that the hemispherical epithelial swelling that we observed in *G. g. domesticus* and *C. livia*, a structure that was strategically

located on the dorsal aspect of the EPPB (i.e. directly in line with the openings of the MVSB) should, by narrowing the diameter of the EPPB, enhance IAV by accelerating the inspired air past the openings of the MVSB.

Molony et al. (1976) found that airflow resistance across the openings of the MVSB was dependent on the  $\text{CO}_2$  partial pressure ( $\text{pCO}_2$ ) in the inspired air, the resistance being high at low values and *vice versa*. Barnas et al. (1978) found that the intrapulmonary smooth muscle was sensitive to changes in the concentration of  $\text{CO}_2$ . The morphological basis for such a  $\text{pCO}_2$ -dependent flow resistance was, however, not given. While the avian trachea has complete cartilages (Fig. 10A,B) that interlock and even ossify with age (e.g. McLelland, 1989), the EPPB has dorsally located cartilaginous plates configured in a C-shape (Fig. 10C,D): the gap between the ends of the cartilages is completed by a smooth muscle, elastic and collagen tissue band. Our observations support the envisaged possible change in the shape and size of the bronchi in the avian lung (e.g. King et al., 1967; King and Cowie, 1969; Cook and King, 1970). This may regulate the physics of the flow of the inspired air in the EPPB itself and that past the openings of the MVSB.

From a morphological perspective, we can only offer circumstantial evidence with regard to the possible control of

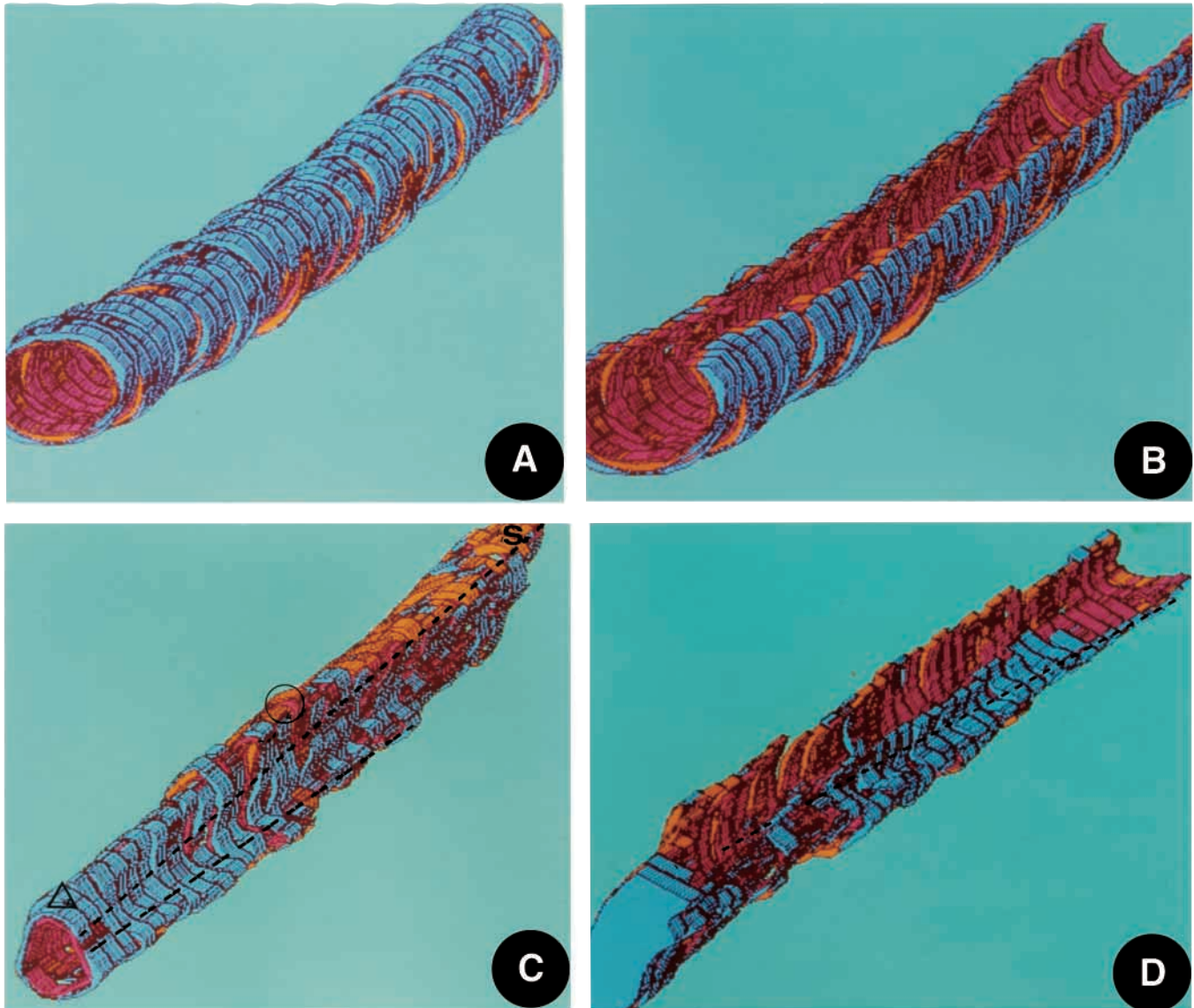


Fig. 10. Three-dimensional computer reconstruction of the trachea (A,B) and extrapulmonary primary bronchus (C,D) of the rock dove, *Columba livia*. (A) Whole trachea; (B) transection to show its cylindrical regular internal morphology. The trachea has complete tracheal cartilages with a constant diameter; the epithelial folds are less conspicuous. Ventral view of the extrapulmonary primary bronchus (EPPB) (C), and a transected view (D), showing its curled configuration (dashed lines). The cartilages (orange colour) are incomplete on the ventral aspect (presenting view) where they are joined by a connective tissue band. This shows that compared with the rigid trachea, the diameter of the EPPB is potentially variable in shape and size. At the syringeal end (s), the extrapulmonary bronchus forms a narrow slit, at the middle it is wider (circle), and towards the origin of the medioventral secondary bronchi (triangle) it is narrow and circular. Red colour, epithelial lining; blue, adventitia; orange, cartilage. Magnification,  $\times 20$ .

the thickness of the epithelial swelling and hence that of the diameter of the EPPB at its location. It is conceivable from its profuse vascularization and presence of relatively thick-walled blood vessels, features that indicate possible sphincteric activity, that through a neuronal mechanism that may be sensitive to airflow velocity and/or  $p\text{CO}_2$  levels in the inspired air (e.g. Osborne et al., 1977) the epithelial swelling may function as a dynamic erectile (cavernous) tissue. Its thickness may be regulated by the haemodynamics of the flux of blood through it (e.g. Weiss, 1972; Ishii and Ishii, 1981). It remains

to be demonstrated whether chemo- or mechanoreceptors exist in or on the swelling itself. Banzett et al. (1991) speculated that during exercise and other conditions that invoke hyperpnea, the segmentum accerelans, which is thick at rest, flattens out to the diameter of the parent bronchus (Wang et al., 1992). This reduces the airflow resistance, lowering the respiratory cost. Wang et al. (1992) considered that the segmentum accelerans might be important for IAV at slow respiratory rates.

In conclusion, as deduced by Banzett et al. (1987, 1991), Butler et al. (1988) and Wang et al. (1988, 1992) in their

theoretical and experimental studies on the respiratory system of the goose *Anser anser*, a 'segmentum accelerans' (a morphological constriction or epithelial swelling of the EPPB) occurs in *Gallus gallus domesticus* and *Columba livia*. We envisage that the modulation of IAV under different respiratory states and circumstances is a result of synergy between structural features and functional processes. These include a syringeal constriction, pressure changes in the clavicular and cranial thoracic air-sacs, gross changes in the shape and size of the EPPB, the presence of epithelial tracts and folds, an epithelial swelling, and narrowing, twisting and angulation of the MVSB. A multifactorial-driven system may impart the necessary flexibility for accommodating the great ventilatory shifts that occur during respiratory changes from rest to exercise, normoxia to hypoxia, and normobaric to hypobaric conditions, which are all states that must be supported by different airflow rates and regimens. It is necessary to study birds of different body sizes and lifestyles to determine the structural features that are fundamental to IAV and to find out whether an allometric correlation exists between their development and the process itself. The segmentum accelerans may play only a small part in a highly integrated functional process.

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