Review Article

The design of the avian respiratory system: Development and Morphology - A review

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Abstract

By every definition birds are extreme animals with singular adaptive morphologies and physiologies.The respiratory system is a good model for studying optimization from a functional perspective because it consists of linked structures with defined design parameters and an overall function that has a measurable upper limit, the maximum rate of oxygen consumption.The investigations of the respiratory tract concentrate on several aspects, viz. bioacoustics, neuroanatomical, respiratory physiology, morphological-ecological analysis of the relation of the respiratory tract structure to the life habits and rarely on the developmental descriptions. The evolution of the vertebrate respiratory system achieved its most efficient state in birds, with their constant volume parabronchial lungs and highly compliant air sacs having low pressure ventilation. These additional characteristics equipped the birds for sustained flight or buoyancy in water. The respiratory organs of birds differ from those of mammals in a number of specific features which are partly associated with the requirements of flight and the great work load that this form of locomotion demands, and partly with the voice production. Differences in the development of this system do exist among different orders or species or even birds of same species.

Key words: Respiratory system, Development, Parabronchi, Lungs

INTRODUCTION

The abilities of birds to sustain flight and to fly in the thin air of high altitude are striking evolutionary accomplishments. The respiratory system is vital to these strenuous feats and thus most research on the form, function, and adaptive significance of the avian lung has rightly focused on adaptations that enable rapid rates of gas exchange.

Since flight is one of the most energetically expensive forms of locomotion, birds have physiological and structural compromise solutions for the required energetic efficiency, environmental demands and lifestyle constraints.

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Birds increase oxygen consumption 10- to 20-fold from rest to flight (Bartholomew, 1954) with their mass-specific aerobic capacities being 2.5–3 times higher than those of non-flying mammals of the same size. To satisfy these high oxygen demands, birds must optimize the structure of the respiratory tract and the cardiovascular system. Although, relentlessly studied for well over four centuries in biology, few organs have withstood as much scientific interrogation as the respiratory apparatus of birds, the lung-air sac system and yet remained profoundly intractable. Historically, the avian respiratory system is highly ranked among the controversial organ-systems and has been investigated by scientists as long as they have been studying comparative anatomy. The functional design of the avian respiratory system remains abstruse, despite concerted efforts to unravel the mysteries of its architecture. In the course of attaining a singular respiratory capacity, the avian lung appears to have contracted certain fundamental structural and functional divestitures. Notably, the lung is noncompliant and takes two inspiratory and two expiratory cycles for the air to traverse the entire system and get out to the trachea. The physiological and anatomical explanations for this mechanism remain elusive and the topographical organization of the air conduits is recondite.

Among the morphoanatomical investigations of birds, a certain attention is devoted to the studies on the respiratory tract. The factors determining the designs of the vertebrate respiratory systems include the physiochemical characteristics of the respiratory medium used, the nature of habitat occupied and the lifestyle pursued. This in turn reflects the structural variations in animals and birds residing in a particular area. In fact, the birds are exceptionally susceptible to infections of the respiratory system. Vast economic losses in the poultry industry have been attributed to mortalities ensuing from pulmonary infections. These deductions have been based on circumstantial evidence and lack resolute experimental basis. The extensive anatomical plan of the lung air-sac system of birds has speculatively been alleged to predispose it to fast diffusion of air-borne diseases while intensifying the spread of harmful effects of toxic air pollutants.

Structural Components of Respiratory System

Air breathing has evolved in many animal taxa and lungs have evolved as an adaptation to hypoxia or anoxic conditions in the early hydrosphere (Randall *et al*., 1981b., Maina, 1988). In lungs, a large surface area is produced by internal subdivision of the parenchyma, giving rise to narrow terminal gas exchange components. The compact, in expansile state of the avian lung has allowed more intense subdivision of the gas exchange tissue into the air capillaries which range in diameter from 8 to 20mm (Duncker, 1974; Maina *et al*., 1982).The normal development of the respiratory organs in birds was determined by an inductive process between the endothelial and the mesenchymal cell elements (Shannon and Deterding, 1997; Hogan 1999). Alcantara *et al*. (2013) stated that the respiratory system organs in chicken began to develop at the fourth day as a disorganized tissue and were undifferentiated. Their complete differentiation was observed at 10 days of incubation.

By 3rd day of incubation in the Kuttanad duck embryo, the olfactory pits were observed at the junction of the lateral and ventral walls of the head and were anterior to the primordia of eyes. By 10th day of incubation the individual parts of the respiratory system were clearly observed with the stereozoom microscope. By day 14 of incubation it was evident that the primary bronchi, secondary bronchi, parabronchi, air sacs and pleura came into existence. By 21st day the parabronchi developed and underwent micro-architectural organization with cavitation that extended peripherally deep into the surrounding mesenchymal tissue all along the lung parenchyma (Firdous *et al*., 2015).

a. Nasal Cavity and Nares

In the embryo of zebra parakeet, olfactory placodes appeared at the 25-26 somite stage (Abraham, 1901) where as in duck Romanoff (1960) reported that the olfactory placodes which formed on the lateral walls of head, anterior to the eyes were first seen at 23-24 somite stage. A transitory depression in the four and fifth day chick embryo on the medial wall of each pit was interpreted as a rudimentary Jacobson's organ. A distinct anlage of jacobson's organ in the black-headed gull and in the European coot persisted up to the stage just prior to hatching. The organ just before hatching of black-headed gull was long and blind canaliculus strewn with stratiform cylindrical or cubical epithelium connected with lumen of the epithelial nasal tubulus by its rostral end (Beer, 1962). Romanoff (1960) explained that by active mitosis and proliferation, the placodes ectoderm gave rise to the sensory or olfactory epithelium and to the olfactory nerves. He also observed that the mesodermal tissue surrounding the nasal pits started to increase in mass on lateral and medial sides of each pit. The mesodermal protuberances adjacent to nasal pits were external and internal nasal processes. By fifth day, palatine process of the maxillary process started to grow and hid choanae from view on eighth day. On eleventh day, two thin plates extended medial ward from the palatine processes, and met in the middle without fusing and formed the split plate characteristic of birds. With the growth of the beak, the nasal fossae were elongated, especially in the vestibular region.

Mathes (1934) reported in domestic fowl that each half of the nasal cavity tends to expand slightly as it passed posteriorly and divided into three compartments, the vestibule, the middle chamber and the antorbital chamber. Das *et al.* (1965) reported in domestic duck that the oval nostrils were located on the dorsolateral aspect of the caudal one third of the bill. Nasal Septum was a very unique feature of petrels (Bang, 1971) but was absent in Japanese quail (Aysun *et al.*, 2007). Yokosuka *et al.* (2009) and Kondoh *et al.* (2011) found in Japanese jungle crow that the nasal cavity was completely divided by the nasal septum into the left and right cavities.

b. Conchae

Street (1937) opined that in chick the inferior concha was first to develop with the primordiumseen as rounded protuberance projecting into nasal cavity from the lateral wall during the fourth day of incubation. On fifth day, the development of superior concha was initiated in the same manner in the fundus of the nasal cavity. Midtgard (1989) reported in chicken that the vascularity of the rostral and middle nasal conchae increased about 4-fold, while there was a progressive decrease in the relative size of the epithelium and connective tissue compartments, during the maturation period. Arteriovenous anastomoses (AVAs) were present already at hatching. Michael (2004) revealed that the olfactory conchae were present with a mostly completed morphology in 8 day old embryos and grew larger by day 12. The inferior conchae were in a primitive state of development at day 8. By day 12, the main structure of the inferior conchae was evident, and by day 14 they seemed to be in their final form. Nemours (1930) observed the presence of three turbinate bones or conchae in domestic fowl. The three compartments of the nasal cavity corresponded with these turbinates and the middle turbinate meets the definition of true turbinate, the others being pseudo turbinate type. Hodges (1974) revealed in domestic fowl that the anterior or ventral turbinate was attached to the dorso-lateral wall of the nasal passage inside the vestibule with slightly curved and strongly convex shape. Middle turbinate originated from lateral wall of the middle chamber as a lammeliform structure, shaped into a spiral of one and one half turns. Dorsal or posterior turbinate was simple, hollow, flattened projection from the wall of the cavity originating above and behind the middle turbinate but slightly overlapping. According to Bang and Wenzel (1985), the avian nasal cavity varied in structure among species and was divided by the anterior, middle and posterior concha with middle one occupied major part. Tasbas *et al.* (1994) also documented the middle nasal concha as the largest of the three conchae in domestic fowl, resembling a scroll. The caudal nasal concha was the smallest nasal concha in coturnix (Fitzgerald 1970), Aysun *et al.,* (2007) and was occasionally missing in Falconiformes and Swifts (King and Mclelland, 1984). According to King and Mclelland (1984) the rostral nasal concha of the domestic fowl, was simple branched, T- or scroll like with an additional vertical lamella of cartilage that arose from the ventral border of the nostril but in Japanese quail Aysun *et al.* (2007) displayed a C-shaped rostral nasal concha. In contrast, the structure corresponding to the posterior (olfactory) concha (Bang 1971., Bang and Wenzel 1985) usually observed in the nasal cavity of birds with well-developed olfaction, was quite indistinct in Japanese jungle crow (Yokosuka *et al.,* 2009) where he identified distinctive anterior and middle concha (MC) in both nasal cavities. In Japanese jungle crow, Kondoh *et al.* (2011) also reported three nasal conchae in each nasal cavity. The anterior concha protruded from the lateral wall near the nares was divided into dorsal and ventral branches, and covered with the keratinized squamous epithelium. The middle concha protruded from the lateral wall over a large area of the nasal cavity and mainly formed a scrolled structure. The posterior concha was distinguished as a small prominence of the lateral wall dorsal to the choana. In Kuttanad ducks each half of the nasal cavity revealed the presence of rostral, middle and caudal conchae. The middle nasal concha was larger and narrower than other two conchae and was slightly dorsal to the rostral concha (Firdous *et al.,* 2014)

c. Nasal Epithelium and Nasal Glands

Street (1937) said that from the early developmental stages itself, the epithelium of the vestibule and the vestibular concha was non-sensory and the olfactory epithelium was confined to superior concha and the olfactory region of nasal cavity. It was also reported that the sensory epithelium was originally present over the portion of the inferior concha but soon receded from it. Weber (1950) found that in 10- day chick embryo the olfactory epithelium was pseudo stratified, with the inner most regions composed of nerve fibers and a region of low sensory epithelium formed a zone of transition between the olfactory and stratified epithelium of the inferior concha. Romanoff (1960) reported that the lateral nasal gland started to develop in the chick on the eighth day of incubation as a solid bud of tissue in the septal wall of the vestibule and attained the lateral wall of the nasal cavity on the tenth day. The seromucous glands in chicken were formed by a process of invagination of the epithelium during the first week after hatching. The glands continued to grow in size and an increased fraction of the cells became mucous-secreting (Midtgard, 1989).

d. Accessory Structures

No Jacobson's organ has been reported in the hatched chick or in the adult fowl (Nemours, 1930). McLelland *et al.* (1968) reported the presence of well-developed thin and flattened lateral nasal gland under the dorsal rim of the orbit in domestic fowl and whose diameter in adult varied from 1 to 2.5mm producing a non-serous, non mucoid secretion. Nasolacrimal duct had a relatively large orifice opening on the lateral wall of the nasal cavity below the middle turbinate. Maxillary sinus or infraorbital sinus was in the form of extensive diverticulum of each side of the nasal cavity.

e. Pharynx and Trachea-Larynx- Glottis Complex

Romanoff (1960) revealed that in domestic fowl the foregut within the head formed pharynx and the branchial region of the pharynx covered the area where the visceral pouches were evaginated as paired lateral expansions. The postbranchial portion of the pharynx was the site of evagination of the laryngo-tracheal groove. This groove was the first indication of the formation of respiratory system, which appeared as a mid-ventral groove in the pharynx of the three day old chick and remained attached to the pharynx only at anterior (laryngeal) end. Rosler (1911) believed that in fowl trachea was probably formed from the rear portion of the groove by the constriction of the pharynx. Locy and Larsell (1916a) reported that in domestic fowl, trachea which originated from laryngo-tracheal groove in the 72 hour chick embryo lay in the median ventral region of the postbranchial division of early pharynx. Towards the end of fourth day trachea became differentiated from the posterior portion of the laryngo-tracheal groove and might be definitely distinguished in an embryo with 39 somites and by the one hundredth hour it was well defined.

The pharynx in domestic duck as reported by Das *et al*. (1965) was directly continuous with the hard plate and had many small caudally directed papillae. McLelland (1965) revealed the presence of a well-defined transverse row of caudally directed papillae at the junction of esophagus. Getty (1975) found that the choanal opening in the avian species was an elongated opening consisting of a triangular caudal part and a slit - like rostral part. Baumel *et al.* (1993) reported in certain groups of birds including Galliformes that the choanal opening remained unfused forming a cleft connecting the nasal cavity to the oral cavity. Aysun *et al.* (2007) reported in Japanese quail that each choana displayed the slit like rostral part and the triangular caudal part, namely intrer-palatine cleft, possessed two openings communicating the nasal cavity with the oral cavity and pharynx.

The larynx in birds prevented the entry of food or any foreign body into the trachea, acted as airway during inspiration and assists the ingestion of solid particles by quickly movement. According to Bradley and Grahame (1960) in fowl, the foundation of the larynx was the cartilaginous ring composed of the cricoid and the arytenoid cartilages which ossified as age advanced. In turkey, duck, fowl, goose (King and McLelland 1984), domestic fowl (Hogg, 1982), denzil cock (Tasbas *et al.,* 1994), mallard (Pierko, 2007), long legged buzzard (Orhan *et al.,* 2010), goose (Onuk *et al.,* 2010) and in stork (Onuk *et al.,* 2011) the laryngeal skeleton consisted of four different cartilages with the cricoid and procricoid as single and the arytenoid as paired one. However, Bock (1978) reported that in corvus, a complex of eight skeletal elements (partially or completely ossified) constituted the skeleton of larynx. In ostrich it was composed of unpaired cricoid and paired arytenoids only (Tadjalli *et al*., 2008; Pasand *et al*. 2010). According to Zweers *et al.* (1981), in pigeon (*Columba livia*) the glottal apparatus was an elastic ring of cartilage with the caudo-medial ridges of the cricoid wings tightly interconnected via the median caudaprocricoidea. The bilateral arytenoids were only hinged to the corpus procricoideus as a result of their particularly shaped articulation facets. The procricoid was tilted by changing the constriction of the ring. The large dilator muscle covered the apparatus as a continuous sheet. The constrictor muscle complex, however, had five discrete sections. Hogg (1982) detected the mineralisation in the laryngeal cartilages in domestic fowl during the early stages as foci or transverse bands. No mineralisation was detected before 105 days post-hatching. In one bird aged 105 days, foci were present bilaterally in the bodies of the arytenoid cartilages only. Mineralisation was next encountered at 126 days post-hatching. Taşbaş *et al.* (1994) reported that in denzil cock, the average distance between the oral part of laryngeal mound and papilla row located transversally at root of tongue was 34-55 mm. Hyolaryngicus, sterno-trachealis, traeheo-laryngeusdorsalis and ventralis muscles were extrinsic and dilator glottis was the intrinsic larynx muscle. Pierko (2007) said that the larynx of mallard and scaup**,** the entrances to the larynx lead through the rima-laryng is surrounded by two labia as labium laryngeumdextrum and labium laryngeumsisnistrum. The larynx was linked muscularly with two hyoid bones ossa-hyoidea. Kirk *et al.* (1993) reported that in Kakapo, Kea and Kaka small papillae guarded the laryngeal opening. Cevik *et al.,* (2007) in Japanese quail reported several cone shaped papillae at each side of the mucosa of the laryngeal mound and margin of glottis. Tadjalli *et al.,* (2008) reported in ostrich that larynx protruded from the floor of the pharyngeal cavity and lay caudal to the tongue with a gap occupied by irregular mucosal plicae. A wide triangular slit as glottis was formed between two arytenoid cartilages. The cricoid cartilage was larger than arytenoid cartilages and forms lateral walls, caudal end and floor of the larynx. In ostrich as reported by Pasand *et al.* (2010), the larynx protruded from the pharynx contained wide glottis without any papillae. Onuk *et al*. (2010) observed in goose that the glottis was split, and circumscribed by the arytenoid cartilage from both sides being 15.32±2.04mm long and was 3.07±0.05 mm wide at the median part. The largest cartilage of the larynx was cricoid which formed the entire ventral and caudo dorsal roof of the larynx which when ossified in the mature goose was approximately 17.22±0.23mm long, 6.24±0.02 mm wide cranially and 11.38±0.32mm wide caudally. Intrinsic dilator and constrictor muscles of the glottis lay between the cricoid cartilage and arytenoid cartilage. The larynx had three pairs of extrinsic muscles; crico-hyoideus, cleido-trachealis and tracheo-lateralis).

Getty (1975) in turkey, fowl, duck and goose, Bock (1978) in Corvus and Kabak *et al.* (2007) in long legged buzzard reported larynx in the form of mound at the caudal end of tongue containing glottis and is covered with numerous caudally directing papillae. Onuk *et al.* (2010) in goose found the laryngeal mound at the caudal side of the larynx divided in half approximately 9.05±0.58mm long by the sulcus laryngealis. Rows of 4-5 cone shaped papillae 25 to 28 papillae per row with tips facing caudally in each half of the laryngeal mound and extending in cranio caudal direction were determined in the sulcus-laryngealis. Nazan and Gulsun (2010) observed in sea gulls a transverse row of papilla called papillae pharynges caudoventrales in the caudal part of laryngeal mound, a sagittal row of papilla around the sulcus laryngeus and a protuberance named crista ventralis in the inner surface of cricoid cartilage.In stork, Onuk *et al.* (2011) reported one to three papillae in the caudal part of laryngeal mound but there was no papilla in the sulcus laryngealis. Crista ventralis was located in the inner surface of cricoid cartilage.

Myers (1917) defined that the trachea in *Gallus domiesticus* ended caudally at the fourth or third ring rostral to the intermediate cartilage of the syrinx. The latter presented four cartilages which united ventrally with the pyramid of the pessulus depending on sex of bird. According to Bradley and Grahame (1960) in domestic fowl a relatively long trachea, composed of complete rings of hyaline cartilage united by narrow membranous ligaments, connected the cranial larynx with the caudal larynx or *syrinx.* The cartilaginous rings were of different sizes, a large ring half overlaps a small ring, and nearly touches the end of the previous small ring. The rings had thick middle portions and thin edges. The ends of the rings were joined by a band of connective tissue. Cover (1953) noticed that in turkey, the trachea had complete, hyaline cartilage rings. The inner surface of each ring was flattened, while the outer surface was flattened on one side and convex on the other side, the transition being dorsal and ventral. The flat and convex sides alternate from ring to ring and overlapped. Johnsgard (1961) reported that the Magpie Goose (*Anser anas semipalmata*) was unique with its externally convoluted trachea, but the syrinx was small and simple in both sexes. Anserinae had symmetrical tracheae in both sexes, which either lacked bullae (Anserini) or had symmetrical bullae which were larger in males than in females. The Coscoroba Swan (*Coscoroba coscoroba*) and the Cereopsis Goose (*Cereopsisnovae-hollandiae*) had trachea of the Anserini type whereas the Freckled duck (*Stictonetta naevosa)* presented an extremely simple and primitive type of trachea and syrinx in both sexes. Tracheal air sacs occurred in some stiff-tail.

McLeod *et al.* (1964) also described the trachea in aves was composed of large number of cartilaginous rings which tend to get ossified with age particularly ventrally. Mennega (1964) in chicken and Ibe *et al.* (2008) in West African guinea fowl reported that the trachea was made up of complete, hyaline rings, which were of two sizes. The large rings almost touched each other, while inside them the smaller rings also nearly touch, halfway between the openings of the large rings forming a double tube. McLelland (1965) reported in *Gallus domesticus* that the diameter of the trachea at the anterior end was greater than the posterior end. In cocks it measured about 175mm in length where as in hens the average length was 160 mm. Ibe *et al.* (2008) in West African guinea fowl reported that trachea laid mid-ventral to the esophagus passed to the right side of the neck as it extends caudally and then returns to the mid-ventral position as it approaches the thoracic inlet. Rajathi *et al.* (2009) concluded that in Japanese quail distal to a length of 1.5 to 2 cm, the trachea was directed slightly towards the right of the median plane with the oesophagus on its left side. Trachea entered the thoracic cavity between the two rami of the furcula.

Mathey (1965) reported in aves that each tracheal ring consisted of a flat, complete ring of hyaline cartilage, the edges of which are wafer-thin, signet shaped with constrictions lying dorsally and ventrally and each ring had one side narrower than other. The number of tracheal rings varied from 108 to 126. The narrow part of one ring fitted inside the wide portion of the wide ring. The only exception to this pattern was the first tracheal and last four rings as reported by McLelland (1965) in domestic fowl. Hogg (1982) studied the trachea in domestic fowl and described it as being continued caudally as the tympanum, which formed part of the syrinx. The numbers of rings ranged from 107 to 138.The vast majority of the rings were complete, occasionally incomplete ring and in some cases partial bifurcation of rings was observed. Mechteld *et al.* (1997) reported that the male trachea of Collared Dove was constructed of 108 rings and had a length of 77 mm, and the female trachea contained fewer than 102 rings and had a mean length of 71 mm. Tracheal rings that were part of the syrinx were often modified to have thickening of the rings over the ventral midline, seen in the most caudally positioned tracheal rings. Pierko (2007) reported in mallard that the tracheal cartilages were closed rings partially overlapping each other with different shapes. Closer to larynx they were elliptical whereas caudally almost circular and linked with an inter-annularis membrane. In West African guinea the number of trachea rings ranged from 119-159and were irregular in size. Larger rings bifurcated at the ventrum into two small rings (Ibe *et al*., 2008).In Japanese quail the trachea had a skeleton of complete cartilaginous rings ranged from 110 to 116 of different sizes connected with each other by narrow annular ligaments. The larger rings almost touched each other and the smaller rings were inside halfway between the openings of the larger rings forming a double tube (Rajathi *et al.,* 2009). Onuk *et al.* (2011) reported in goose, there were 137-140 cartilage rings in the trachea and the rings in the anterior half of trachea could nest into each other in dorsal and ventral directions. Laterally the cartilage rings in middle of trachea contacted the previous or following rings and were "H"-shaped and some rings were dorsally and some rings were ventrally forked.

Garside (1968) has shown in domestic fowl that ossification of the tracheal rings may be initiated as early as 15 weeks of age progressing upto 104 weeks of age. In the studies of Hogg (1982), in domestic fowl the first indication of mineralisation was encountered at 98 days post-hatching then at 105 days, and at 112 days and in all birds examined thereafter. The process began at the caudal end of the tracheal series and spread cranially. The first ring was not involved until 126 days. The rings at the caudal end became fully mineralised whereas those in the cranial half of the trachea usually remained not more than 50 per cent mineralised, and often less, throughout the growing period. Pierko (2007) in mallard and Rajathi *et al.* (2009) in Japanese quail reported that both sides of trachea were covered by tracheo-lateralis muscle. Close to the end of the trachea there were right and left cleido-trachealis muscle and at the very end of the trachea were right and left sterno-laterales muscle. Besides trachea was covered with fourth muscle as cleido-hyoideus muscle located in the upper part of the trachea by the larynx.Onuk *et al.* (2010) observed in goosethat the three muscles *viz.,* sternotrachealis*,* cleidotrachealis and tracheolateralis allowed movement of the trachea. Sternotrachealis was narrow, thin structure, approximately 2.21±0.03 mm wide. Tracheolateralis was approximately 4.28±0.07 mm wide originated from cricoid cartilage of the larynx and the cleidotrachealis was approximately 4.20±0.05 mm wide originated on the clavicular.

f. Syrinx

Tymms (1913) reported that on the ninth day of incubation in fowl and eighth day in sparrow within the dense mesoblast, concentrations began to assume ring like form. It was also found that in the region of bifurcation of trachea, these rings became specialized to form the supporting structure of the syrinx. The pessulus formed between conjoining bronchi on the eleventh day of incubation. By the 12th day tracheobronchial rings appeared. As the rings of the syrinx developed further, supporting framework like membranes became differentiated and the first to appear was membrane externae between last tracheal ring and first bronchial semiring. By the fifteenth day of incubation of chick, the muscles of the syrinx started developing (Romanoff, 1960). Alcantara *et al.* (2013) stated that the respiratory system organs in chicken were completely differentiated at the 10 days of incubation, however, until 19 days the syrinx was not observed.

Johnsgard (1961) reported that Anatinae exhibited sexual dimorphism in the syrinx, and males of most species except stiff-tails (Oxyurini) possessed asymmetrically enlarged syrinxes (bullae). Males of most Anatinae possessed entirely osseous bullae; partially membraneous (fenestrated) bullae were in all pochards and most sea ducks. The marbled teal and pink-headed duck also possessed fenestrated bullae which were intermediate between the dabbling duck and pochard (*Aythyaferina*). The syrinx is the vocal organ of songbirds, located at the base of trachea (Koch, 1973; Konig, 2001). Syrinx has been classified to be tracheobronchial in most common birds such as duck (Frank *et al*., 2007), hen (Hummel, 2000., King, 1989., Nickel *et al*., 1977), ostrich (Yıldız *et al*., 2003), Bursa roller pigeon (Yıldız *et al*., 2005), white turkey (Arican *et al*., 2007; Khaksar *et al.,* 2012), goose (Onuk *et al*., 2010), long-legged buzzard (Kabak *et al.,* 2007), quails (Bayram and Liman, 2000; Çevik *et al*., 2007) and in sea gulls (Ince *et al*, 2012).Studies reported that the number of cartilages in syrinx could be eight (Warner, 1972b; Lockner and Youngner, 1976) or ten (Frank *et al*., 2007). Frank *et al.* (2007) described this variation in the number of the rings depended on the fusion of the cartilages and concluded this variability to be normal due to the structural difference between male and female syrinx.

Bayram and Liman (2000) reported that quails had a tracheo-bronchial syrinx since it was based on both tracheal and bronchial elements. Two tracheal syringeal cartilages were attached at both ends to the pessulus in the tympanum. The internal or medial tympaniform membranes were present on the medial wall of the bronchus on either side of and behind the pessulus. Yildiz *et al.* (2003) in ostrich, Yildiz *et al.* (2005) in pigeon and Khaksar *et al.* (2012) in female and male turkey observed that, the syrinx was composed of three different cartilage groups, namely tympanum, tracheao-syringeal cartilages and bronco-syringeal cartilages. The pessulus did not contain any ossified or cartilaginous tissues and was made up of a double folded mucous membrane extending dorso-ventrally from median walls of primary bronchus into the cavumsyringis.

In pigeon the tympanum was formed from 5 oval-shaped cartilage rings pressed dorso-ventrally. The average length of the tympanum was 4.11 ±0.09 cm. An interbronchial ligament connected the right and left bronchus. Intrinsic muscles were absent but two extrinsic muscles, sternotracheal muscle located above pessulus and tracheolateral muscle located at the side of the trachea were seen (Yildiz *et al.,* 2005).Frank *et al.* (2007) reported in mallard that the syrinx consisted of a tympanum, a pessulus, medial tympaniform membranes, interanular membranes, an interbronchial ligament (bronchi desmus), and broncho-syringeal cartilage semi-rings. The syringeal valve was at the right lateral side of the tympanum by using frozen sagittal section. In male, the pessulus was massive and showed an elongated oval, transparent area ventrally. Khaksar *et al.* (2012) concluded that the tympanumin in male and female turkey was composed of two tracheal cartilage rings. Tracheo-syringeal cartilages were composed of two cartilagous rings where latero-lateral length was longer than dorso-ventral length; four on each side were C-shaped. The syrinx was composed of two medial (internal) tympaniform membrane and two lateral (external) tympaniform membranes. There was no tympanic bulla in the turkey's syrinx. Yilmaz *et al*. (2012) reported in mallard that the tympanum was composed of four tracheal cartilage rings different from those described in the Bursa roller pigeon (Yıldız *et al*., 2005), long-legged buzzard (Kabak *et al*., 2007), sea gulls (İnce *et al*., 2012), goose (Onuk *et al*., 2010) and Japanese quails (Çevik *et al*., 2007). The pessulus in the mallard was composed of boney tissue as in singing birds (Frank *et al*., 2007; Taşbaş *et al*., 1994; Warner, 1972b), but different from that in ostrich (Yıldız *et al*., 2003) and chickens (King, 1989). In sea gulls (*Larus*spp.) as reported by Ince *et al.* (2012), five trachea-syringeal cartilages were fused completely and shaped tympanum. Broncho-syringeal cartilages were formed from seven C shaped cartilage rings. The lateral tympaniform membrane was observed between first and second cartilage rings of broncho-syringeales. Medial tympaniform membrane was placed between the pessulus and 7th broncho-syringeal cartilages.

Hogg (1982) found mineralization of syrinx in domestic fowl at 98 days post-hatching. In all cases it was present only in the pessulus and the bases of the left and right first bronchial syringeal cartilages. Three birds showed bilateral separate centres in the shaft of the first bronchial syringeal cartilage. Two birds showed centres of mineralisation in the cartilages of the primary bronchi caudal to the three which constitute the bronchial syringeal cartilages. In one bird, these centers were present in the fourth and fifth cartilages.

g. Extrapulmonary Primary Bronchi

Batt (1926) reported in domestic fowl that the structure of the primary bronchus changed rapidly inside the lung. The cartilaginous rings were replaced by cartilaginous plates lying longitudinally within the wall. Payane and King (1959) and Akester (1960) reported in birds that primary bronchus enters the lung at hilus together with pulmonary artery and vein. Primary bronchus does increase in diameter in the second quarter of its intrapulmonary part there was no vestibule present. King (1957) reported in birds that pulmonary aponeurosis was pierced by the primary bronchus, by the pulmonary blood vessels and by the connections of the air sacs. Hodges (1974) reported in domestic fowl that bronchi pass diagonally backwards and upwards from the syrinx enter the lung on the medial edge of the ventral surface just anterior to midpoint of the length of the lung. The cartilaginous rings changed into circular or oval in cross section and did not overlap. They were roughly 'C' shaped as they do not pass round the medial side of the bronchi. On approaching to lung they get reduced on ventral side.

h. Lungs

Romanoff (1960) found that, in chick at the end of fourth day or at 41 somites the lungs were small, smooth pouches extending caudally along each side of the esophagus.

The distal end of the mesobronchus was enlarged to form the abdominal air sac. On fifth day of development, the lung began to show surface irregularities. At the distal end, a protuberance represented the beginning of the lobe containing mesobronchus. From day 8th day to 13th day of incubation lung changed to a rectangular organ. In domestic fowl, the lungs were paired from the very beginning and firstly appeared during the third day of chick incubation as on each side of the ventral surface of the primitive fore- gut or pharynx just caudal to the fourth pharyngeal pouch and below the broader branchial region of the foregut (Goldin and Opperman, 1980).Adamson (1997) observed that the lung-air sac system of birds at hatching was practically mature as against the mammalian lung where intensive growth of the terminal airways and important structural changes occurred postnatally. Maina (2003) revealed that at third day of incubationin *Gallus domesticus,* well defined mesothelium bordered the mesenchyme around the lung buds. The endoderm budded to provide the lining membrane of the bronchial tree. The lungs reached their definitive topographical locations in the coelomic cavity on day six and on day seven, lungs rotated, attached onto the ribs and by eighth day was deeply inserted.

In the developing avian lung, differentiation of mesenchymal cells into angiogenetic cells termed “vasoformative cells” (Gonzalez-Crussi, 1971) occurred very early. Hiruma and Hirakow (1989) observed that in the chick embryo, the pattern of vasculogenesis varied according to the developmental stage, the body region, local environmental conditions and proximity to certain cellular elements such as the endoderm. Locy and Larsell (1916a) reported that the pulmonary vein was the first to appear along blood vessel. The pulmonary artery was formed between the fourth and fifth days from two parts *viz*. The proximal end came from the sixth aortic arch and the distal end beginning in the lung wall and growing to meet the sprout from the aorta. De Ruiter *et al.,* (1993) reported in avian embryo that the splanchnic plexus consisted of endothelial cells and precursors were present around the foregut before the lung buds develop. This plexus gave rise to the pharyngeal arch arteries, the ventral pharyngeal veins, the pulmonary vessels, and the bronchial vessels, including the intrapulmonary vessel network. The splanchnic plexus was transiently connected to the systemic arteries and veins. The bronchial arteries and veins developed in the second period from these transient vessels. Makanya and Djonov (2007) stated that the pulmonary vasculature in domestic fowl originated from the splanchnic plexus by a process of vasculogenesis and angiogenesis. During the last week of incubation, together with the formation of air capillaries, the pulmonary vasculature underwent rapid growth by combining sprouting to a process of intussusceptive angiogenesis.

Payane (1960) reported in domestic fowl that lungs were spongy structures present in the antero-dorsal region of the thoracic cavity. They were closely apposed to the ribs and vertebral column so that dorsally and laterally the substance was strongly indented by the second to sixth pairs of ribs.Hodges (1974) in domestic fowl observed that ventral surface of lung was slightly convex, covered by thin; double membrane of pleura and below, the lungs and separating them from the lower part of the thorax was the pulmonary aponeurosis, a musculo-tendinous sheet.

i. Bronchi

Juillet (1912) reported in chick that the sixth day of incubation marked the formation of buds from the primary lung tree representing the beginning of the secondary branches of the bronchial tree. The first bud from intrapulmonary bronchus was the primordium for first entobronchus and behind this was the smaller bud for second entobronchus. Afterward, third and fourth buds initiated the corresponding entobronchi. Locy and Larsell (1916a) stated that on the seventh day chick incubation the primordia of the ectobronchi appeared as a series of six to ten buds from the wall of the embryonic vestibulum, below the level at which entobronchi formed. Minute branches projected from the parabronchi into the lung parenchyma formed air capillaries and appeared on fourteenth and sixteenth day of development. Romanoff (1960) reported that in chick four entobronchi appeared on sixth day of incubation were larger and more conspicuous divisions of the bronchial tree. They were ventral in distribution. Six laterobronchi (Ectobronchi) from bronchial tree arised from the middle portion of the mesobronchus at the region of the expanded embryonic vestibulum. Two groups of dorsobronchi, four or five larger ones and twenty smaller ones were arranged in two rows with larger ones at the middle. Visschedijk (1968) reported the significant difference in the degrees of pulmonary development at hatching between altricial and precocial birds. In precocial birds the development of lungs was at a relatively more advanced stage which was critical for the survival of the chicks of the precocial birds since they don’t get parental care after hatching. Jones and Radnor (1972) found that during the last 2 to 3 days incubation, the air and blood capillaries anastomosed and interdigitated profusely in birds. It was also reported that in the chicken, the type II (granular) pneumocytes were numerous from day 17 and at hatching the atrial, infundibular, and air capillary epithelial surfaces are lined by large quantities of trilaminar material. Scheid and Piiper (1986) revealed that the bronchi in birds were arranged partly in parallel and partly in series with each other, and unidirectional airflow within the lungs permits a gas exchange that is more efficient than the exchange in mammals. The earliest indication of the bronchial tree was seen in the hollow buds that formed the endoderm lining the lung pouches in chicks by third day of incubation. At 4th day of incubation bronchial tree was simple cylindrical tube of endoderm. At the proximal end of the lung bud a small part just outside the mesenchymal swelling formed the primordium of the extrapulmonary bronchus (Maina, 2003).

Payane and King (1959) and Akester (1960) reported in bird’s primary bronchus increased in diameter in the second quarter of its intrapulmonary part there was no vestibule present. The primary bronchus after the point of entry to lung immediately gave rise to four large dorsal secondary bronchi. Posteriorly along the primary bronchus two further groups’ arose. These together consisted of sixteen ducts, about eight of which arose from the dorsal surface of the primary bronchus and about eight arose from its ventral surface. A third group of about thirty secondary bronchi as caudolateral secondary bronchi arose from the posterior half of the primary bronchus laterally and were generally small in diameter. Numerous tertiary bronchi arose from secondary bronchi and which in turn gave rise to air capillaries (King, 1957).

Bretz and Nielsen (1971) revealed that in aves the description of gas conduits (channel) in the avian respiratory system consisted of three levels of bronchi. The first level was primary bronchus or mesobronchus, secondary bronchi branched off from the primary bronchus and were cranio-medial and caudodorsal bronchi, which connected to the lung parenchyma. Tertiary bronchi (parabronchi) were branches at the level where gas exchange with the blood takes place, and with their surrounding air capillaries they made up the bulk of the lung parenchyma. Gerrit and Clark (1972) reported that in common crackle inside the lung the mesobronchus immediately gave rise to four ventrobronchi six dorsobronchi branched from the medial side of the mesobronchus and laterobronchi as discrete secondary branches of the mesobronchus. The largest laterobronchus came off the ventral surface of the mesobronchus anteriorly curved posteriorly and entered the posterior thoracic sac. Duncker (1974) found in domestic fowl that at the lung hilus the primary bronchus gave off four ventrobronchi, and posteriorly seven to ten dorsobronchi and the laterobronchi. Parabronchi originated from the internal surface of these secondary bronchi, connected ventrobronchi to dorso- and laterobronchi. The three anterior air sacs were connected to the ventrobronchi. The posterior thoracic and the abdominal air sacs were connected to the large latero-bronchus and to the end of the primary bronchus. Maina (1988) reported in aves that bulk of the intrapulmonary air flows through the parabronchial lumen and then centrifugally diffuse into the exchange tissue through the atria, the infundibula, and the air capillaries. The flow of blood was centripetally from the inter-parabronchial arteries, then into the intra-parabronchial arterioles, and finally into the blood capillaries, which together with the air capillaries constituted the functional terminal gas exchange units.

j. Air Sacs

In the adult avian lung there were five air sacs, all paired except interclavicular. The cervical and interclavicular arose anteriorly while the three pairs were on the caudal and ventral surfaces of the lungs. The first air sacs appeared in the 6.25 day chick embryo as projections of the lung wall. The abdominal and cervical sac came from the first entobronchus. The anterior thoracic and interclavicular sac appeared as bud of the third entobronchus (Larsell, 1914). According to Mania (2003) in domestic fowl, the abdominal air sacs appeared earliest by 5th day followed by the cervical ones on 6th day and other air sacs by 10th day. After hatching, no further consequential structures formed.

King (1957) on his extensive review of the pneumatic bones of fowl considered that the cervical bones except atlas and axis, the thoracic vertebrae except the fifth, the lumbro-sacral mass, the pelvic girdle, the first two vertebral ribs, the plate and the cranial processes of the sternum, the humerus and the distal half of the coracoid were aerated by air sacs. According to Akester (1960) the air sacs in domestic fowl were single cervical and interclavicular and paired anterior thoracic, posterior thoracic and abdominal. They were thin walled and connected to lung by primary bronchus (abdominal) by branches of the secondary bronchi (cervical, interclavicular and anterior thoracic) or by parabronchi. Murray and Fisher (1967) described in Laysan albatross the vertebrae were pneumatized as far anteriorly as the axis and as far posteriorly as the last sacral vertebra. The atlas, the coccygeal vertebrae and pygostyle were not pneumatic. Gerrit and Clark (1972) reported in common crackle that the abdominal, posterior thoracic, and cervical sacs were similar to those described for other birds. The interclavicular and anterior thoracic sacs were fused into one unpaired sac. All sacs except the cervical had several parabronchial connections to the lung and one direct connection with either the mesobronchus or a major branch of it. Mennega *et al.* (1964), Getty (1975) and Tasbas *et al.* (1994) did not mention any diverticula of the cranial thoracic sac in domestic birds. Nickel *et al.* (1977) noted that diverticula of cervical sacs pneumatized all the cervical vertebras in the domestic fowl. Ellenberger and Baun (1974) showed that the volume of the abdominal sac was larger at the right in domestic fowl but Murray and Fisher (1967) showed that the left was having a greater volume than the right side in Laysan albatross.

Kurtul *et al,* (2004) reported in rock partridge that all the air sacs except the cervical sac were paired, whereas the right and left clavicular sacs were ventrally fused. The cervical was located cranial to the lungs and ventral to the last two cervical and first thoracic vertebrae. It communicated with the lung via the first medioventral bronchus. The paired cranial thoracic sac possessed a distinct costal impression on its surface and was present underneath the lateral wall of the body. These were roughly triangular in shape and twice larger than caudal thoracic sacs and aerated by the first, second and fourth medioventral bronchi. The paired caudal thoracic sac received air via the second lateroventral bronchus and had no diverticula. The abdominal air sac extended from the caudal border of the lungs to cloaca and was the largest of all the sacs. The sac was connected to lungs via the third, fourth and fifth lateroventral bronchi. Cevik *et al.* (2006) opined that in mallard ducks the cervical air sacs with its diverticula was aerating the axis and the first two ribs. Cranial thoracic air sacs were smaller than the caudal sacs pneumatising the second to seventh ribs by their diverticula. The caudal thoracic air sac had no diverticulum. The left abdominal air sac had two portions, the cranial and caudal sacs, the later aerating the last three ribs and synsacrum, the former being smaller and narrower. The right abdominal sac was bigger than left sac.

Orhan *et al.* (2010) reported in long legged buzzard that cervical sac communicated with lungs via the first medioventral bronchus. The clavicular had several diverticula, which were divided into intrathoracic and extrathoracic. The cranial thoracic was paired extended to the sternal ribs at lateral to the lungs lateral and was ventilated through bronchi medio -

ventrales. The caudal thoracic sac was quite small without any diverticula and group of parabronchi and bronchi lateroventrales aired this sac. The abdominal sac was largest occupying most of the peritoneal cavity and was connected via lungs through lateroventral bronchi. Onuk *et al.* (2010) reported seven air sacs in goose. Cranial, caudal thoracic and abdominal were paired whereas cervicoclavicular sac was single. Cranial and caudal thoracic sac contained no diverticula and did not aerate any bones. The left and right abdominal sacs were of equal in size and located symmetrically.

Conclusion

The evolution of the vertebrate respiratory system achieved its most efficient state in birds, with their constant volume parabronchial lungs and highly compliant air sacs having low pressure ventilation. Together, properties like unidirectional and continuous ventilation of the gas exchange tissue, gas exchange designs like the crosscurrent and the multicapillary serial arterialization systems and highly refined pulmonary morphometric parameters such as a thin blood-gas barrier and a large respiratory surface area and capillary blood volume accord high gas exchange efficiency in the avian lung, permitting active flight even under extreme conditions of high altitude. These additional characteristics equipped the birds for sustained flight or buoyancy in water. The respiratory organs of birds differ from those of mammals in a number of specific features which are partly associated with the requirements of flight and the great work load that this form of locomotion demands, and partly with the voice production

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