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Development of the Respiratory Tract in Red Sokoto Goat (Capra Hircus): Histological Perspective

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ABSTRACT

The foetal development of the respiratory tract in the red Sokoto goat was investigated in this study using morphological techniques. Sections of the respiratory tract were obtained from the foetuses of 40 apparently healthy red Sokoto goats that were grouped into the first term, early 2nd term, late 2nd term, and 3rd term (n = 10/group). Laryngeal glands formed in the early 2nd term and also secreted neutral mucin within the same period, while apical budding and proliferation of the naïve epithelium led to the formation of stratified squamous epithelium just at the beginning of the 3rd term. The trachea consisted of a bi-stratified epithelium at foetal days (FD) 53 and later became ciliated pseudostratified columnar epithelium during the early 3rd term. At FD 102, the glandular epithelia contained bluish-stained areas, while the glandular lumina contained acidic mucins. The lungs of red Sokoto goats were at the pseudo-glandular stage at FD 54, canaliculi stage between FDs 71-76, terminal sac stage between FDs 76 – 104, and alveolar stage from FD 129. The structural changes in the respiratory tract of this breed are essential changes needed for neo-natal and post-natal functions. The lungs were structurally mature in the 3rd term and could support the animal even in preterm kids.

Keywords

larynx, trachea, lungs, foetal development, red Sokoto goats

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Abbreviations

FD(s): foetal day(s)

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Introduction

Goats are one of the most valuable livestock species present in many parts of the world. The Red Sokoto goat (RSG) is the most abundant breed of goat in Nigeria, particularly in Northern Nigeria [1]. This breed is also present in the Northern part of the Niger Republic and Cameroon [1]. RSG possesses a characteristically dark red coat colour with occasional occurrence of lighter coat colour. Several ecotypes of Red Sokoto goats, possessing varied coat colours such as dark red, light red, brown, light brown, black, and variegated, have also been reported [2, 3]. The goat breed has unique adaptive traits that make them most suited to the harsh environmental conditions of the tropics and are highly valued for their meat and skin.

The respiratory system has two functional parts: the conducting part which conveys, moistens, and warms the air passing to the lung, and the respiratory part, where gaseous exchange occurs. The upper respiratory tract is made up of the nasal cavity, oral cavity, pharynx, and their associated structures, while the lower respiratory tract consists of the trachea, bronchi, bronchioles, and alveoli. The respiratory system develops from the primitive gut tube which is an endodermal structure that forms during the lateral folding of the embryo [4]. The expression of Nkx2-1 (Titf1) in the ventral wall of the foregut marked the earliest signal for the development of the respiratory system and results in the specification of future trachea and lungs locations [5]. An out-pocketing of the proximal part of the foregut gives rise to the respiratory diverticulum which later bifurcates into two buds that eventually become the left and right primary bronchi [4]. After the lung buds form, the trachea bud appears and undergoes further morphological transformations, including tube separation, elongation, and diameter expansion [5]. The initial lung bud comprises of an endodermal epithelium that is surrounded by splanchnic mesoderm-derived mesenchyme [6]. Further lung development involves controlled cross-signalling between the epithelium, mesenchyme, and mesothelium [6, 7]. The Wnt signalling is indispensable for embryonic lung progenitor proliferation [8]. The maturation of fetal lungs for normal post-natal life also depends on gene expression [9]. The transcription factors, TTF-1 (thyroid transcription factor 1), CCAAT-binding proteins (or C/EBPα), FoxA2 (Foxhead box protein A2), and proteins such as Hopx, and Hdac2 are key regulators of gene expression needed for the modulation of lung maturation [9-11].

The timing and the pattern of epithelial differentiation during gestation varies among species. There are five morphological phases of development for most mammal lungs, namely the embryonic phase, pseudo-glandular phase, canalicular phase, terminal sac phase, and alveolar phase. In fetal bovine lungs, the typical features of the pseudo-glandular, canalicular, and alveolar stages of lungs were observed from days 84 – 98, 154 – 164, and 224 – 266 of gestation, respectively [12]. In sheep, the alveolar phase of lung development is established 4 weeks before birth [13]. The timing and pattern of development of the various respiratory tissues of caprine have not been reported. Thus, this study aims to investigate the morphological development of the larynx, trachea, and lungs in the fetuses of red Sokoto goats using histological and histochemical techniques.

Results

Histology of the larynx

The laryngeal walls consist of a modified mucosal layer, skeletal muscles, and cartilages. The laryngeal mucosa exhibited two bilateral folds (vocal folds/cords) and two upper pairs of folds known as vestibular folds (false vocal cords) (Figure 1). At FD 53, the forming epithelium of the laryngeal mucosa showed somewhat bi-stratified epithelial cells. The lamina propria mucosae was a mesenchymal tissue devoid of glands. Areas of naïve skeletal muscles were observed (Figures 1A, 1B). At FD 71 the vocal cord areas consisted of an epithelium with a basal area and an apical area. The basal epithelial area contained a single layer of basal cells that rested on a basal membrane, while the apical aspect of the epithelium was lined by stratified epithelial cells containing squamous to round nuclei. The subjacent areas showed lamina propria mucosae with glands and bundles of forming skeletal muscles (vocalis muscles). Vestibular folds were observed (Figure 1C). At FD 76, there were apical buddings of the stratified epithelium. The lamina propria mucosae contained glands which increased in population at FD 98 (Figure 1D). At FD 98, the nuclei of the topmost layer of the epithelium were more squamous than round. At FD 104, the laryngeal mucosa was largely lined by a well-defined stratified squamous epithelium. The population of glands in the submucosa increased while thick bundles of skeletal muscles were key constituents of the laryngeal wall (Figures 1E, 1F).

PAS-Alcian blue histochemistry of larynx

Following PAS-Alcian blue staining, there were no goblet cell areas at FD 99 of development. However, the observed glandular lumina contained magenta-stained secretions (Figure 2A). At FD 104, few areas of bluish-stained goblet cells were observed in the epithelium, while more magenta-stained glandu-

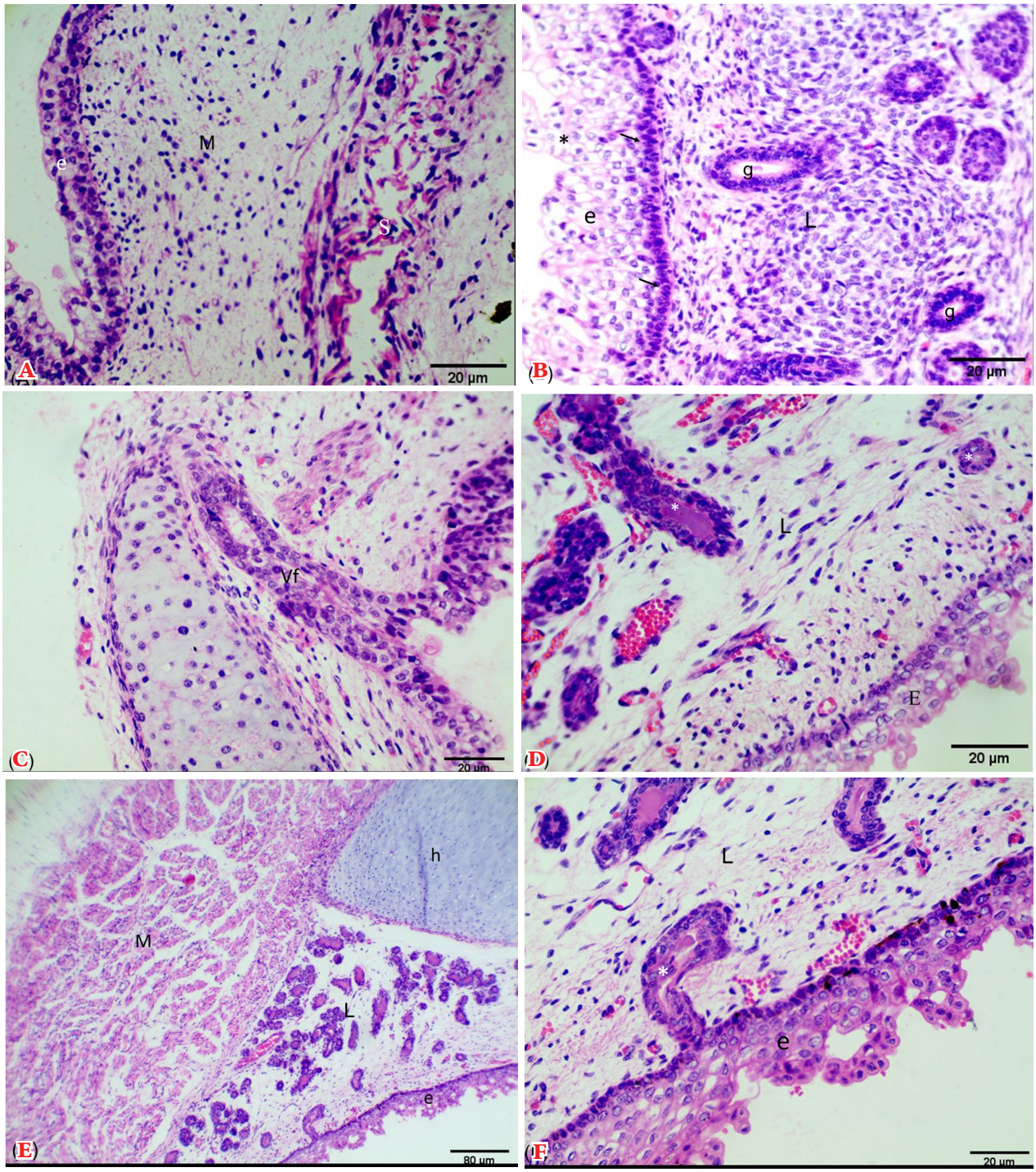

Figure 1.
1A, the larynx at FD 53 showing forming epithelium (e), mesenchymal tissue area (M), and naïve skeletal muscle area (S), H&E stain, x400. 1B, the larynx at FD 69 shows the forming of the epithelium (e) with basal (arrows) and apical (asterisk) areas and lamina propria mucosae (L) with glands (g). H&E stain, x400. 1C, the larynx at FD 71 showing the vestibular fold (Vf). H&E stain, x400. 1D, the larynx at FD 98 shows stratified squamous epithelium (E) and lamina propria mucosae (L) with glands (asterisks). H&E stain, x400. 1E, the larynx at FD 104 shows stratified squamous epithelium (e), lamina propria mucosa (L) with many glands, bundles of skeletal muscles (M), and hyaline cartilage (h), H&E stain. x100. 1F, the larynx at FD 104 shows stratified squamous epithelium (e), lamina propria mucosae (L), and invaginating gland (asterisk). H&E stain, x400

lar lumina were observed (Figure 2B).

Histology of the trachea

The trachea of the red Sokoto goat was made up of four tunics, namely tunica mucosa, tunica submucosa, tunica muscularis, and tunica adventitia (Figures 2C and 2F). The tunica mucosa consisted of lamina epithelialis mucosae, lamina propria mucosae, and lamina muscularis mucosae, while the tunica submucosa contained C-shaped hyaline cartilages whose ends are bridged by smooth muscles.

At FD 53, the lamina epithelialis mucosae was a

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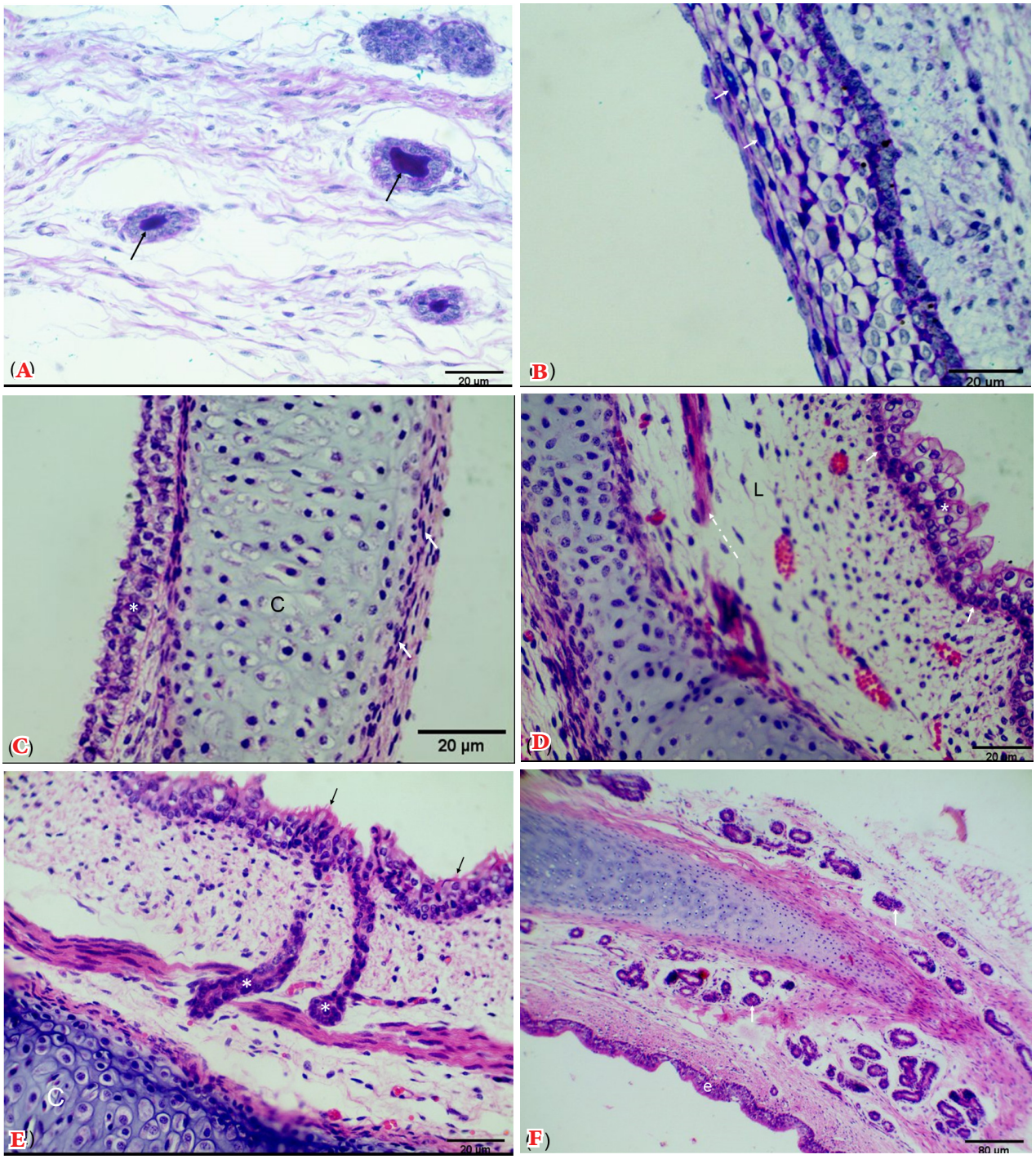

Figure 2.
2A, the larynx at FD 99 showed glandular lumina with magenta-stained secretions (arrows), PAS-Al stain, x400. 2B, at FD 104, the larynx showed bluish-stained areas within the epithelium (arrows), PAS-Al stain, x400. 2C, the trachea at FD 53 showing bi-stratified epithelium (asterisk), hyaline cartilage (c), and smooth muscle cells (arrows), H&E stain, x400. 2D, micrograph of the trachea at FD 80 showing basal (arrows) and apical (asterisk) epithelial areas, lamina propria mucosae (L), lamina muscularis mucosae (dotted-arrow), H&E stain, x400. 2E, the trachea at FD 102 showing tracheal epithelium with apical cells (arrows) and invaginating glands (g), H&E stain, x400. 2F, the trachea at FD 130 shows a substantial population of glands (arrows) in the lamina propria and submucosal areas and ciliated pseudostratified columnar epithelium (e), H&E stain, x100.

bi-stratified epithelium with basal columnar and apical cuboidal to columnar epithelial cell layers. A thin layer of lamina muscularis mucosae closely associated with the cartilaginous rings was observed, while islands of smooth muscle cells existed between the tips of the cartilages (Figure 2C). At FD 71, cells within the bi-stratified epithelium became more staggered, with additional apical dome-shaped binucleated cells forming an extra layer. At FD 80, the lamina muscularis mucosae was more clearly delineated and partly separated from the cartilaginous ring (Figure 2D). At

FD 98, epithelial cells invagination into the wide lamina propria mucosae formed a few glands.

At FD 102, the lamina epithelialis mucosae was a pseudostratified columnar epithelium that showed scanty cilia. Several glands extended from the epithelium throughout the length of the lamina propria mucosae and to the submucosa (Figure 2E). At FD 130, the tracheal epithelium consisted of pseudostratified columnar epithelium with an apical brush border appearance (Figures. 2F, 3A). Each C-shaped cartilage exhibited three lateral, medial, and distal surfaces.

PAS-Alcian blue histochemistry of trachea

Between FDs 53 – 102, staining with PAS-Alcian blue showed no positive reaction within the epithelium. Within the above timings, no goblet cell areas were obvious (Fig. 3B). However, at FD 102, the glandular epithelia contained a bluish-stained area, while the glandular lumina contained bluish-magenta secretions (Figure 3C). At FD 130, distinct bluish-stained goblet cells were found within the tracheal epithelium. The glandular epithelia of the trachea exhibited bluish-magenta stained areas (Figure 3D).

Histology of the lungs

At maturity, the lungs are composed of parenchyma, branches of the bronchial tree (consisting of primary bronchi, secondary (lobar) bronchi, and tertiary (segmental) bronchi), pulmonary arteries, and veins. The segmental bronchi give rise to bronchioles that later forms the terminal bronchioles, respiratory bronchioles, alveolar ducts, alveoli sac, and alveoli (Figure 4)

Early 2nd term

At FD 54, the lung of the red Sokoto goat was at the pseudo-glandular stage (Figure 4A). Here, the developing lungs appear as mesenchymal tissue that

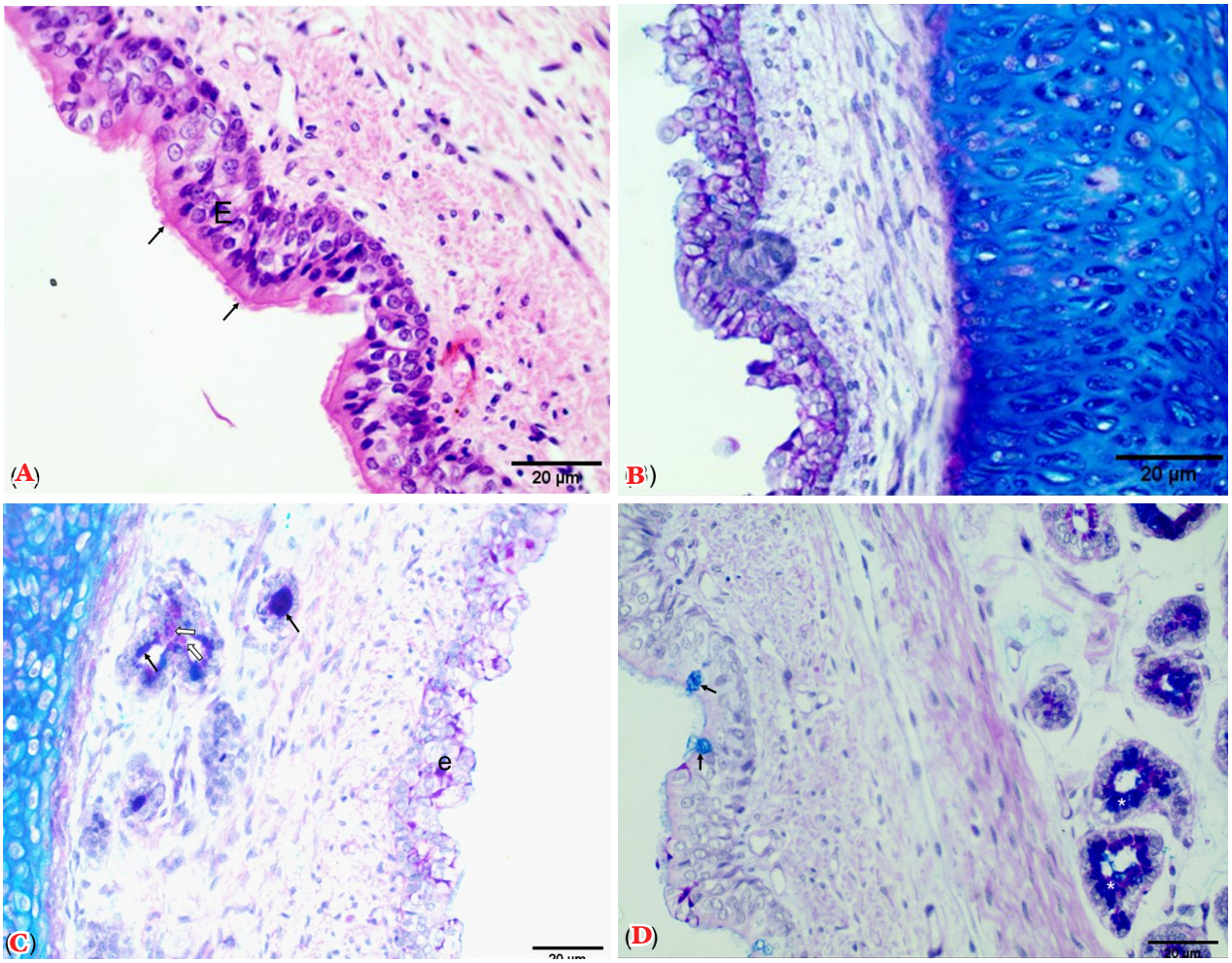

Figure 3.
3A, the trachea at FD 130 showing ciliated (arrows) pseudostratified columnar epithelium (E). H&E stain, x400. 3B, the trachea at FD 80 showing negative PAS-AL blue reactions, PAS-Al stain, x400. 3C, the glandular lumina of the trachea at FD 102 showed bluish (black arrows) and magenta-stained (white arrows) areas, PAS-AL stain, x400. 3D, the trachea at FD 130 shows bluish-stained goblet cells (arrows) and bluish-stained glandular epithelial areas (asterisks). PAS-Al stain, x400.

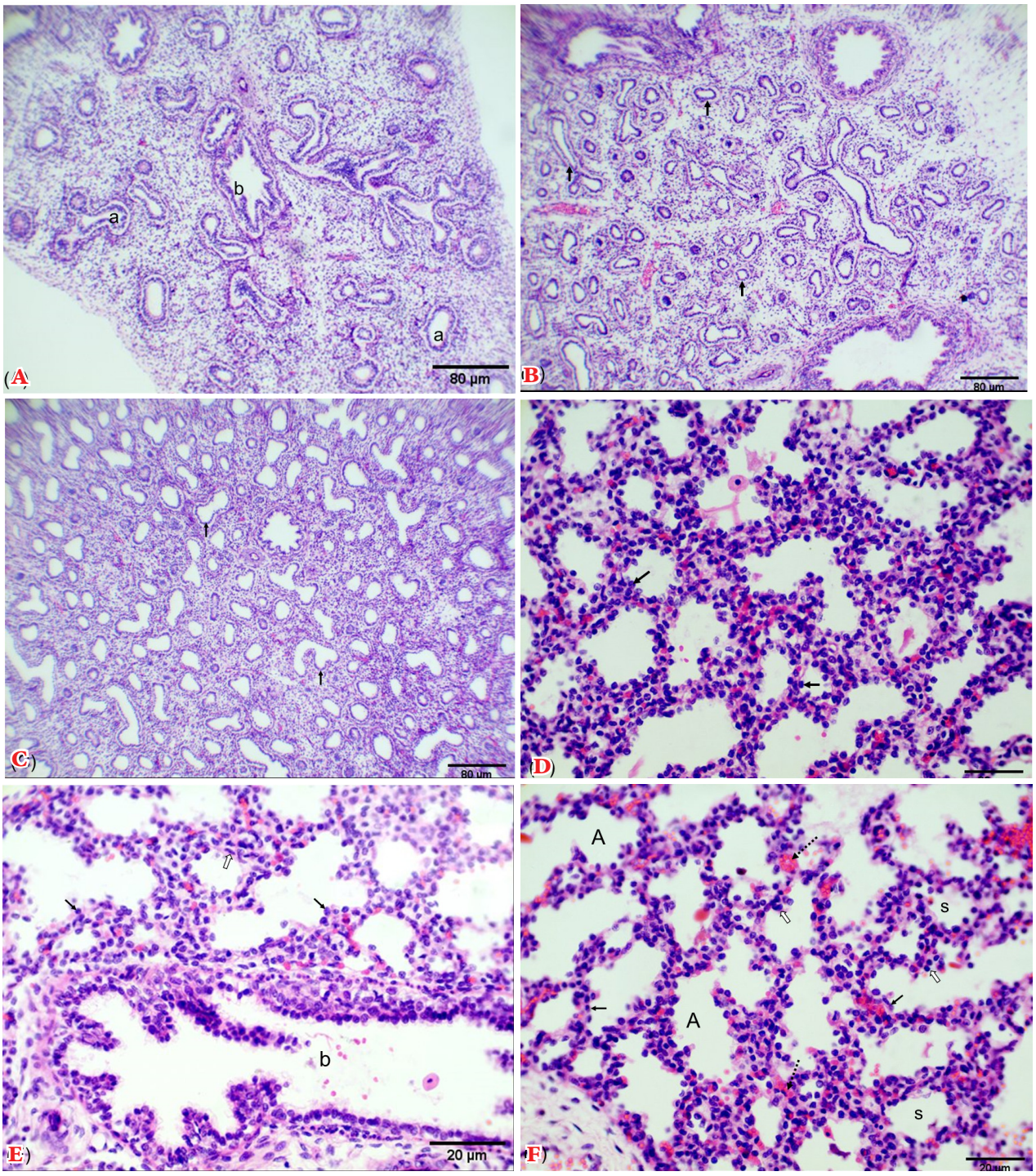

Figure 4.
4A, the lung (FD 54) at pseudo-glandular stage showing mesenchymal tissue with expanding airways (a) and bronchiole (b), H&E stain, x100. 4B, the lung (FD 71) at canalicular stage showing diffusely distributed canaliculi (arrows) within the lung tissue, H&E stain, x100. 4C, the lung (FD 76) at the canalicular stage, transitioning to the terminal sac stage. Note the budding terminal sac (arrows). H&E stain, x100. 4D, the developing lung (FD 99) at terminal sac stage showing sacs lined by simple cuboidal epithelia (arrows), H&E stain, x400. 4E, the lung (FD 104) at terminal sac stage showing bronchiole (b), alveolar sacs with type 1 (white arrows) and type II (black arrows) pneumocytes, H&E stain, x400. 4F, the lung (FD 129) at late terminal sac or alveolar stage showing alveolar sacs (S) and alveoli (A) with type I (black arrows) and type II (white arrows) pneumocytes. Note the blood capillaries (segmented arrows). H&E stain, x400.

contains exocrine glands. All branches of the bronchial tree and bronchioles were present (including terminal bronchioles). At FD 71, the developing lung was at the canalicular stage (Figure 4B). The mesenchymal tissues of the developing lungs contained a large population of mesenchymal cells, with canaliculi widely distributed within the lung tissues.

Late 2nd term

At FD 76, the lung was in the late canalicular stage, transitioning to the terminal sac stage (Figure 4C). Several canaliculi were diffusely distributed, but terminal sacs were beginning to bud. At FD 99, the developing lungs were in the terminal sac stage (Figure 4D). A large population of terminal sacs budded off from the respiratory bronchioles were observed. The terminal sacs were largely lined by simple cuboidal epithelium.

Third term

At FD 104, the developing lungs of red Sokoto goats were in the terminal sac stage (Figure 4E). At this stage, a large number of alveolar sacs were formed from the respiratory bronchioles and were lined by cuboidal epithelial cells. The walls of the sacs had a rich supply of capillaries that were increasingly associated with the epithelium. Areas of type I pneumocytes and type II pneumocytes were observed. At FD 129, the lungs were either in the late terminal sac stage or alveolar stage, meaning that they were transitioning to the alveolar stage (Figure 4F).

Discussion

The framework of the larynx of the red Sokoto goat was fully established in the early 2nd term. Though naïve, a bi-stratified epithelium was clearly seen at FD 53 with basal and upper layers. The laryngeal basal layer may initiate the stratification process of the epithelium and also remain as stem cells for epithelial renewal. In most epithelia, the basal cells serve as multipotent progenitors capable of renewing the epithelia [14, 15]. In mouse embryos the basal layer-initiated stratification at embryonic day 10.5 to form the periderm [16]. At around the 71st day of gestation in this study, the upper layer of the laryngeal epithelium proliferated, largely by apical budding to first form large, hollow cells with small flat to oval nuclei. Later in the 2nd term, the foetal larynx was composed of stratified squamous epithelium. In humans, squamous epithelium develops in the 2nd trimester of fetal life and has been associated with programmed activation of certain genetic signals within the endodermal cells [17]. It is believed that a primitive swallowing ability develops in foetuses [18], thus, the stratified squamous epithelium developed in this study may serve mechanical purposes.

The structure of the larynx in the red Sokoto goat included vocal folds that were similarly lined by an epithelium that varied in structure with age. The vocal cord lamina propria contained laryngeal glands which were first observed in the early 2nd term (around FD 69) in this study. Earlier, the glands formed by epithelial invaginations and proliferated to populate the lamina propria. The observation of the magenta-stained secretions (after PAS-Alcian blue staining) in the glandular lumina at FD 99 shows the onset of neutral mucin secretions which may lubricate the foetal larynx. Bluish-stained areas were seen within the epithelium in the 3rd term. It is unclear if these are cells or orifices of developing glands with a secretory content of acidic mucin. Naïve vocalis muscle areas were observed in the early second term as islands of forming muscles. The vocalis muscle is a key constituent of the true vocal fold which aids phonation [19]. We observed that the naïve vocalis muscle area became bundles of skeletal muscles in 104th day old red Sokoto goats. These muscles, together with the formed cartilages as well as vestibular folds consolidated a complex laryngeal structure just before birth. Mechanical signals from swallowing and breathing were earlier thought to guarantee a more complex/mature larynx [18, 20]. But in this study, the already established complex laryngeal structure fingers the influence of genetic factors than just mechanical factors. According to Jadcherla et al. [21], the swallow peristaltic activity begins in fetal life, thus, the fetal larynx is required to prevent liquid aspiration.

The tracheal epithelium of the red Sokoto goat was poorly developed in the 1st and 2nd terms, most probably because the respiratory system of foetuses is largely nonfunctional. The pattern of development of the tracheal epithelium followed a similar trend as that of the larynx. However, at FD 53, the bi-stratified epithelial lining of the trachea contained basal columnar, and apical cuboidal to columnar-shaped cells. The trachea forms the conductive part of the respiratory system and consists of the ciliated pseudostratified columnar epithelium (respiratory epithelium) in 104-day-old foetuses of red Sokoto goats. The respiratory epithelium which forms in the 3rd term is preparatory for post-natal protective roles. The constituent goblet cells of the respiratory epithelium, its secretory products, and as well as glandular secretions toward birth will likely drive mucociliary clearance of dust and pathogens after birth. The distinct bluish-stained goblet cells in PAS-Alcian blue preparations at FD 130 showed secretion of acidic mucin, while the bluish, bluish-magenta stained glandular areas are indicative of acidic-neutral mucin secretions. These secretions

Structural development of the respiratory tract

will synchronize to defend the respiratory system. Among other cells like goblet cells, basal cells, and neuroendocrine cells, ciliated cells are the most abundant cells of the tracheal epithelium [8, 23].

Five morphological stages of lung development previously recognized in prenatal mammalian lung development included embryonic, pseudo-glandular, canaliculi terminal sac, and alveolar stages. In the current study, the lungs of the red Sokoto goats were at the pseudo-glandular stage at FD 54, canaliculi stage between FDs 71-76, terminal sac stage between FDs 76 – 104, and alveolar stage from 129 days of gestation. This observation is at variance with the report of pseudo-glandular, canaliculi, terminal sac, and alveolar sac stages in sheep, which were reported between 40-90, 95-120, 120-140, and from 140 foetal days, respectively [7]. In experimentally reared perinatal goats of Assam [23], late canaliculi, terminal sac, and alveolar stages were observed at gestation days 116, 139, and 149, respectively. The reports on the varied timing of lung development may represent breed/species-specific features of lung development and may also reflect environmental influences. According to Greenough [24], intra- or extra-thoracic compression, abnormal fetal breathing movement, and reduction in amniotic fluid volume, which may impair antenatal lung growth will adversely affect normal lung functions postnatally. Thus, in this study, the structural maturation of the lungs of red Sokoto goats is obvious in the 3rd term of development and thus prepares the lungs for normal post-natal life. In the late 3rd term, the onset of the alveoli stage is obvious, but it is believed that the lung has a life-long alveolization ability to facilitate any required lung regeneration [25].

Type 2 pneumocytes are considered the major source of both types II and I pneumocytes [26, 27]. In this study, the terminal sacs and the alveoli observed in the 3rd term were composed mostly of type I pneumocytes than type II. Although type II pneumocytes also occurred, there were fewer in population than type I cells. It is unclear in this study when type II pneumocytes first form. However, popular opinion suggests that they arise from the distal tubules during canalicular and saccular stages [28, 29]. The flat appearance of type I cells in this study is typical of the shape of the cells in the mammalian lung. Later in the 3rd term, type I cells were intimately associated with alveolar capillaries in an arrangement that will facilitate the onset of gaseous exchange. The endothelial cells, basement membrane of the type I pneumocytes, basement membrane of the alveolar capillaries, and the endothelial cells of the capillaries form the gaseous exchange barrier in the alveolar wall [28]. Markers of type I pneumocytes are podoplanin (T1α) and aquaprin5 (Aqup5) [26, 29].

In conclusion, the structural modifications observed within the larynx, trachea, and lung in this study highlight essential changes needed for normal post-natal function of the respiratory system in the red Sokoto goat. While four of the five stages of lung development were obvious between FD 54 and 129, the lungs of the red Sokoto goat were structurally mature at FD 129 in readiness for the first breathing exercise.

Materials & Methods

Animals

The intact gravid uterine and their adjoining tissues were obtained from 40 healthy pregnant red Sokoto goats (Figure 5) slaughtered at the Nsukka municipal slaughterhouse, Ikpa, Nsukka Local Government Area, Enugu State. Nsukka is located at 6.86 degree North Latitude, 7.39 degree East longitude, 7.39o East longitude [30]. The gravid uteri were transported to the Department of Veterinary Anatomy, Faculty of Veterinary Medicine, University of Nigeria, Nsukka for the collection and processing of samples from their fetuses. The fetuses were grouped into the three terms, namely: days 0-50 (first term), 51-100 (second term), and 101-150 (third term). The second term was subdivided into 2, namely: days 51-75 (early second term), and 76-100 (late second term).

Figure 5.
Photograph of the red Sokoto goat showing phenotypic traits of the breed.

Gross anatomy

After the exteriorization of the fetuses, the crown-rump length (CRL) was measured using a thread and meter rule. The distance from the top of the head, passing through the dorsal aspect of the neck, and the curvatures of the spine to the root of the tail represented the CRL. The gestational age (or fetal age) was estimated using the formulae [31]:

$y = 2.74x + 30.15$

The y denotes gestational age in days, and the x is the CRL (cm).

The sections of the larynx, trachea, cranial, middle, and caudal lobes of the lungs were obtained and processed for histological evaluation.

Histological procedures

The sections of the larynx, trachea, and lung were excised and fixed in 10% neutral-buffered formalin for 48 hours. Thereafter, the fixed tissues were dehydrated in the graded concentration of ethanol and cleared in xylene. The cleared tissues were embedded in molten paraffin wax and mounted for sectioning with a rotary microtome. Five micrometer thick sections were obtained and stained with haematoxylin and eosin (H&E), and periodic acid Schiff-Alcian blue at pH 2.5 (PAS-Alcian blue) stains for light microscopy. The staining protocols were according to the methods described by Sheehan and Hrapchak [32] and Mepham [33]. The Motic binocular light microscope was used to evaluate the histological features of the tissue sections. Photomicrographs were captured using an Amscope® digital camera (United Scope LLC) attached to the Motic binocular light microscope.

Authors' Contributions

A.F.U. conceived and planned the experiments. A.F.U., C.L.O., and E.E.U. carried out the experiments. A.F.U. planned and carried out the simulations. A.F.U., C.L.O., and E.E.U. contributed to sample preparation. A.F.U., C.L.O., and E.E.U. contributed to the interpretation of the results. A.F.U. took the lead in writing the manuscript. All authors provided critical feedback and helped shape the research, analysis and manuscript.

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Conflict of interest

The authors declare that there is no conflict of interest.

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