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The abdominal air sac ostium of the domestic fowl: a sphincter regulated by neuro-epithelial cells? *

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INTRODUCTION

Information on the microscopic structure of the ostia connecting the lung to the air sacs in birds is scarce. The ostium of the abdominal air sac in the domestic fowl consists of a direct connection of the primary bronchus into the air sac and several indirect connections between the air sac and the parabronchi. It is generally agreed (King, 1966; King & Molony, 1971; Duncker, 1971; Carlson & Beggs, 1973; Hodges, 1974) that the walls of the avian air sacs are lined by a simple squamous epithelium backed by a very thin layer of collagen and elastic fibres, except at the ostia where the epithelium becomes columnar and ciliated. The existence of a ring of smooth muscle around the ostia of the air sacs in general seems to have been explicitly mentioned only by King & Molony (1971). However, Duncker (1971) mentioned an increase in the smooth muscle of the wall of the primary bronchus just before the ostium of the abdominal sac, and a similar increase in the wall of the lateroventral secondary bronchus which forms the direct connection to the caudal thoracic sac. Duncker suggested that these muscles could regulate bronchial diameter. The presence of granule-containing cells in the walls of air sacs or their ostia has apparently not been reported.

This paper describes the histological and ultrastructural characteristics of the ostium of the abdominal air sac of the domestic fowl. It reports the presence of a ring of smooth muscle in the wall of the ostium, and the occurrence of innervated granule-containing cells within both the epithelium and the lamina propria. It also calls attention to structural features suggesting a defence function relative to inspired air.

MATERIALS AND METHODS

Light and transmission electron microscopy

Six chicks one day old and 6 adult chickens were killed by barbiturate overdose. Within one minute after death, the caudal surface of the lung was exposed and fixed *in situ* with 4% glutaraldehyde in 0·06 M phosphate buffer, pH 7·4 at 4 °C. After 10 minutes the tissue forming the ostium of the abdominal air sac was removed, immersed in the same fixative for a further 30 minutes, and cut into smaller pieces which were postfixed in 2% Dalton's chrome osmic acid for 1½ hours. The tissue was then dehydrated in a graded series of ethanols, passed through propylene oxide and embedded in Maraglas.

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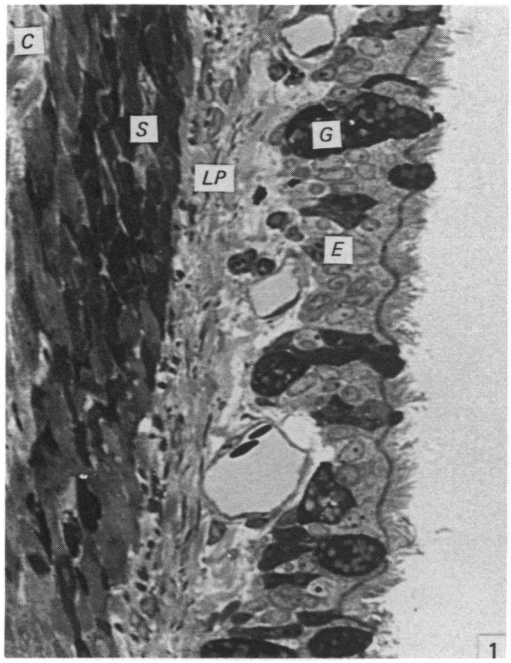


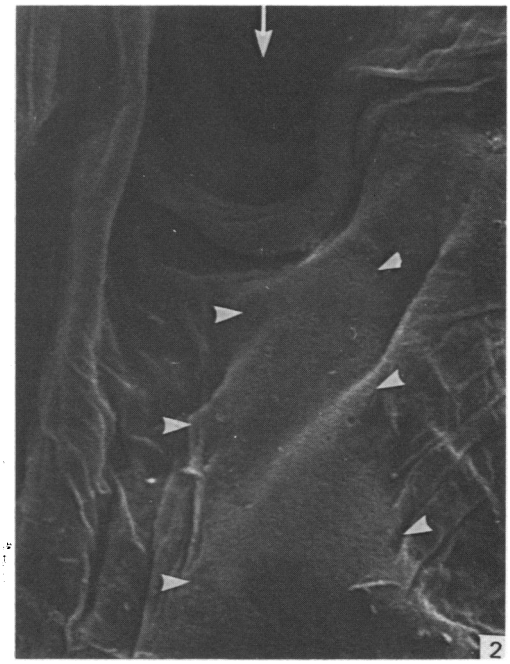


Fig. 1. The layers of the abdominal ostium are shown. *E*, ciliated, pseudostratified epithelium containing goblet cells (*G*); *LP*, connective tissue and blood vessels of lamina propria; *S*, layer of smooth muscle fibres; *C*, connective tissue of submucosa. 1 μm toluidine blue stained section. × 560.

Fig. 2. Scanning electron micrograph of the ostium opening into the abdominal air sac. Ridges of ciliated epithelium (bounded by arrowheads) extend from the ostium (arrow) as velvety bands. × 900.

Sections 1 μm thick were cut and stained with toluidine blue for light microscopy. Areas were selected for examination by transmission electron microscopy. Thin sections of these areas were cut and stained with uranyl acetate and lead citrate.

Scanning electron microscopy

The ostium of the abdominal air sac was obtained as above from a further six one day old chicks and three adult chickens. The ostium was placed in the glutaraldehyde fixative for 30 minutes and postfixed in 2 % Dalton's chrome osmic acid for 1 hour. The tissue was then dehydrated in a graded series of ethanols, transferred to a 50 % mixture of ethanol and amyl acetate, and taken through two changes of amyl acetate. The tissue was dried using a Balzer's critical point drying apparatus and sputter-coated with gold/palladium. The specimens were examined by scanning electron microscopy.

The nomenclature to be used follows that of the *Nomina Anatomica Avium* (Baumel *et al.* 1979).

RESULTS

The lumen of the ostium was lined by a typical respiratory epithelium of pseudostratified, ciliated columnar cells with goblet cells (Fig. 1). This mucociliary epithelium extended from the ostium, and continued as wide bands (Fig. 2) across the adjacent air sac wall which otherwise was lined by a simple squamous epithelium. Beneath the epithelium of the ostium was a richly vascularised lamina

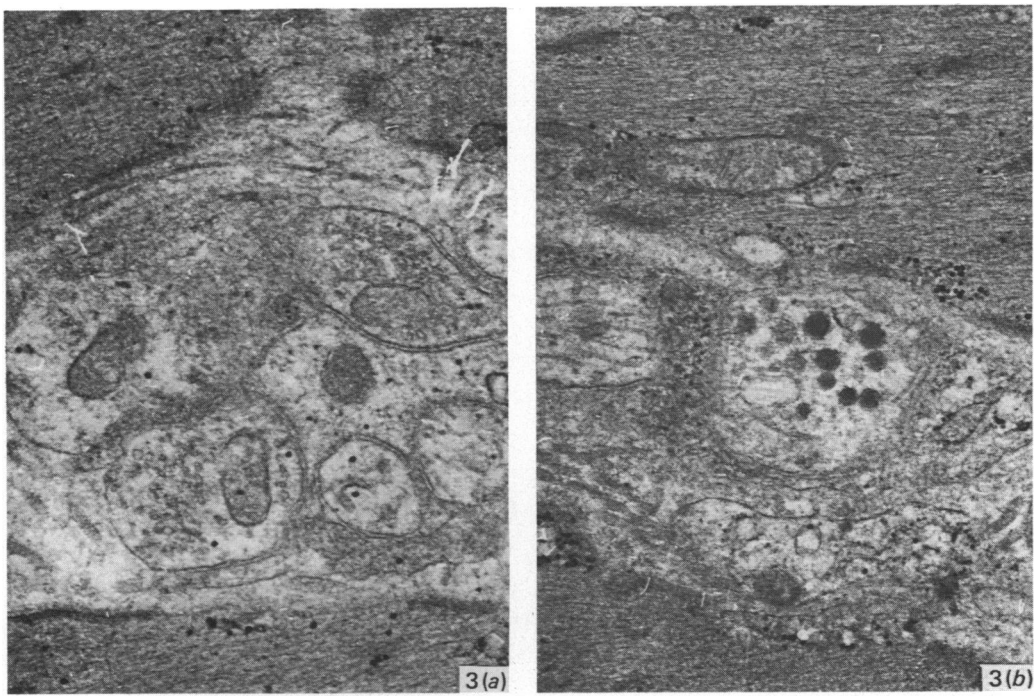


Fig. 3(*a–b*). Axon varicosities closely associated with the smooth muscle of the ostium, containing small agranular vesicles (*a*) or large granular vesicles (*b*). ×27000.

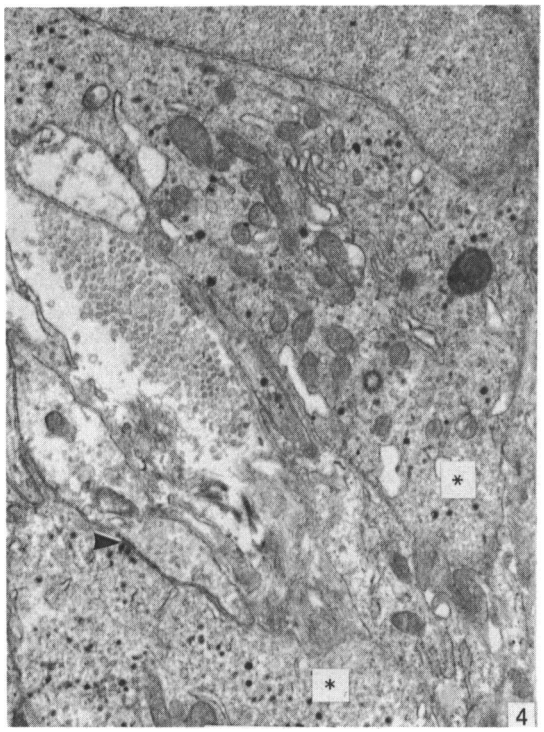
propria which contained a nerve plexus of fine bundles of mostly unmyelinated axons. Most regions of the lamina propria contained only a few fibroblasts, plasma cells and mast cells. However, there were areas of defensive tissue containing relatively abundant macrophages, lymphocytes and plasma cells.

There was a substantial layer of well innervated smooth muscle beneath the lamina propria (Fig. 1). Although it varied in thickness and was interrupted in some places by strands of connective tissue, it formed a sphincter-like ring round the ostium. The axons innervating the muscle were essentially of two types: one contained typical cholinergic vesicles (Fig. 3*a*); the other type was characterised by large dense-cored vesicles about 80–120 nm in diameter (Fig. 3*b*), similar in appearance to those of peptidergic axons.

The connective tissue beneath the muscle layer appeared typical of a tunica submucosa, being dense with prominent bundles of collagen. This layer also contained large blood vessels, nerve bundles of both myelinated and unmyelinated axons, occasional ganglia and, especially in the adult fowls, adipose tissue.

Some areas of the tunica submucosa were bounded by a simple squamous or cuboidal epithelium which probably belonged to the adhering wall of the caudal thoracic air sac. In other areas, the tissue beneath the tunica submucosa consisted of typical exchange tissue.

Cells containing numerous dense-cored granular vesicles were observed in the region of the ostium, particularly at the direct connection of the primary bronchus with the abdominal air sac. An abundance of granular vesicles typifies peptidergic neurons and peptide endocrine cells for which a common origin, neuroectoderm, has been proposed (Pearse & Takor Takor, 1976), and therefore the granular cells of the



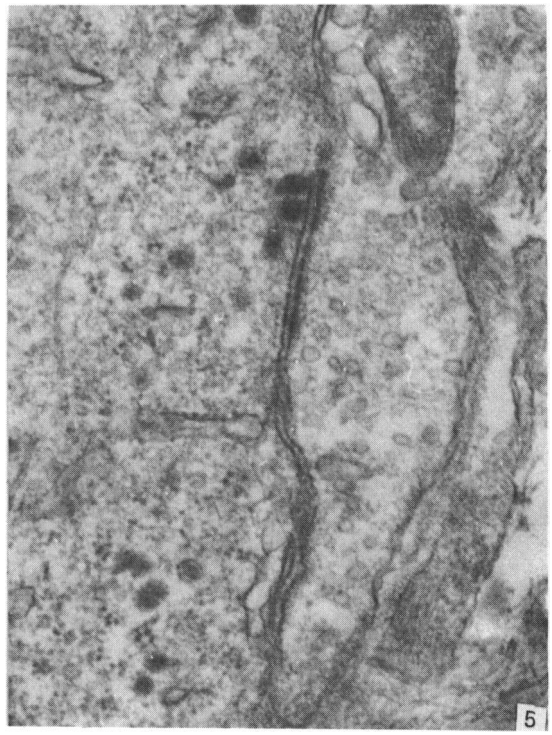


Fig. 4. Part of a ganglion in the submucosal layer of the ostium showing portions of two Type I granule-containing cells (asterisks). An axon terminal, containing small agranular vesicles, synapses with one of the granular cells (arrowhead); the synapse is shown in Fig. 5. ×13000.

Fig. 5. Detail of the synapse shown at the arrowhead in Fig. 4. ×47000.

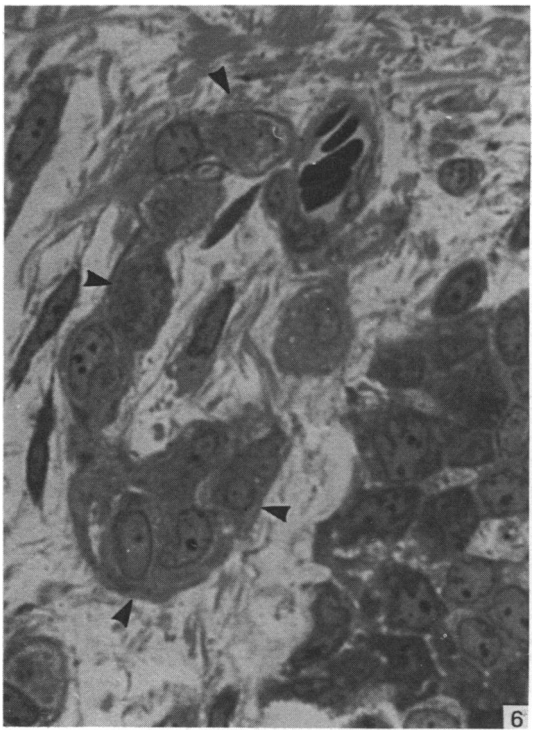
ostium are referred to here as neuro-epithelial cells. It was possible to classify these cells into three types on the basis of their morphology and their location.

Type I neuro-epithelial cells

These cells (Fig. 4) were observed within the ganglia in the submucosal layer, and their features were similar to those of small, granule-containing cells associated with mammalian sympathetic ganglia. The cytoplasm contained numerous small granular vesicles approximately 80–100 nm in diameter (Fig. 4). These cells were surrounded by many axon profiles. Some of the axonal varicosities contained large, dense-cored vesicles, approximately 120 nm in diameter; others possessed small, agranular vesicles, about 60 nm in diameter, and only the latter type were seen to make synaptic contact with the Type I cells (Fig. 5).

Type II neuro-epithelial cells

The second type of granule-containing cell lay within the lamina propria and was characteristically arranged in cords or clusters of three or more cells (Fig. 6). Usually they were near capillaries which were fenestrated in the region closest to these cells (Figs. 6, 8). Typically the cells possessed two or more prominent nucleoli in evenly dispersed euchromatin, with a thin peripheral rim of heterochromatin (Figs. 6, 7). A few of the cells appeared to be binucleate. The cytoplasm (Fig. 7) contained many evenly distributed, large, dense-cored vesicles, approximately 100–



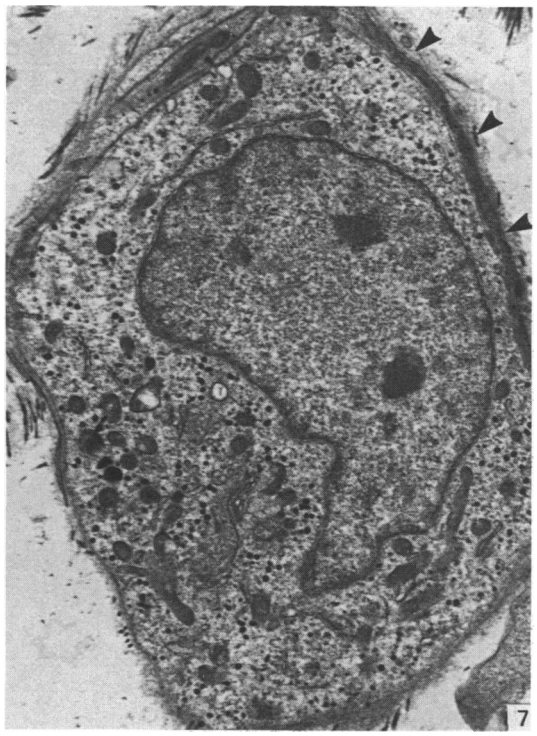


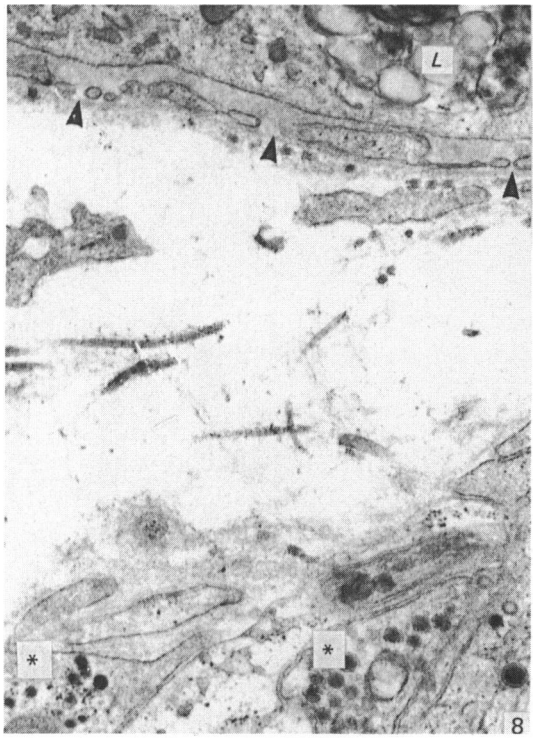
Fig. 6. A cord of nine Type II cells (arrowheads) in the lamina propria of the ostium. At the top, a capillary lies near one of the cells. The basal region of the pseudostratified epithelium is on the lower right. 1 μm thick, toluidine blue stained section. × 1300.

Fig. 7. A typical Type II cell closely surrounded by slender cell processes containing electron-dense cytoplasm (arrowheads). × 8100.

120 nm in diameter, a prominent Golgi complex, some cisternae of rough endoplasmic reticulum, many ribosomal rosettes and occasional bundles of microfilaments. Short cytoplasmic protrusions containing granular vesicles were typical of most cells. One cell possessed an elongated process which terminated in a bulbous portion and contained a prominent axial bundle of microfilaments (Fig. 9). The cells were closely surrounded by slender electron-dense processes of cells similar to Schwann cells (Fig. 7). Several axon profiles were intimately associated with the Type II cells, and some were expanded into axonal terminals which contained many small mitochondria and aggregations of small agranular vesicles about 60 nm in diameter (Fig. 10). Axon profiles, containing dense-cored granular vesicles about 120 nm in diameter, were occasionally observed in the vicinity of these cells but not in very close contact.

Type III neuro-epithelial cells

These cells could not be identified in the sections stained with toluidine blue, but were readily recognised in thin sections examined in the electron microscope. The cytological features of these cells (Figs. 11, 12, 13), in particular the size of the granular vesicles, were similar to those of the Type II cells in the lamina propria, except that they usually contained only one nucleolus. Serial sections suggested the presence of two varieties of Type III cells, depending on their location in the



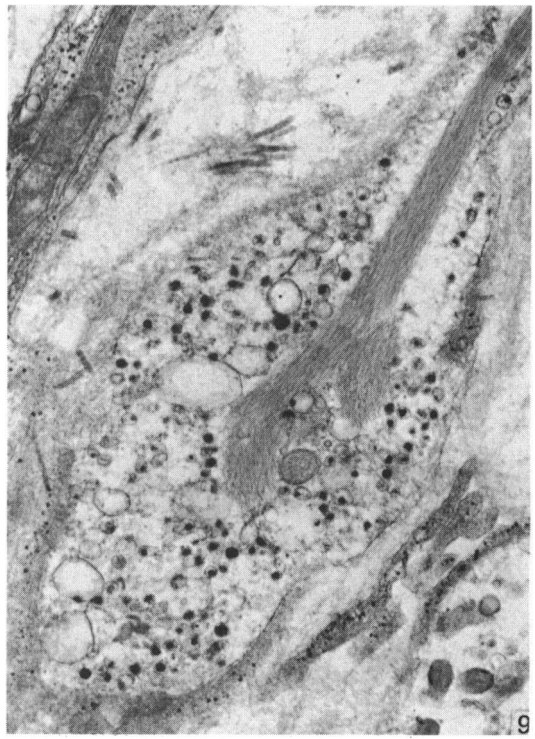


Fig. 8. Part of a fenestrated (arrowheads) capillary near Type II cells (asterisks). *L*, leukocyte in capillary. × 26000.

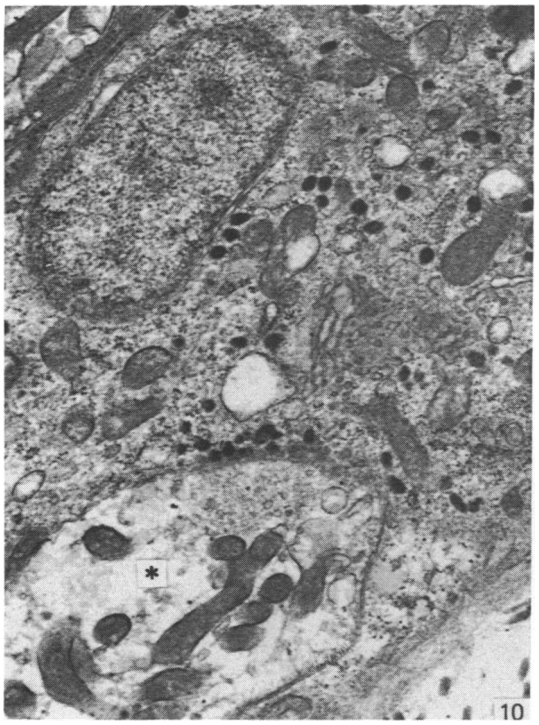
Fig. 9. The bulbous terminal portion of an elongated process of a Type II cell. A compact bundle of microfilaments lies axially within the process. × 16000.

epithelium and whether or not they were associated with axons. One variety appeared to consist of columnar cells extending from the base of the epithelium (Fig. 11), though none was seen to reach the surface and scanning electron microscopy of the epithelial surface did not reveal their presence within the epithelium. They were not associated with axons. The cells formed many small processes which interdigitated with the adjacent epithelial cells. Although often present in small groups of three or four, the individual cells only rarely made contact with each other and were usually separated by portions of electron-dense epithelial cells (Fig. 12). The other variety of Type III cells was basal in position and was closely associated with axon terminals. These axonal profiles contained many small agranular vesicles, about 60 nm in diameter, and several small mitochondria (Fig. 13).

DISCUSSION

We believe this to be the first report on the ultrastructure of the ostium of an avian air sac. It describes three main features, i.e. numerous neuro-epithelial cells, a thick band of well innervated smooth muscle encircling the ostium, and defensive tissue.

Neuro-epithelial cells have not previously been observed in the wall of the ostium of the abdominal air sac of the domestic fowl, although similar cells have been found in the epithelium of several other regions of the respiratory system of the domestic



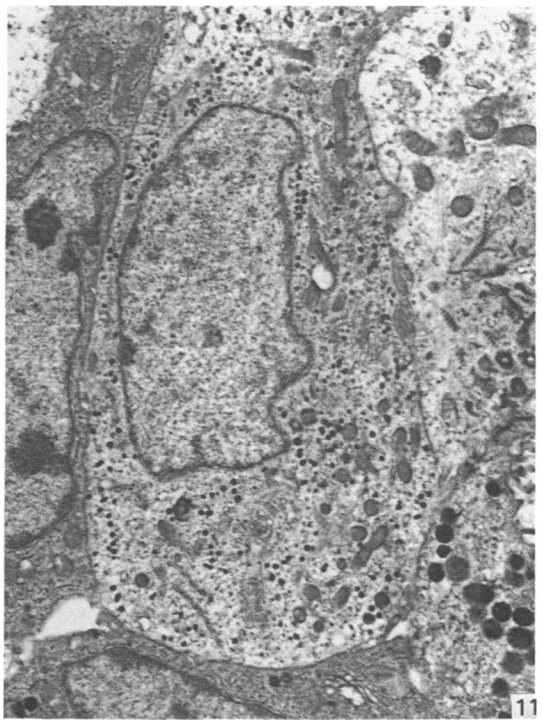
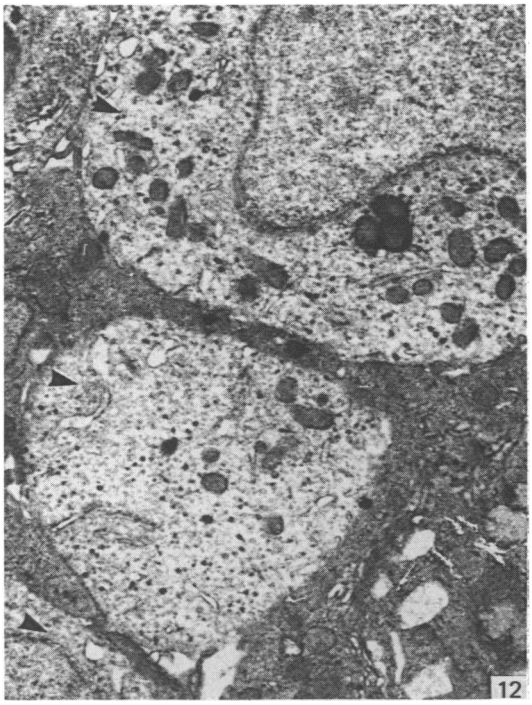


Fig. 10. Part of a Type II cell is closely associated with an axonal terminal (asterisk), which contains several mitochondria and aggregations of small agranular vesicles. A group of granular vesicles appears to have assembled in the cytoplasm of the Type II cell close to the axon. × 18300.

Fig. 11. A Type III cell within the pseudostratified epithelium of the ostium. Note the adjacent electron-dense epithelial cells which are commonly associated with this type of granular cell. × 8000.

fowl, especially in immature birds but also in adults. Thus they occur in the trachea (Walsh & McLelland, 1974), and in the primary bronchus and secondary bronchi (Cook & King, 1969*a*, *b*; Wasano & Yamamoto, 1979). They can be found relatively constantly in adults at the roots of the medioventral secondary bronchi (King *et al.* 1974), and they also occur though less regularly at the roots of the mediodorsal secondary bronchi but never in the terminal parts of the secondary bronchi or in the walls of the parabronchi (D. Z. King, unpublished observations). In the trachea (Walsh & McLelland, 1974) and in the wall of the primary bronchus and the roots of the secondary bronchi (Cook & King, 1969*a*, *b*; King *et al.* 1974) some of them are closely apposed to axonal endings with synaptic complexes. These published observations have therefore established that neuro-epithelial cells are widely distributed throughout the major airways of this species of bird, and hence it is not unexpected to find them in the ostium of an air sac, and especially at the direct connection of the primary bronchus with the abdominal air sac.

In the present study, however, three types of neuro-epithelial cells were identified on the basis of their general morphology and location. The cells of Type I differ from those found elsewhere in the walls of avian airways, since they are not intra-epithelial but are situated in ganglia in the submucosa: they are similar in location and ultrastructure to the small intensely fluorescent (SIF) cells observed in various



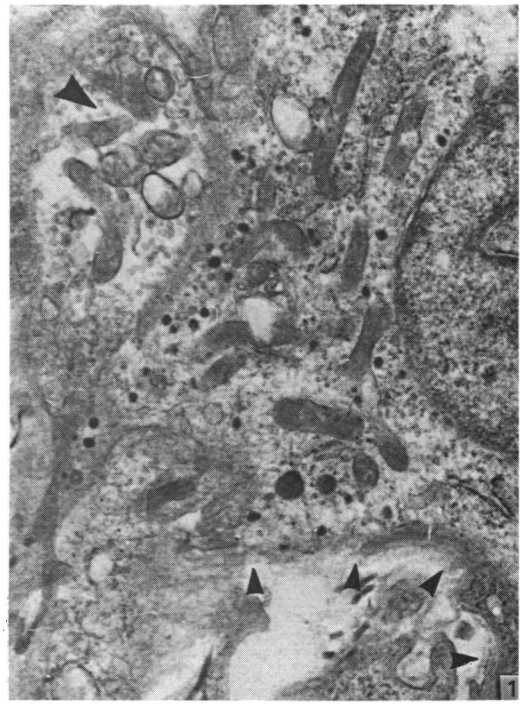


Fig. 12. An oblique section through a group of Type III cells (arrowheads) within the ostial epithelium. Serial sectioning established that these are three distinct cells. They are separated from each other by thin profiles of epithelial cells characterised by electron-dense cytoplasm. × 5600.

Fig. 13. A Type III cell in the basal region of the ostial epithelium. An axonal terminal (large arrowhead) containing mitochondria and small agranular vesicles is associated with the Type III cell. The small arrowheads indicate the basal lamina of the epithelium. × 12500.

mammalian autonomic ganglia (Matthews, 1976, 1980; Autillo-Touati & Seite, 1980). Ultrastructurally Type II and Type III cells closely resemble each other. However, the Type II cells again appear to be distinct, since they are situated in the lamina propria rather than in the epithelium and are associated with fenestrated capillaries. On the other hand the Type III cells do resemble the neuro-epithelial cells found elsewhere in avian respiratory epithelium. They appear to include two different types of cell, i.e. clusters of non-innervated columnar cells and basal cells closely associated with axons. The cells of Types II and III are morphologically similar to APUD cells (Pearse, 1969), thus indicating a possible endocrine function. The tendency for the Type II cells to be associated with fenestrated capillaries is consistent with this suggestion. On the other hand, some of the Type II and Type III cells were associated with axons. Innervated granule-containing cells with similar ultrastructural characteristics occur in the avian carotid body (King, King, Hodges & Henry, 1975), where they are believed to be involved in chemoreceptor activity; similar innervated granular cells are also found in avian Grandry corpuscles, where they are associated with mechanoreceptor activity (Gottschaldt, 1985). Thus it is possible that the innervated granular cells are involved in sensory functions. The possibility of dual endocrine and sensory functions has been suggested in previous studies of neuro-epithelial cells in the respiratory tract of birds (King *et al.* 1974; Wasano & Yamamoto, 1979).

Neuro-epithelial cells have also been observed in the respiratory epithelia of amphibians (Rogers & Haller, 1978; Goniakowska-Witalińska, 1981), reptiles (Scheuermann, De Groodt-Lasseel, Stilman & Meisters, 1983), and in various species of mammals; in all these groups they tend to form prominent aggregations known as neuro-epithelial bodies (Lauweryns, Cokelaere & Theunyck, 1972; Hage, 1976; Wasano, 1977; Cutz, Chan & Sonstegard, 1978; Hung, Chapman & Mestemacher, 1979; Edmondson & Lewis, 1980; Wasano & Yamamoto, 1981; Hoyt, Feldman & Sorokin, 1982; Hoyt, Sorokin & Feldman, 1982; Sorokin, Hoyt & Grant, 1982). By a neuronal anterograde tracing technique, Bower, Parker & Molony (1978) detected labelled structures in the extrapulmonary primary bronchus of the domestic fowl which were suggestive of neuro-epithelial bodies, but King, King & Griffiths (1977) showed by series of sections of the extra- and intra-pulmonary primary bronchus of the domestic fowl that neuro-epithelial bodies similar to those found in mammals are not present in the airways of this species. Thus birds may be an exception among the air breathing vertebrates but other avian species should be investigated.

From the physiological point of view, the salient microscopic features of the ostium of the abdominal air sac can be summarised as follows. The ostium is enclosed by circular smooth muscle which is well innervated; Bennett & Malmfors (1970) have reported that adrenergic nerves are associated with the ostia of the air sacs of the domestic fowl. Granular cells are present in the wall of the ostium, especially at the direct connection to the primary bronchus. Some of these cells form synapses with axonal endings. Airflow through the ostium may be influenced by a sphincter-like action of its innervated muscle ring, and this may be regulated by local hormonal effects or reflex nervous control originating from the granule-containing cells and their associated axons.

Histopathologically the ostium of the abdominal sac may contribute to the protection of the bird against inspired microorganisms and particulate matter. Goblet cells are present at the ostium, and together with the ciliated cells, both on the air sac surface as bands and within the ostium, they appear to constitute a continuous mucociliary carpet extending from the air sac through the ostium, along the primary bronchus, and up the trachea. During irritative challenge this carpet has been shown to be augmented by metaplasia of the squamous epithelial cells of the abdominal air sac into areas of new ciliated cells with goblet cells (Lucas & Denington, 1961; Lucas, 1970). In addition, the aggregations of macrophages, lymphocytes and plasma cells in the lamina propria of the ostium is in contrast to the lack of defensive tissue found in the lung of the domestic fowl (D. Z. King, personal communication). The presence of this tissue in the ostium indicates that the area is particularly vulnerable to infection, a not surprising finding since most of the inspired air in this species goes directly through the ostium into the abdominal air sac.

SUMMARY

A microscopic study of the ostium of the abdominal air sac of the domestic fowl has shown that the ostium has a sphincter-like ring of well innervated smooth muscle. Three types of neuro-epithelial cell characterised by their content of numerous large granular vesicles are found in the wall of the ostium. Type I cells are present within the submucosal nerve plexus and appear to be morphologically similar to SIF cells. Type II cells occur in the lamina propria, in clusters or cords, are often associated with fenestrated capillaries, and have synaptic contact with axonal

terminals containing small agranular vesicles. The cells of Types I and II are not intra-epithelial and therefore differ from the cells which have been found elsewhere in the respiratory tract of the domestic fowl and other vertebrates. Type III cells are intra-epithelial, and some of those in the basal region of the epithelium are associated with axon terminals. Type III cells are similar in ultrastructure and location to neuro-epithelial cells found elsewhere in the major airways of the domestic fowl. They also resemble cells in neuro-epithelial bodies in amphibian, reptilian and mammalian lungs, although neuro-epithelial bodies have not been found in the lung of this species of bird. The morphology of the ostium suggests that it may have a sphincter-like function, possibly regulated by the neuro-epithelial cells. The presence of a mucociliary epithelium and defensive tissue in the lamina propria indicates that the ostium is the site of defence mechanisms.

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