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A microscopic study of the tracheal epithelium of *Testudo graeca* and *Pseudemys scripta elegans**

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INTRODUCTION

Since the pioneering ultrastructural descriptions of tracheal cilia (Engstrom, 1951; Engstrom & Wersall, 1952) and the ultrastructural studies of Rhodin & Dalhamn (1956) and Rhodin (1959), an extensive literature has accumulated on the ultrastructure of the tracheal epithelium of mammals. Thus, this area has been carefully studied in the rat (Rhodin & Dalhamn, 1956; Breiphol, Herberhold & Kerschek, 1975; Jeffery & Reid, 1975; Marin, Lane, Gordon & Drummond, 1979), mouse (Hansell & Moretti, 1969; Pack, Al-Ugaily, Morris & Widdicombe, 1980; Pack, Al-Ugaily & Morris, 1981), hamster (Kennedy, Desrosiers, Terzaghi & Little, 1978; Gabridge, Agee & Cameron, 1977; Becci, McDowell & Trump, 1978; Carson, Collier & Hu, 1980), guinea-pig (Inoue & Hogg, 1974; Dalen, 1983), rabbit (Konradova, 1966; Plopper *et al.* 1983), cat (Tandler, Sherman, Boat & Wood, 1983*a*, *b*), sheep (Mariassy & Plopper, 1983, 1984), monkey (Wilson, Plopper & Hyde, 1984) and man (Rhodin, 1959, 1966; Miani, Pizzini & De Gasperis, 1971). The avian extrapulmonary airways have also been widely described (Purcell, 1971; Walsh & McLelland, 1974). However, little attention has been paid to the tracheal epithelium in reptiles. References are few and refer only to lizards (Tesik, 1984).

In the present paper, the tracheal epithelium of two Chelonia (*Testudo graeca* and *Pseudemys scripta elegans*) have been studied by means of conventional light microscopic, histochemical, immunocytochemical and ultrastructural techniques. The endocrine cells in the epithelium and the alterations, produced by hibernation, in the tracheal epithelium of *Testudo graeca* have been especially considered.

MATERIALS AND METHODS

Light microscopy

The Chelonia were killed by injecting an overdose of sodium pentobarbitone into the peritoneal cavity.

Tracheas from adult specimens of 6 *Pseudemys scripta elegans* and 8 *Testudo graeca* in non-hibernating (4) and hibernating (4) periods were fixed by immersion in Bouin's fixative. The samples were then processed and embedded in paraffin wax. The sections, 5 μm thick, were stained with haematoxylin and eosin, PAS (Martoja & Martoja, 1970), alcian blue (AB) at pH 2·5 and pH 1 (Pearse, 1985), aldehyde fuchsin (AF) (Gabe, 1968), alcian blue (pH 2·5)–PAS (AB–PAS) (Ganter & Jolles, 1969), alcian blue at pH 2·5 after methylation and saponification (Met + Sap + AB 2·5) (Pearse, 1985), high-iron diamine (HID) (Spicer, 1965), high-iron diamine–alcian blue at pH 2·5 (HID–AB) (Spicer, 1965) and Grimelius silver nitrate stain (Grimelius, 1968).

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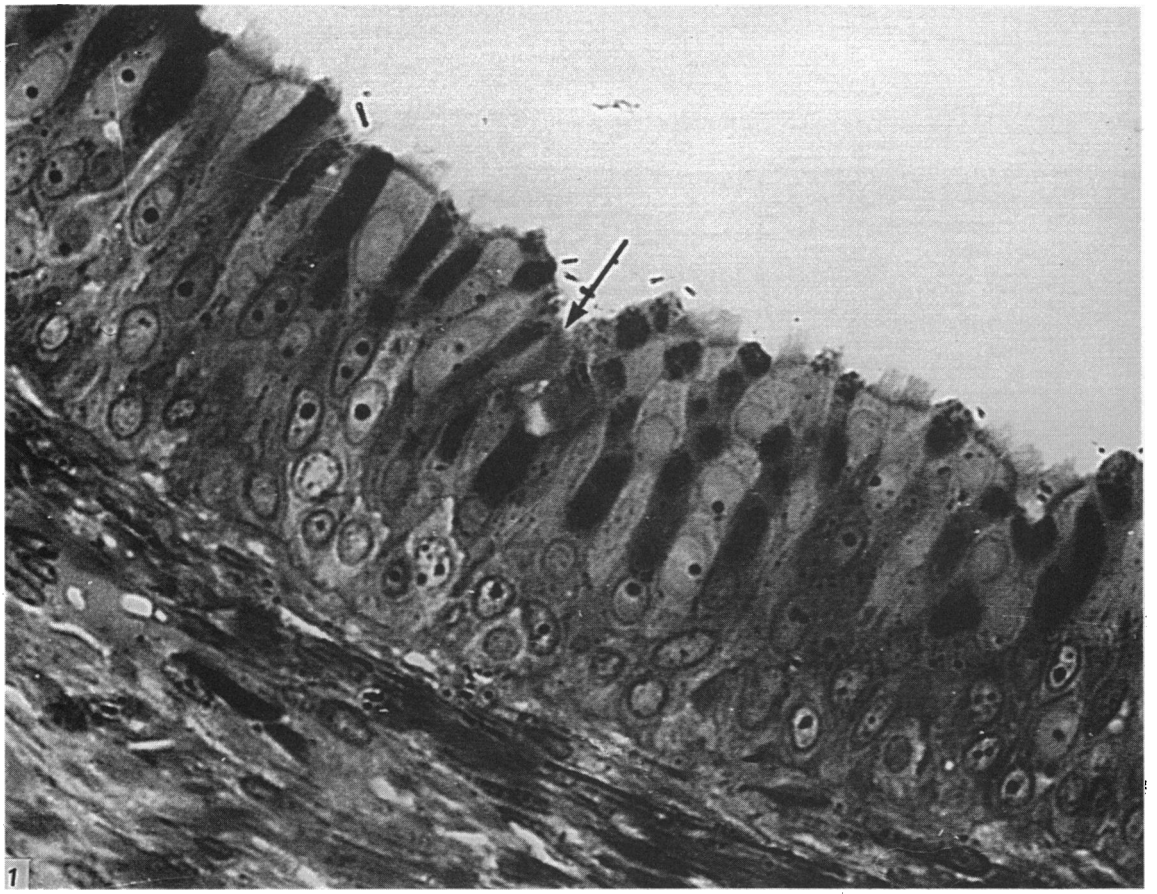


Fig. 1. Tracheal epithelium of *Testudo graeca*. Basal, ciliated and mucous cells are present. Note depression in the epithelium (arrow). Toluidine blue. × 480.

Immunocytochemistry was performed according to the PAP method (Sternberger, 1979) using rabbit antibodies to bombesin (1:10000), leu-enkephalin (1:4000), met-enkephalin (1:4000), calcitonin (1:5000) and serotonin (1:10000). Specific controls included: (1) preabsorption of the antibodies with the corresponding antigen, (2) normal serum from a non-immunised rabbit as the first layer.

Electron microscopy

Before fixation in Bouin's fluid, 1 mm thick sections were obtained at different levels of the trachea: laryngotracheal junction, superior, middle and inferior portions of the trachea and tracheal bifurcation. The samples were fixed in 2·5% glutaraldehyde, postfixed in 1% osmium tetroxide, dehydrated in acetone and embedded in Epon 812. Ultrathin sections were cut using a Reichert–Imy Ultracut ultramicrotome and stained with uranyl acetate and lead citrate. Electron microscopy was performed with a Zeiss EM/10 cR.

RESULTS

Light microscopy

Both species showed a pseudostratified columnar epithelium (Fig. 1). Three cell types were observed: basal, ciliated and mucous. In non-hibernating *Testudo graeca*,

Table 1. *Distribution of mucosubstances in tracheal epithelium of Testudo graeca and Pseudemys scripta elegans*

	PAS	A-PAS	AB pH 2.5	AB pH 1	AF	AB-PAS	M-S-AB	HID	HID-AB
Mucous cells of *Testudo graeca*	P	P	B	B	V	BP	B	N	BN
Mucous cells of *Pseudemys scripta elegans*	P	P	B	0	0	PB	B	0	B

P, PAS-positive; B, AB-positive; N, HID-positive; BP, a mixture of AB- and PAS-positive mucins with AB-positive mucins predominating; PB, a mixture of PAS-and AB-positive mucins with PAS-positive mucins predominating; BN, AB-positive predominating over HID-positive mucins; V, AF-positive; 0, negative.

abundant clear basal cells were seen; these cells were not, however, observed in hibernating *Testudo graeca* or in *Pseudemys scripta elegans*. In hibernating *Testudo graeca* marked intercellular spaces were found.

Histochemical techniques for mucosubstances enable some differences between these species to be established. Thus, mucous cells in *Testudo graeca* were positive with the techniques detecting neutral mucins, sialomucins and sulphated mucins while in *Pseudemys scripta elegans* the cells were positive only for neutral mucins and sialomucins. The results are summarised in Table 1.

Both species showed argyrophil cells diffusely distributed along the trachea (Fig. 2). The cells were located in the basal portion of the epithelium and processes were occasionally observed passing towards the lumen.

No calcitonin, bombesin, met- or leu-enkephalin-immunoreactive cells were observed; however, small serotonin-containing cells could be seen (Fig. 3).

Electron microscopy

Pseudemys scripta elegans and *Testudo graeca* showed basal, ciliated, mucous and endocrine cells (Fig. 4), corresponding to those described by light microscopy.

Both species had ciliated cells (Fig. 5) with a clear cytoplasm showing numerous electron-dense mitochondria in the apical portion. Basal bodies and cilia were similar to those found in mammals. Among the cilia, microvilli were usually present, being more frequent next to the junctional complexes. Lipid droplets could be observed in the ciliated cells of *Pseudemys scripta elegans*. Beneath the cilia, abundant small granules with a mucous-like appearance were present (Fig. 6).

The mucous cells were very electron-dense, being characterised by the secretory granules of their apical portion. Secretory granules could be seen in *Pseudemys scripta elegans* and *Testudo graeca* in different states of maturation (Fig. 7). In *Testudo graeca*, mucous granules with a dense core were frequently observed (Fig. 7). The granules coalesced and were secreted by means of a merocrine mechanism.

Basal cells were characterised by the intermediate filaments around the nucleus and by an electron-dense cytoplasm (Fig. 8). In non-hibernating specimens of *Testudo graeca*, abundant 'clear basal cells' with an electron-lucid cytoplasm were observed. These cells were not detected in hibernating animals (Fig. 9).

Endocrine cells had a typical pyramidal shape with a cytoplasmic process passing towards the lumen (Figs. 10, 11). The main morphological characteristic of the endocrine cells was the presence of basally located secretory granules with a thin halo

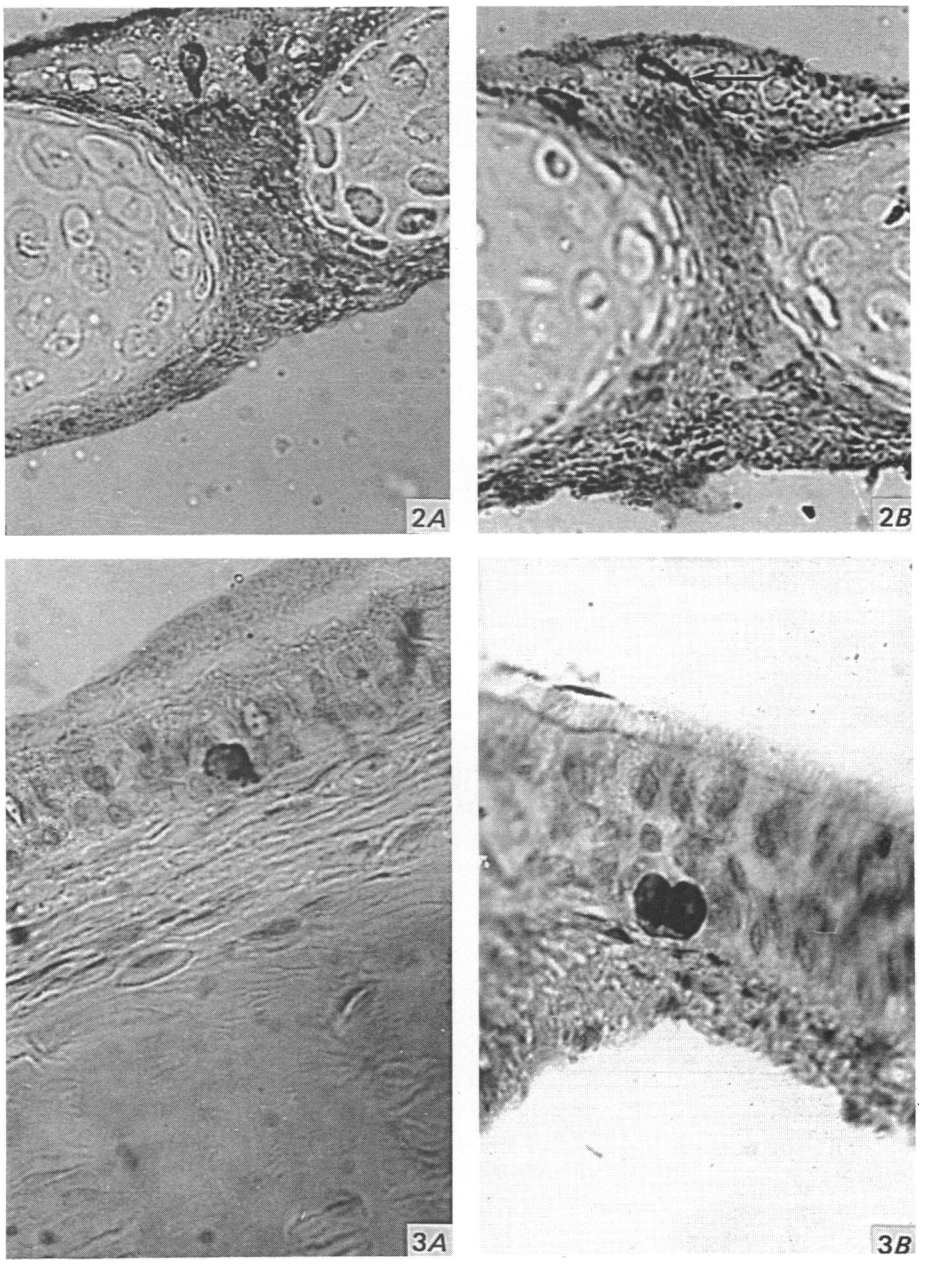


Fig. 2(*A–B*). *Pseudemys scripta elegans*. (*A*) Argyrophil cells in the tracheal epithelium. ×480. (*B*). Argyrophil cell showing a short lateral process (arrow) ×480.

Fig. 3(*A–B*). 5HT-immunoreactive cells in the tracheal epithelium. (*A*) *Pseudemys scripta elegans*. (*B*) *Testudo graeca*. ×480.

surrounding an electron-dense core. The granules were very small (mean diameter, 90–120 nm). No contacts between endocrine cells and nerve terminals could be seen.

In both species, intra-epithelial plasma cells were identified. These cells had abundant rough endoplasmic reticulum containing a granular material indicating active synthesis of immunoglobulins (Fig. 12).

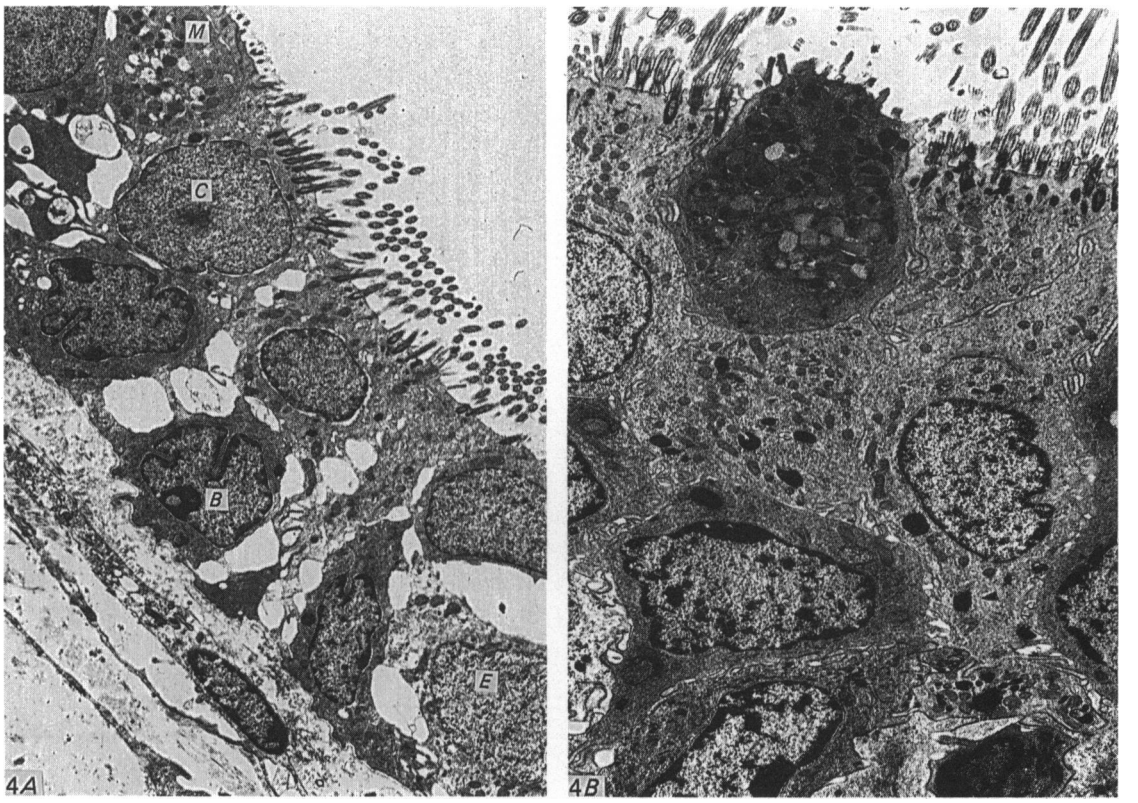


Fig. 4(*A–B*). (*A*) Hibernating *Testudo graeca*. The tracheal epithelium shows wide intercellular spaces. Four cell types are present: ciliated (*C*), mucous (*M*), basal (*B*) and endocrine (*E*). × 5000. (B) Non-hibernating *Testudo graeca*. No marked intercellular spaces are noted. × 10000.

In hibernating *Testudo graeca*, abundant myelin bodies could be observed in the epithelial cells (Fig. 13).

DISCUSSION

The tracheobronchial epithelium of the animals studied has four cell types: basal, ciliated, endocrine and mucous, having the structure typical of the respiratory epithelium.

Some morphological differences in the respiratory epithelium have been found between different species of mammals; however, no differences have been detected between the two species of turtles from distinct families and habitats. Cells currently observed in the mammalian tracheobronchial epithelium (Clara cell, serous cell, brush cell, etc.) were not found in the epithelium of these species, neither were intra-epithelial glands nor 'intermediate type cells' similar to those described in birds (Walsh & McLelland, 1974).

Regarding the trachea of other reptiles, our results differ from those of Tesik (1984) in *Lacerta vivipara* and *Lacerta agilis*. These species have a tracheal epithelium of differing thickness and stratification depending on the area (over the cartilaginous or over the membranous zones). In the animals studied, no differences were found; the epithelium, from the larynx to the extrapulmonary bronchi, had a similar structure

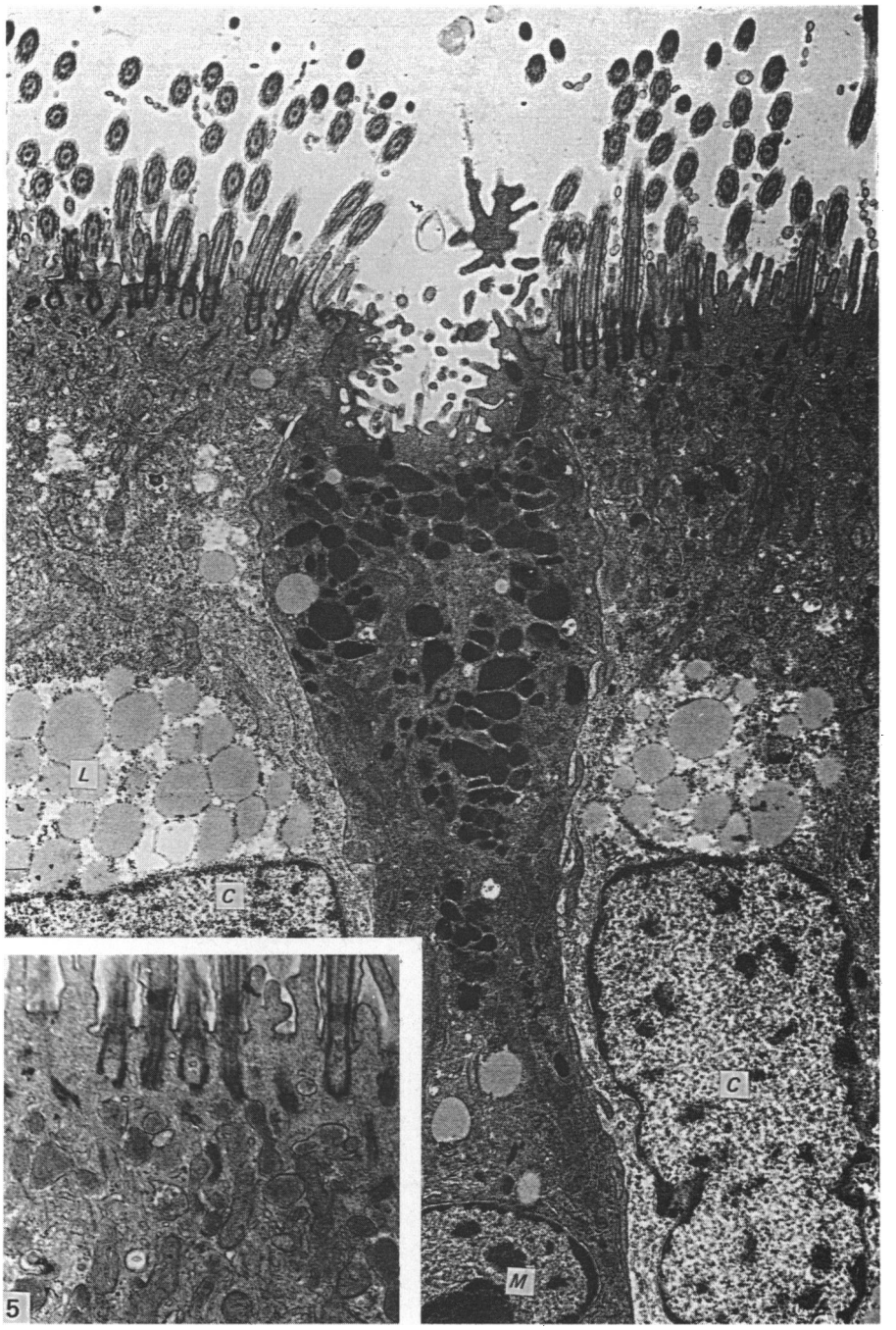


Fig. 5. Tracheal epithelium of *Pseudemys scripta elegans*. Ciliated cells (*C*) showing microvilli and lipid granules (*L*). The mucous cell (*M*) is characterised by electron-dense granules, apical microvilli and a marked electron density. × 10000. Inset shows apical pole of a ciliated cell with small dense granules of mucous appearance. × 30000.

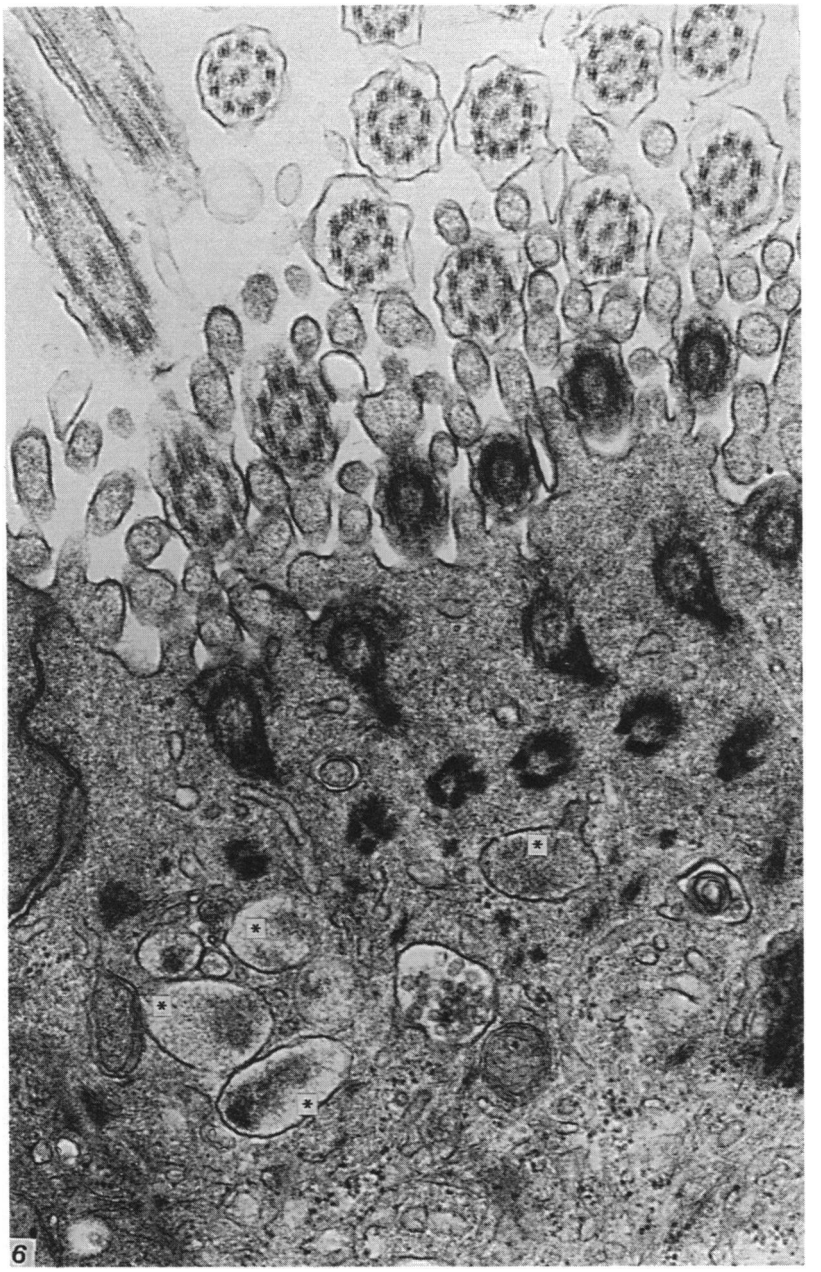


Fig. 6. Apical zone of a ciliated cell from *Pseudemys scripta elegans* showing granules of low density of mucous appearance (*). × 46 500.

with no differences between the cartilaginous and the membranous zones. Tesik (1984) observed, in addition, a cell type (the most abundant) called 'granular cells', but this cellular type was not observed in the Chelonia studied here.

Studies on mucosubstances of the respiratory tract are numerous. Mucins of mouse, rat, hamster, rabbit, dog, pig, monkey and man have been previously described (McCarthy & Reid, 1964; Spicer, Chakrin, Wardell & Kendrick, 1971; Baskerville &

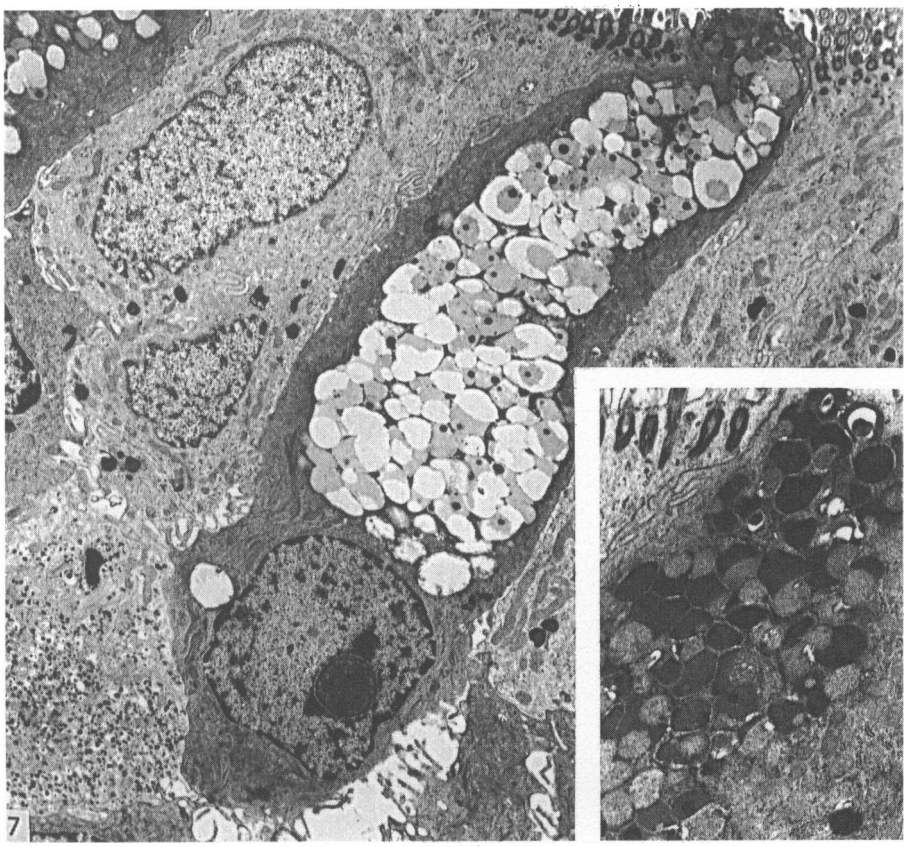
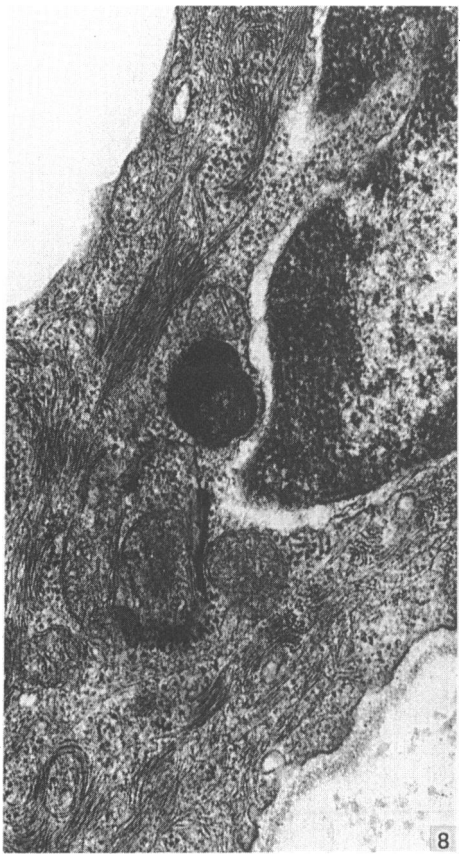


Fig. 7. Mucous cell of *Testudo graeca*. The central and apical portions of the cell are filled by mucous granules with a dense core. × 10000. Inset shows the mucous granules. Note the different electron density of the granules. × 12500.

Reid, 1975; Kennedy *et al.* 1978; Spicer, Schulte & Thomopoulos, 1983; Plopper *et al.* 1984; George, Nishio & Plopper, 1984). There are some differences (of unknown origin) between these animals; sulphated mucins are very abundant in rabbit, dog and monkey, although they are not found in the hamster (Kennedy *et al.* 1978).

Similarly, the reptiles considered in the present study had a different composition of mucosubstances in the tracheal epithelium, sulphomucins being found in *Testudo graeca*, while the tracheal cells of *Pseudemys scripta elegans* contained only sialomucins.

In the mammalian trachea, the presence of endocrine cells is well recognised (Ericson *et al.* 1972; Cutz, Chan, Wong & Conen, 1975), these being diffusely distributed throughout the trachea and having morphological similarities to the endocrine cells of lung neuro-epithelial bodies (Sonstegard, Cutz & Wong, 1976). These cells apparently contain serotonin (5HT) (Dey, Echt & Dinerstein, 1981), and secretory granules of different size and shape, depending on the species (Cutz *et al.* 1975). In the present work, we describe, for the first time, the presence of endocrine cells in the extrapulmonary airways of Chelonia. These cells are similar to those found in the neuro-epithelial bodies of the lung of *Pseudemys scripta elegans* (Sheuermann, De Groodt-Lasseel, Stilman & Meisters, 1983). The immunocytochemical technique used in this study suggests that the tracheal endocrine cells contain 5HT, as do those of the trachea of higher vertebrates (Dey *et al.* 1981).



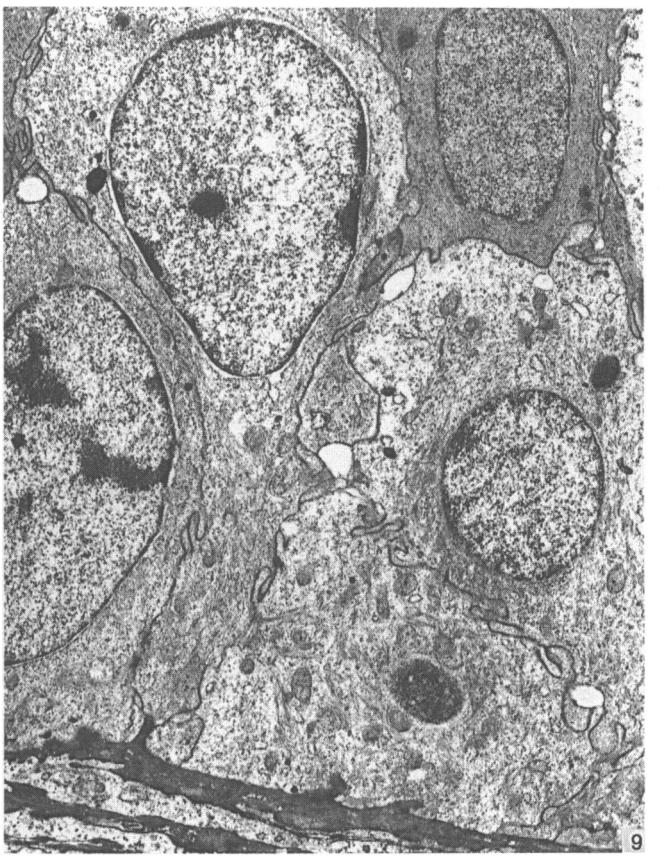


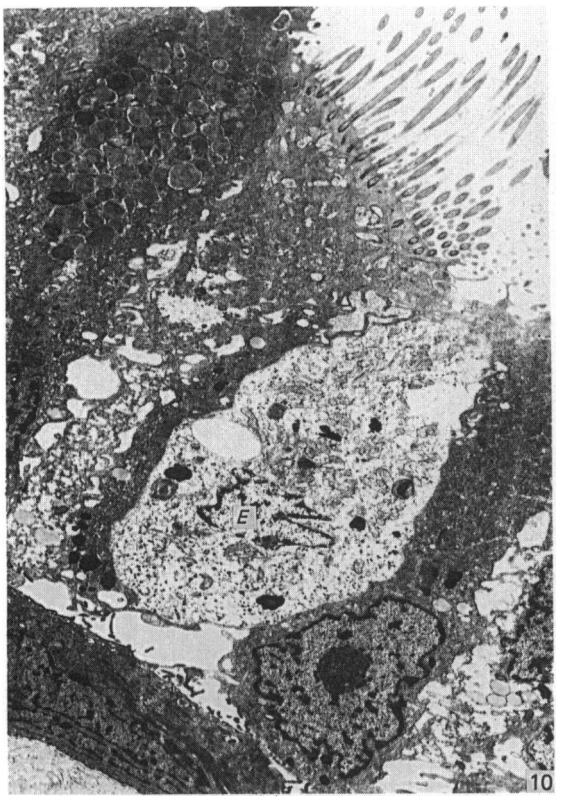
Fig. 8. Basal cell of hibernating *Testudo graeca*. The cytoplasm shows abundant free ribosomes and bundles of filaments. × 23700.

Fig. 9. Low electron-dense cells in the basal portion of the tracheal epithelium of non-hibernating *Testudo graeca*. × 12000.

The tracheobronchial lamina propria of mammals usually has abundant lymphocytes and plasma cells. These have not been observed in the turtles studied. The presence of intra-epithelial plasma cells suggests a primitive system of immune defence.

As distinct from the non-hibernating state, when hibernation occurs the following characteristics in the tracheal epithelium of *Testudo graeca* were noted:
(1) No clear basal cells were found, possibly because of a decrease in the regeneration of the epithelium, (Breeze & Weeldon, 1977). (2) The junctions and foldings between the epithelial cells were fewer. A similar finding has been described by Rhodin (1966) and Wilson *et al.* (1984) in higher vertebrates. These authors suggest that this may be due to the increase in the exchange of fluids between the epithelium and the lumen. (3) Abundant myelin bodies appeared in the epithelial cells, probably due to autolytic processes during hibernation, as noted by Geuze (1971) in the gastro-intestinal tract of *Rana esculenta*.

In conclusion, the trachea of *Testudo graeca* and of *Pseudemys scripta elegans* has a similar structure to that of mammals and differs from the reptiles so far studied.



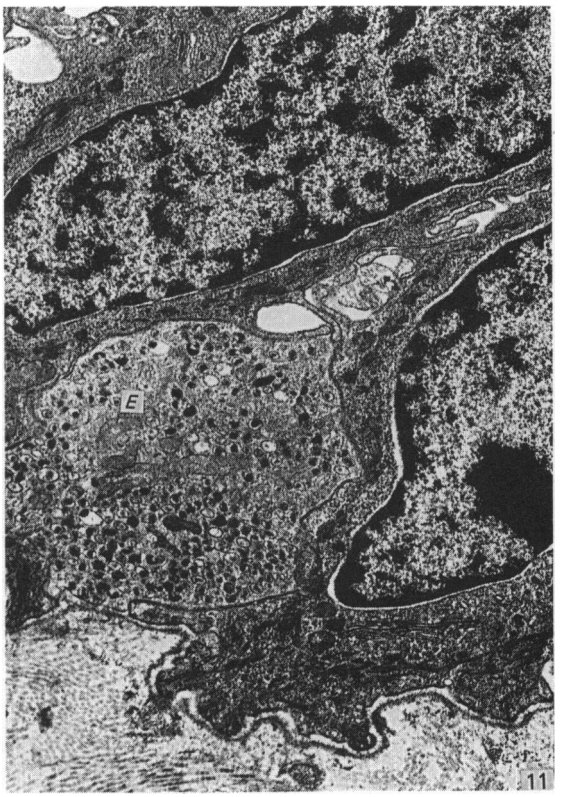


Fig. 10. *Pseudemys scripta elegans*. Endocrine cell (*E*) with an apical prolongation towards the tracheal lumen. × 6000.

Fig. 11. Portion of an endocrine cell (*E*) in the basal zone of the tracheal epithelium of *Testudo graeca*. × 8000.

SUMMARY

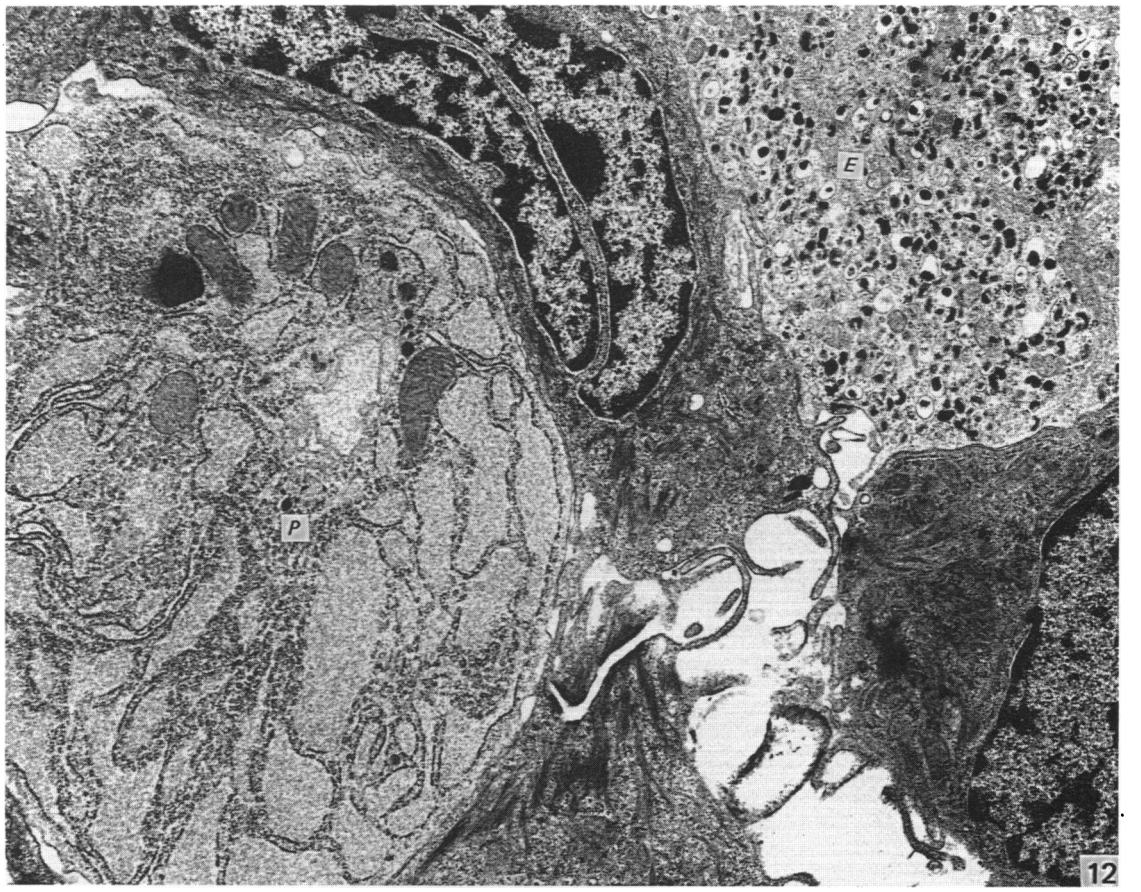
The tracheal epithelium of *Testudo graeca* and *Pseudemys scripta elegans* was studied by means of light and electron microscopy, histochemistry and immunocytochemistry.

Three cell types were detected by conventional light microscopy: mucous, ciliated and basal. The Grimelius silver argyrophil technique was positive in a population of tracheal cells. By immunocytochemistry, serotonin-containing cells were identified. The mucous cells of *Testudo graeca* contained sialomucins and sulphomucins; however, only sialomucins were detected in *Pseudemys scripta elegans*.

By electron microscopy four cell types were observed: mucous, ciliated, basal and endocrine. Plasma cells were also found. The differences between the species studied lay mainly in the ultrastructure of the ciliated cells, the mucous granules and the presence of a special type of basal cell called 'clear basal cells' in non-hibernating specimens of *Testudo graeca*.

During hibernation, the tracheal epithelium of *Testudo graeca* showed the following changes: (1) Myelin bodies were present in the cytoplasm. (2) The intercellular spaces were remarkably widened. (3) No 'clear basal cells' were present.

In conclusion, the tracheal epithelium of the reptiles studied showed a pattern similar to that described in mammals but some differences from reptiles previously studied were found.



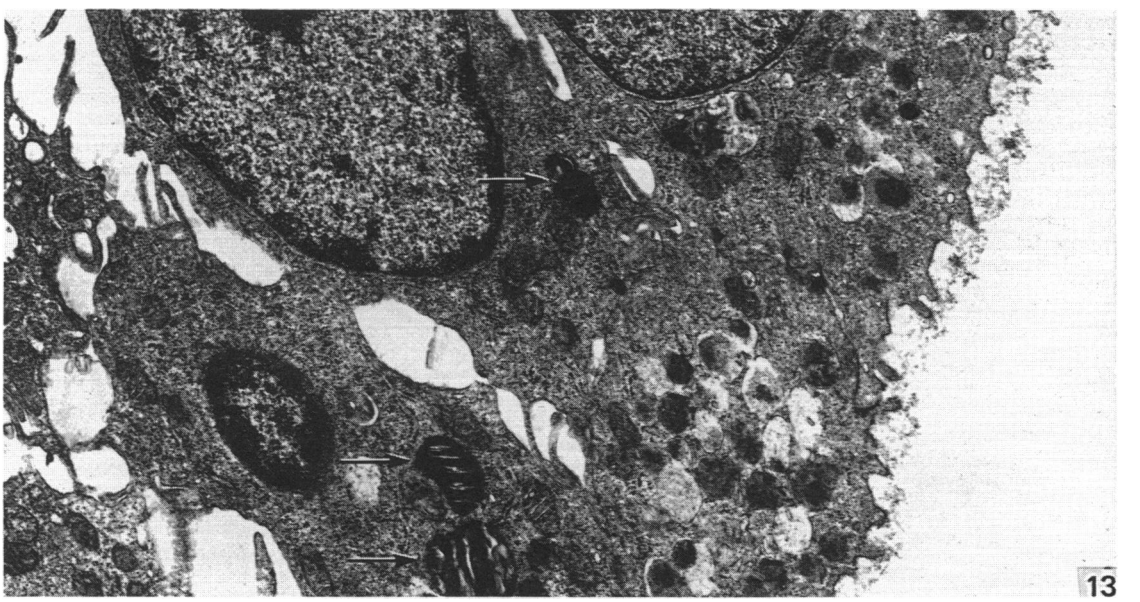


Fig. 12. *Testudo graeca*. Plasma cell (*P*) with distended cisternae of endoplasmic reticulum. A portion of an endocrine cell (*E*) is also shown. × 10000.

Fig. 13. Mucous cells in the trachea of hibernating *Testudo graeca*. Several myelin bodies (arrows) are noted in the cytoplasm. × 12000.

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