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Cilia in the porcine bile ductule: motile or sensory?

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Summary. Oligociliated epithelial cells or cells with a solitary cilium were observed lining hepatic bile ductules in pigs. The cilia were situated in the midst of microvilli, and arose from a basal body that was located in the vicinity of the free surface of the epithelium. The axonemal pattern revealed in transverse sections of the cilia was 7+1, 8+1, 8+2 or 9+0. Although devoid of the classical axoneme pattern, we assume some of the cilia to be motile, and other to be sensory structures that would assist bile formation and secretion.

Key words: Liver ultrastructure, Oligociliated cells, Solitary cilium, Bile ductule, Porcine

Introduction

Oligociliated cells occur in many locations in vertebrates, for instance, in rat articular chondrocytes (Vidinov and Vasilev, 1985), and intrahepatic bile ductules of rats (Tansy et al., 1977). Similarly, solitary cilia are present on epithelial cells including intrahepatic bile ducts, rete testes, intercalated ducts of the pancreas (Fawcett, 1981).

Kinocilia are found on the surface of many fixed epithelial cells, for example, on tracheal cells. In such a locality these structures aid in the movement of liquid (mucus) and small particles along the cells lining the airways (Darnell et al., 1990). Another example of a propulsion function was reported by Tansy et al. (1977) where cilia in the bile ductules of the rat play an important role in the movement of bile. Ohata et al. (1982) proposed that solitary cilia in avian intrahepatic biliary ducts have a sensory function which detects «mechanical impulses induced by alteration of the bile flow and chemical and physicochemcial changes in the bile passing through the ductule». Indeed, many sensory endings including those specialized for light and sound transductions, are derived from solitary cilium.

The object of this report is to provide evidence for the occurrence, and detailed ultrastructure of cilia in the hepatic bile ductules of the pigs.

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Materials and methods

Animals

Twenty, 3-month-old, Yorkshire pigs, the same animals as were used by Shahidi (1983) for a study on the effects of fatty diets on the liver, were utilized in this work.

Electron microscopy

The animals were euthanized by exsanguination preceded by stunning. Samples, 2-3 mm^3 from the left lateral, the largest lobe of the liver, were harvested and fixed in 2.0% buffered (0.1M phosphate buffer; pH 7.3) glutaraldehyde, overnight. The samples were washed in several changes of buffer, and postfixed for 1 hour in 2% osmium tetroxide and dehydrated in ascending grades of ethanol. The samples were transferred to a solution of propylene oxide, propylene oxide and Epon, and then to Epon. The liver specimens and Epon were placed in gelatin capsules and left in an oven at 60 °C, overnight. Further details of the sample processing are included in a symposium paper (Singh and Shahidi, 1986).

Semithin sections (ca. 1 μm) were obtained using glass knives on a Sorvall ultramicrotome (MT2B model) and stained with toluidine blue on glass slides. Favourable areas were selected for ultrastructural analysis by examining up to 10 specimens from each animal. Thin sections were cut on an ultramicrotome and contrasted with uranyl acetate and lead citrate, and examined and photographed in a Jeol Electron Microscope (JEM-100 S) at 80 kV. Photomicrographs were printed on multigrade Ilford photographic paper.

Morphometry

Measurements on the cilia were made by a nomogram developed by Ghadially et al. (1981). In this procedure, size of the object is determined by measuring the image size of an object on an electronmicrograph at a known magnification, and calculating the object size

with a nomogram.

Results

Solitary and oligociliated cells were observed in the bile ductules of pigs. The cilia were situated amongst the microvilli present on the epithelium (Figs. 1, 2). The cilia were considerably longer in length than the microvilli (Fig. 2) and were easily distinguishable. Each cilium that could be traced back to its cell of origin was seen to arise from a basal body located close to the free surface of the epithelium as illustrated in Fig. 1. There was a basal foot extending from the basal body (fig. 1). The axoneme was composed of central and peripheral microtubules (Fig. 3). A 7+1, 8+1, 8+2 or 9+0 axonemal pattern was revealed in the transverse sections of round or ovoid cilia profiles. The average diameter of the cilia was calculated to be 0.3 μm (range 0.25-0.40 μm). It was

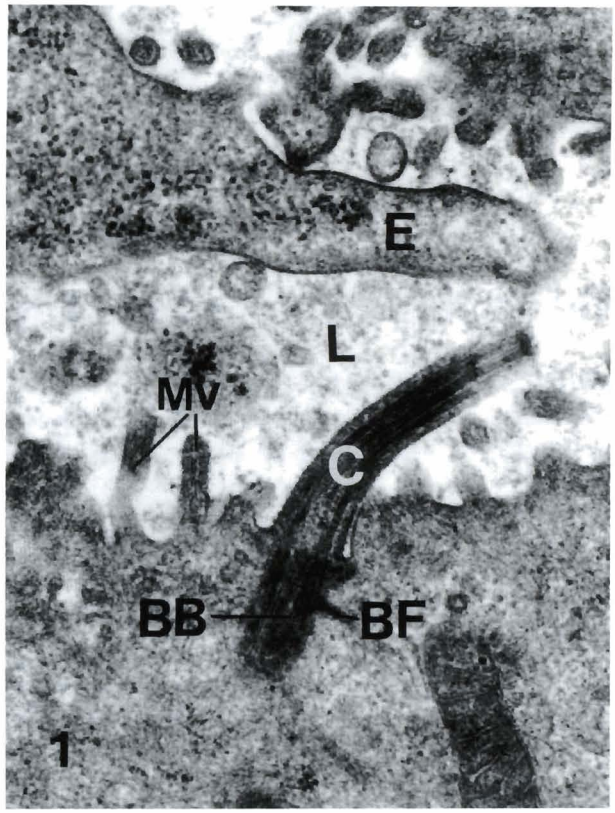

Fig. 1. Profile of a solitary cilium (C), sectioned obliquely, is illustrated amongst the microvilli (MV) in a hepatic ductule lumen (L). E: portion of a ductule epithelial cell; B: basal body; BF: basal foot. x 30,000

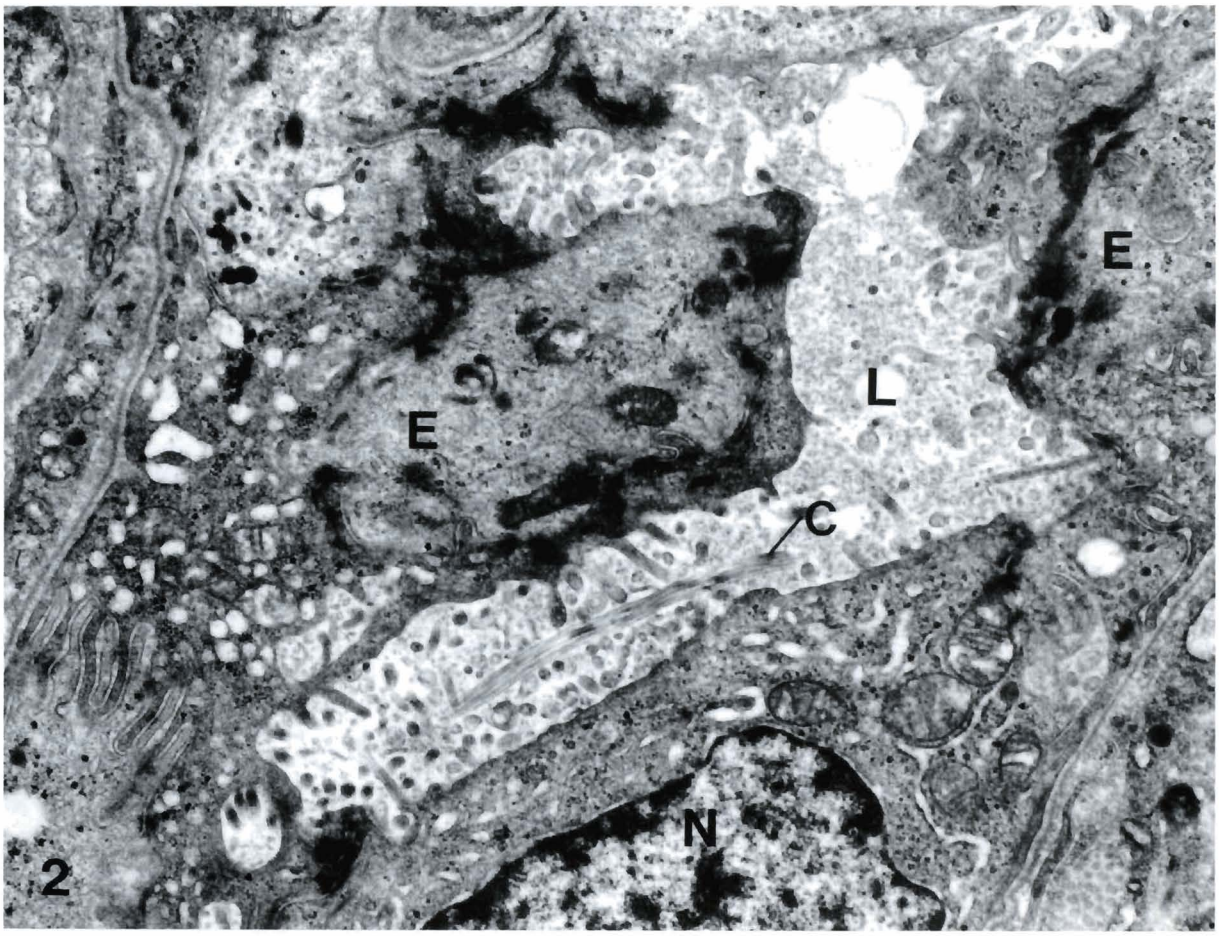

Fig. 2. Solitary cilium (C) is seen in a longitudinal section in the midst of numerous microvilli. E: portion of ductule epithelium; L: ductule lumen; N: portion of the epithelial cell nucleus. x 15,000

not uncommon, by way of frequency, to detect the ciliated epithelial cells.

Discussion

Occurrence of oligociliated cells in the bile ductule of porcine liver is reported the first time in the present study. The cilia were situated in the midst of short microvilli, and were seen to arise from a basal body, with a basal foot extending from it that was located located near the free surface of the epithelium. The axonemal pattern revealed in transverse sections of the cilia was 7+1, 8+1, 8+2 or 9+0. Ross and Romrell (1989) stated that there may be several hundred cilia located on a ciliated cell. In our study either a single (solitary ciliated) or a few (oligociliated) cells were revealed. The ultrastructure of classical kinocilia has been well documented (Fawcett, 1981, 1994; Afzelius, 1983; Griepp and Robbins, 1988).

Classical cilia are 6-10 μm long processes that extend from cells (Fawcett, 1981). The central portion of a cilium is the axoneme with a 9+2 configuration, 9 represents doublet microtubules situated around the periphery and 2 represents the two centrally located microtubules (Afzelius, 1983; Griepp and Robbins, 1988; Fawcett, 1994). Cilia described in our study were not the classical type; morphometrically speaking, the average diameter of these structures was 0.3 μm which is similar to that of a kinocilium. It was only with the presence of a 9+2 axonemal pattern that cilia were considered motile (Odor and Blandau, 1985; Griepp and Robbins, 1988). However, Odor and Blandau (1985) observed single cilia that were beating on monolayers of cultured oviductal epithelium from early postnatal pigs. These cilia had an axonemal pattern other than the classical pattern, some of which were 9+0, 8+1 or 7+2. We suggest that the porcine bile ductule cilia may be motile since some of the transverse section images of the cilia in the present work demonstrated a 9+0 or 8+1 pattern.

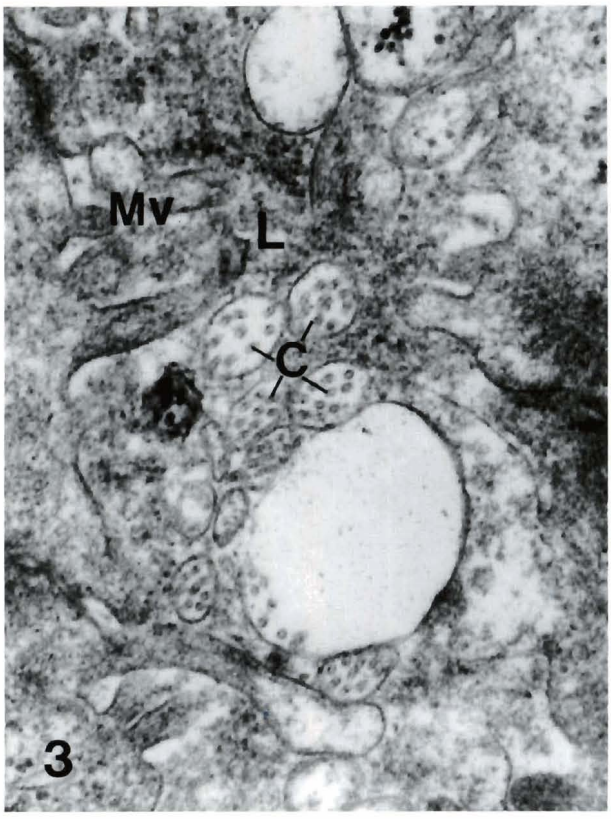

Fig. 3. Several profiles of cilia (C), cut transversely, are situated next to microvilli (Mv). Various axonemal microtubule patterns are depicted in the profiles. L: ductule lumen. x 40,000

When viewed in transverse section the apex of the respiratory cilium is oval.

Approximately 0.50 μm below the apex peripheral microtubules begin to exist as doublets. This change occurs at what is referred to as the transformation zone (Rautiainen et al., 1984). Images of some cilia seen in Fig. 3 in the present study were sectioned at the transformation zone since a doublet configuration of microtubules was depicted in the axoneme profiles. Often a basal foot is observed extending from the basal body (Ohata et al., 1982; Afzelius, 1983; Odor and Blandau, 1985; Griepp and Robbins, 1988), as demonstrated in the present work (Fig. 1).

Cilia tend to have differing functions depending on their location. Oligociliated cells occur in many locations in vertebrates, for example, on rat articular chondrocytes (Vidinov and Vasilev, 1985), intrahepatic bile ductules of rats (Tansy et al., 1977) and pigs (Shahidi, 1983). Epithelial cells including those of intrahepatic bile ducts, rete testes, intercalated ducts of the pancreas (Fawcett, 1981), oviducts (Odor and Blandau, 1985), osteocytes (Federman and Nichols, 1974) and biliary ducts of some avian species (Ohata et al., 1982) have single cilium. If cilia in the osteocytes are motile, this could possibly explain the fast flowing of extracellular fluid through Haversian system canaliculi (Federman and Nichols, 1974). Cilia are also located in various «excretory» ducts such as the rete testis, the intercalated ducts of the pancreas and intrahepatic bile ducts. It is speculated that the function of the solitary cilium found in these locations is to cause agitation of fluid in the excretory ducts (Fawcett, 1981). Tansy et al. (1977) contemplated that in rat these cilia may be important in the movement of bile, and suggested that these processes may aid in the secretion, absorption and perhaps even the propulsion of the bile. The solitary cilium in the avian intrahepatic biliary duct was thought to have a sensory function where it detects changes in the flow of the bile (Ohata et al., 1982). Both kino- and sensory cilium types have been noted by researchers including Fawcett and Porter (1954), Ohata et al. (1982) and Moran and Rowley (1983). Taking into account the earlier findings and our present observations, we assume that cilia that are present in the porcine bile ductules may serve a dual

purpose; the motility may be involved in the transport of bile, and these cilia may also function as sensory structures and aid in the formation and secretion of bile.

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