CILIA AND VESICULAR PARTICLES
IN THE ENDOCRINE PANCREAS
OF THE MONGOLIAN GERBIL

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ABSTRACT
Though the general appearance and the cellular composition of the pancreatic islets of the Mongolian gerbil (Meriones unguiculatus) conformed to those of most other rodent species, some peculiar ultrastructural details were found. Thus there were diversiform, mainly vesicular particles with varying electron opacity in these islets. The vesicular particles showed a clear association to cilia which seemed to possess a basic fiber pattern of 9 + 0. The basal bodies were localized in the cytoplasm of the islet parenchymal cells, most often in the β-cells, and the vesicular particles occurred in the portions of cilia that were protruding into intercellular spaces. The cilia were often swollen, and the vesicular particles were mainly found in the space between the ciliary membranes and the longitudinal fibers. A few vesicular particles could be seen inside and sometimes seemingly in contact with these fibers. Occasionally, there were morphologically similar structures in the cytoplasm of adjacent β-cells. The vesicular particles were differentiated from the vesicles occurring in nerve structures by their larger size, as well as by their heterogeneous shape and electron opacity. The nature of the vesicular particles and the significance of their presence in cilia and in the cytoplasm of some of the islet cells remain unknown. Among other possibilities, it is, however, suggested that the vesicular particles may represent secretory material.

INTRODUCTION
The Mongolian gerbil (Meriones unguiculatus) is a rodent species that is becoming increasingly used in various fields of current research (17). Because another member of the subfamily Gerbillinae with similar natural habitat, the sand rat (Psammomys obesus), has been found to develop diabetes mellitus (12) and morphological alterations of the pancreatic islet cells (11, 13), my intention was to find out whether the endocrine pancreas of the Mongolian gerbil offered some features of interest for diabetes research. In a pilot morphological study, it was soon observed that, although the light microscope picture of its pancreatic islet cells essentially conformed to that of other rodents (3), the fine structure of its endocrine pancreas showed some unusual characteristics. The most conspicuous of these were the frequent occurrence of ciliated parenchymal cells and the apparent association between the cilia and vesicular structures with peculiar appearance. Cilia have been found in many organs and cells in which their presence is unexpected and their function is unclear. In previous communications from this laboratory (4, 6), it was stated that, although cilia in endocrine cells might play some role for cell renewal or might be rudimentary structures, their significance remained dubious. This prompted a more detailed study of the islet parenchyma of the Mongolian gerbil, with particular attention to cilia and vesicular structures.

To the best of my knowledge, there are no previous reports on the pancreatic islet morphology...
of the Mongolian gerbil. The adenohypophysis of this species is known to contain ciliated cells with unknown significance (14). Any association between these cilia and vesicles has, however, not been reported.

**MATERIALS AND METHODS**

The study was performed on 23 adult healthy Mongolian gerbils (*Meriones unguiculatus*). These animals were of both sexes and at an age of 3-19 months. They were kept on a standard laboratory diet (AB Ewos, Södertälje, Sweden) and drinking water ad lib.

The following ultrastructural procedures were used. The animals were sacrificed, and specimens were taken from the pancreas and fixed by immersion in 1% osmium tetroxide in 0.34 M Veronal acetate buffer adjusted to pH 7.2-7.4. After fixation, the specimens were rinsed, dehydrated with ethanol, and embedded in Epon 812. For trimming the blocks and for identification of the islets, adjacent thick (1 μ) sections were stained with toluidine blue and examined under a light microscope. The sections were cut on an LKB Ultrotome III and stained with uranyl acetate and lead citrate prior to examination in a Siemens Elmiskop IA and/or 101.

**RESULTS**

The pancreatic islets were composed of β-cells situated in the central portion and of α1- and α2-cells localized peripherally. Occasional cells without granules were intermingled among the other cells. Mitotic figures were not observed.

The interstitial spaces between the islet parenchymal cells, mainly those situated between the β-cells, were often dilated and contained numerous small particles (Fig. 1). In addition to these particles, whole cilia or remnants of cilia occurred interstitially. Many ciliary structures could be seen close to each other and close to the small particles (Fig. 2).

The small particles were mainly of vesicular nature and were tentatively called vesicular particles (Fig. 3). Their size varied considerably. Most of them were round, oval, elongated, or completely irregular, whereas a few possessed semilunar or annular shape. Small vesicles arranged in a circular fashion were also found. The interior of the vesicular particles was either electron translucent or more or less electron opaque,

![Figure 1](image-url) Intercellular area between pancreatic islet β-cells of Mongolian gerbil, showing vesicular particles (V) of varying size and shape. Some of these particles have an electron-translucent interior, whereas others are electron opaque in the central part. Close to the vesicular particles are fibers (F) which seem to be of ciliary nature. In the β-cells are a few secretory granules (g). X 24,500.
and the electron opacity was either homogeneous or varying. The electron-opaque portions comprised the whole or only part of the space limited by the vesicular membranes. Rather seldom was there an electron-opaque central core with an electron-translucent halo between this core and the vesicular membrane. Such configurations were reminiscent of secretory granules in endocrine cells. Membranes and/or minute vesicles could be seen within the vesicular particles.

As mentioned above, there was a close spatial relationship between vesicular particles and cilia. The basic fiber pattern of the cilia seemed to be 9 + 0. Their basal bodies were located in the cytoplasm of the endocrine cells, often near the surface. The cilia protruded for a shorter (Fig. 4) or longer (Fig. 5) distance into intercellular spaces. The portions that were situated outside the cells were often swollen and exhibited a ground substance with low electron opacity. Within the intercellularly localized cilia, vesicular particles were diffusely distributed, often in large number, between the membranes and the central longitudinal fibers. There were no clear connections between these particles and the ciliary membranes. Some vesicular particles were found inside the longitudinal fibers (Figs. 6 and 7), and a few seemed to be connected with them (Fig. 8). Small elements with vesicular appearance were occasionally seen in the interior of the basal bodies (Fig. 9). Whether these elements were of the same nature as the vesicular particles was difficult to clarify.

In the interstitial spaces there were nerve structures. The vesicular particles differed from the vesicles in the nerve endings, mainly in that the latter were smaller and rather homogeneous in shape, size, and electron opacity (Figs. 10 and 11).

Structures morphologically similar to the vesicu-
lar particles were recorded in the cytoplasm of some β-cells, either as diffusely scattered (Fig. 12) or localized (Fig. 13) bodies. These were tentatively called intracytoplasmic vesicular particles. Sometimes they occurred close to fibrillar material or endoplasmic reticulum that, at least partly, seemed to be of agranular type. Infrequently, they appeared within bi- or trilamellar membranes possessing moderately electron-opaque interspaces (Fig. 14). Any clear association between intracytoplasmic vesicular particles and one or more cytoplasmic organelles was, however, not found.

When it was possible to determine their cellular origin, the cilia in the presently investigated animals most often occurred in β-cells, rather seldom in α1-cells, and only infrequently in α2-cells. Cilia with associated vesicular particles were recorded in β-cells and seldom in α1-cells, whereas no vesicular particles were seen within the few cilia that were observed in α2-cells. Intracytoplasmic vesicular particles were only found in β-cells. Occasionally, β-cells with cilia and/or vesicular particles contained intranuclear rods (5).

**DISCUSSION**

The association between the vesicular particles and cilia was substantiated by the occurrence of these particles in the ground substance of cilia, as well as the close spatial relationship and possible connections between them and ciliary fibers. Whether the structures with vesicular appearance that sometimes were seen in the central part of the intercellular space between islet β-cells, showing vesicular particles with varying size, shape, and electron opacity; some of them are annular; others contain membranes or smaller vesicles. A few fibrous structures can also be seen. X 33,000.
Figure 4  Part of islet β-cell containing typical secretory granules (g) and a cilium (C) protruding into an intercellular space. The part of the cilium that is situated outside the cell is swollen and contains vesicular particles (V). × 50,000.

Figure 5  Part of islet β-cell showing a cilium (C) with its basal body localized close to the cell surface. The cilium that protrudes into an intercellular space is swollen. The connections between the ciliary membrane and the cell membrane are clearly seen. In the cilium between the longitudinal fibers and the membrane are vesicular particles. × 50,000.
Figure 6 Interstitial area between islet $\beta$-cells, demonstrating a swollen cilium with a longitudinal section of its basal body situated close to the surface of one $\beta$-cell. The cilium is studded with vesicular particles that also occur centrally to the longitudinal fibers at the base (arrow). $\times$ 35,000.

Figure 7 Interstitial space in an islet, showing a swollen cilium with vesicular particles, some of which are arranged in a circular fashion. The cilium with its fibers is sectioned transversely. At least one vesicular particle is seen centrally to these fibers (arrow). $\times$ 36,500.
Figure 8. Islet ß-cells with typical secretory granules. In the interstitial spaces are more or less easily distinguishable ciliary fibers (F) and vesicular particles (V). Inset: higher magnification of transverse section of one of the cilia with two vesicular particles seemingly in contact with the longitudinal fibers. × 24,000. Inset, × 74,000.

Figure 9. Basal body (b) and basal portion of cillum (C) with distinct membranes in an islet ß-cell. In the interior of the basal body are a few small structures with vesicular appearance. × 53,000.

Figure 10. Intercellular area in an islet. Nerve ending (N) has vesicles that, compared with the neighboring vesicular particles (V), are smaller and rather homogeneous in shape and electron opacity. × 17,500.

Figure 11. Another intercellular area in an islet, demonstrating membrane-bounded vesicular particles (V), a nerve ending (N), and unmyelinated nerve fibers (nf). The structural differences between the vesicular particles and the nerve structures are evident. × 19,000.
**Figure 12** Portions of islet β-cells; in one of these are cytoplasmic structures (CV) which are morphologically similar to vesicular particles. In the neighboring interstitial space are membrane-bounded vesicular particles (V). × 33,500.

**Figure 13** Islet β-cell containing a localized collection of structures (CV) which are morphologically similar to vesicular particles. Close to these cytoplasmic particles, fibrillar material (to the left) and agranular endoplasmic reticulum (to the right) can be seen. In the interstitial spaces vesicular particles (V) and ciliary fibers (F) occur. × 34,000.
basal bodies were of the same nature as the vesicular particles was not possible to determine with certainty, but this remains a possibility. The vesicular structures that were present in the cytoplasm of some β-cells showed structural similarities to the vesicular particles and may be identical to these. If so, it can be speculated that these structures represent secretory material formed in endocrine cells, from which they are transported to cilia that assume a swollen appearance and possibly subsequently rupture. On the other hand, the vesicular particles may represent material that is resorbed from the interstitial spaces and is transported in the opposite direction. Although the vesicular particles may be secreted or resorbed elements, it cannot be excluded that they are formed in loco and are stationary in cilia and cytoplasm, respectively.

Whether the vesicular particles are transported (secreted or resorbed) or not, the present study gives no definite suggestion as to their nature. Inasmuch as some of them bear morphological resemblance to secretory granules, e.g. in endocrine cells, they may be the structural counterpart of some biochemical agent. The fact that they, by morphological criteria, could be differentiated from the vesicles occurring in nerve endings seems not to preclude the possibility that they are of neurosecretory nature. Furthermore, the vesicular particles may represent cellular organelles, degenerated or not. Their rather large size and diversiform shape speak possibly in favor of the latter supposition.

Contrary to the findings in the Chinese hamster (4) where cilia of 9 + 2 type were recorded in the islet β-cells, the Mongolian gerbil was found to possess cilia probably of 9 + 0 type (with or without vesicular particles) also in the α1- and α2-cells.
Vesicular particles were not observed in the cilia of the Chinese hamster. It seems, thus, that the distribution and possibly also the significance of cilia in the endocrine pancreas vary in different species. The frequency of cilia in the pancreas of the Chinese hamster appeared to be higher in states of regeneration. Studies on the pancreas of duct-ligated rats have, however, not disclosed any obvious increase of ciliated cells, though there was evidence of neoformation of endocrine cells (7, 10). Obvious signs of islet cell neoformation were not found in the presently investigated animals. This further supports the supposition of the existence of species differences related to the occurrence and significance of ciliated endocrine cells. Previously, it has been suggested that cilia in endocrine cells have chemoreceptor (13), sensory (2, 18), or motile (8) abilities. They have further been proposed to be nonfunctioning rudimentary structures (9). Modified bulbous cilia containing minute, apparently rather homogeneous vesicles have been observed in the crown cells of saccus vasculosus of fishes (1, 16). These cilia have been thought to have a secretory function (1). The present finding of diversiform vesicular particles in association with cilia gives no reason to believe that the latter are rudimentary structures or have motile properties.

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