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Invited Review

The glomerular peripolar cell: a review

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Summary. There is now morphological evidence from several species that the peripolar cell is a distinctive glomerular cell which may have a secretory function, although a secretory product has not been identified. Peripolar cells, like other glomerular epithelial cells, probably absorb plasma proteins from the glomerular filtrate. Peripolar cells may participate in regulation of sodium balance and the changes in renal function which occur at the time of birth. They are ideally situated to monitor the composition of the glomerular filtrate and/or the calibre of the glomerular arterioles. The relationship between peripolar cells and other granulated glomerular epithelial cells must be clarified, however their morphology and unique anatomical site is suggestive of a specialised function.

Key words: Kidney, Glomerulus, Peripolar cell

Introduction

In 1979, Ryan described the granulated peripolar cell at the vascular pole of the sheep glomerulus (Ryan et al., 1979). It was suggested that the peripolar cell may be a secretory cell which secretes into the glomerular filtrate and may be part of the juxtaglomerular apparatus (JGA). This has not been universally accepted however, largely because other glomerular epithelial cells become granulated in some human and experimental discases. The purpose of this paper is to review the evidence that the peripolar cell is indeed a unique glomerular cell.

Anatomy of the peripolar cell

Light microscopy

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Peripolar cells are identified by their intracytoplasmic granules and their position in the reflection of Bowman's capsule at the vascular pole, where they are interposed between the visceral and parietal epithelial cells (Ryan et al., 1979) (Figs. 1-3). The granules stain positively with toluidine blue, purple with aldehyde fuchsin and Bowie's stain, usually red but occasionally blue with Lendrum's martius scarlet blue and magenta with the periodic acid-Schiff technique (Ryan et al., 1979; Gardiner and Lindop, 1985). Peripolar cells and the renin-containing cells of the JGA are often separated only by the basement membrane of Bowman's capsule (Gardiner and Lindop, 1985), but with care it is possible to distinguish the two. Peripolar cells are prominent and numerous in sheep (Fig. 2) but are present in smaller numbers in almost all other mammals studied (Gall et al., 1986; Mbassa, 1989) including humans (Gardiner and Lindop, 1985) (Fig. 3). Peripolar cells have also been identified in chickens (Morild et al., 1988), amphibians (Hanner and Ryan, 1980) and in elasmobranch fish (Lacy and Reale, 1989). Peripolar cells appear to be most prominent in species which have sparse renin-containing cells (Ryan et al., 1982).

Examination of serial sections of individual glomeruli is a reliable method of demonstrating peripolar cells (Gardiner and Lindop, 1985; Morild et al., 1988). We have found that 65% (range 20-100%) of sheep glomeruli contain at least one peripolar cell and some may contain up to 6 (Kelly et al., 1990). In sheep, peripolar cells are seen in average of 12% of glomeruli in a random histological section (Gall et al., 1986). There is wide variation in numbers of peripolar cells not only between apparently normal animals of the same species but also between glomeruli in the same kidney. In many animals, peripolar cells are sparse and difficult to find. In the normal parts of human nephrectomy specimens, granular peripolar cells were found in only 12% (range 3-28% of serially-sectioned glomeruli (Gardiner and Lindop, 1985). In the human kidney a maximum of two

peripolar cells are present in each glomerulus. However a random section of normal human kidney is unlikely to contain a single peripolar cell.

Transmission electron microscopy

In all species, the peripolar cell rests on the basement membrane of Bowman's capsule between the parietal and visceral glomerular epithelium with its free surface exposed to the urinary space (Fig. 4). Peripolar cells form junctional complexes with visceral and parietal epithelial cells and, where present, other adjacent peripolar cells (Ryan et al., 1982; Gardiner et al., 1986). In humans the peripolar cell may partly overlie adjacent parietal epithelial cells (Fig. 4). The peripolar cell contains the organelles associated with the synthesis and secretion of protein namely rough endoplasmic reticulum, Golgi apparatus, free ribosomes, and microtubules. In our experience however these organelles are rarely well-developed in cells with conspicuous granules. Peripolar cells sometimes have surface microvilli and single cilia (Ryan et al., 1982).

The intracytoplasmic granules are generally round but occasionally have a more irregular shape (Fig. 4). There is a wide variation in size; they measure 100-2000 nm in diameter in most species but they may be as large as 4000 nm in the axolotl (Hanner and Ryan, 1980) and newborn lamb (Mitchell et al., 1972). The granules are membrane-bound and some granules contain small vesicles adjacent to the investing membrane (Gardiner et al., 1986; Morild et al., 1988). They usually have a dense fibrillogranular substructure, but some have a pale matrix, and a paracrystalline substructure has been noted in the axolotl (Hanner and Ryan, 1980) and elasmobranch fish (Lacy and Reale, 1989). Granule contents are secreted by exocytosis into the urinary space (Ryan et al., 1982; Hill et al., 1983).

Scanning electron microscopy

Scanning electron microscopy (SEM) confirms that peripolar cells are a distinctive population of cells which are applied to the vascular pole, more often to the afferent arteriole (Gibson et al., 1989; Kelly et al., 1990). Up to 10 peripolar cells can be found forming a complete collar around the vascular pole of the sheep glomerules. They are easily distinguished from both podocytes and parietal epithelial cells. In sheep, peripolar cells are large cells (Kelly et al., 1990). They have a bossellated surface due to the closely packed cytoplasmic granules bulging into the cell membrane (Fig. 5).

In rats (Gibson et al., 1989), peripolar cells have a bipolar, dendritic shape. Long tapering processes extend from ovoid or pyramidal cell bodies and embrace the glomerular arterioles (Fig. 6). They have a relatively smooth surface, often covered with abundant microvilli. Peripolar cells in guinea pigs and humans have a similar surface morphology (Figs. 7, 8). In rats, over 40% of glomeruli contain at least one peripolar cell and up to 3 cells can be found around a single vascular pole. By light microscopy peripolar cells are difficult to identify in rat glomeruli (Gall et al., 1986). This suggests that there is a larger population of non-granulated peripolar cells in the rat (and possibly other species) which are identifiable by SEM but not by light microscopy.

Distribution of peripolar cells within the renal cortex

There are well known structural and functional differences between superficial and juxtamedullary glomeruli, (Beeuwkes et al., 1981); for instance there are significantly more renin-containing cells in superficial JGAs than deep JGAs in some species such as the rabbit (Wurfer et al., 1988). It has been suggested that peripolar cells are larger and more frequent in outer cortical glomeruli (Gardiner and Lindop, 1985; Gall et al., 1986; Gibson et al., 1989), although not in all species (Morild et al., 1988). We have shown that the apparent preponderance of peripolar cells in the outer layers of the renal cortex may be due to the greater frequency of glomeruli within the superficial cortex (Kelly et al., 1990).

Embryology

In fetal sheep granulated peripolar cells appear at 53 days gestation (Mitchell et al., 1982); this precedes the appearance of the renin-secreting cells of the JGA. Peripolar cells arise from the lower limb of the S-shaped body and form a cuff around the vascular pole in newborn lambs. Granulated peripolar cells are increased in number from 12 hours after birth until up to 4 days postpartum (Alcorn et al., 1984; Gall et al., 1986). The increase is greater in fetal sheep which are treated in utero with dexamethasone (Alcorn et al., 1984).

Peripolar cells are also prominent in newborn rats on the first day after birth (Gall et al., 1986) regardless of the period of gestation (Dhiab al Naimy and Bearn, 1980). In fetal and neonatal rats granules occur in glomerular epithelial cells which are initially adjacent to the vascular pole (and by definition, peripolar cells) but later in fetal life and after birth granulated epithelial cells are also identified distant from the hilum. Dehydration and cortisone administration increase the number of granulated epithelial cells (Dhiab al Naimy and Bearn, 1981a, 1986) but their numbers decrease after maternal adrenalectomy (Dhiab al Naimy and Bearn, 1981b). The granulation of glomerular epithelial cells may therefore be dependent on adrenal function (Dhiab al Naimy and Bearn, 1981a).

In summary, peripolar cells increase in number immediately after birth. Other glomerular epithelial cells may also become granulated. These changes may reflect the dramatic alteration in renal function which

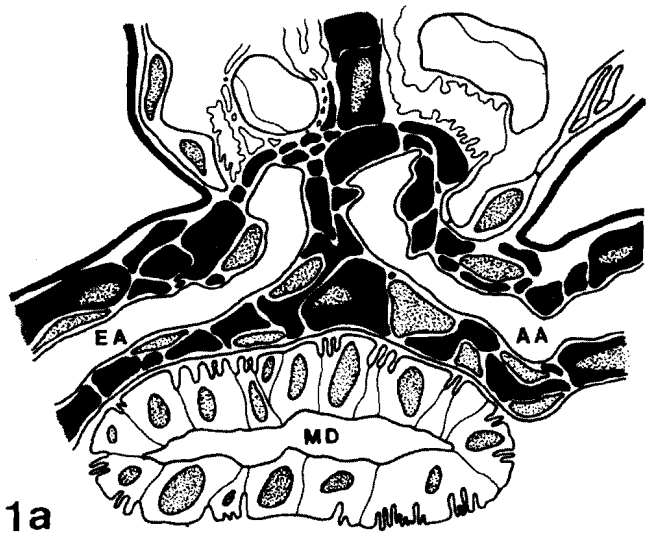

Fig. 1a. Diagram of the juxtaglomerular apparatus (JGA) before the discovery of the peripolar cell. It consists of the afferent arteriole (AA) and efferent arteriole (EA) and the macula densa (MD). The renin-containing granular myoepithelioid cells are situated in the afferent arteriole and occasionally in the efferent arteriole. **b.** The peripolar cell (arrow) is a granulated cell which is situated at the vascular pole between the visceral and parietal glomerular epithelium. It may be part of, or could interact with the other components of the JGA.

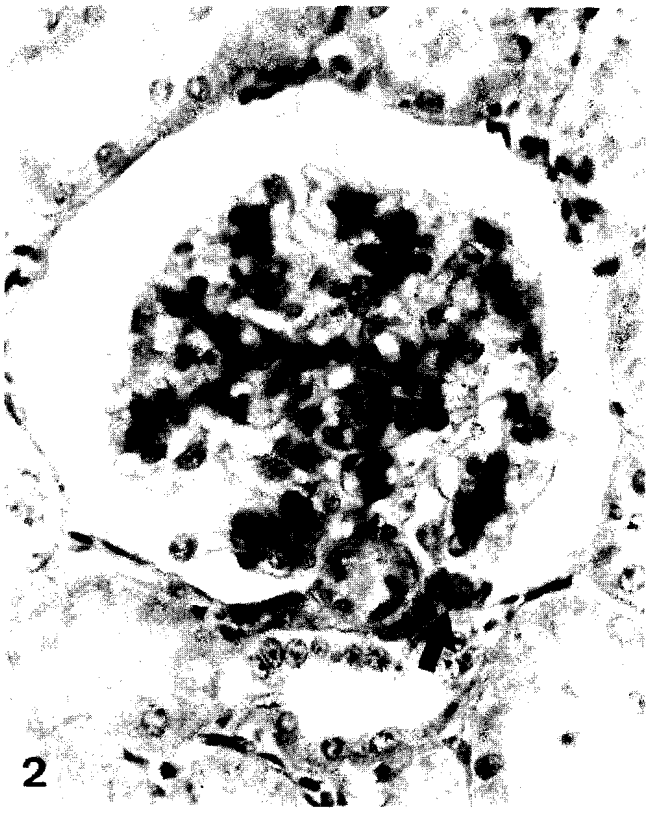

Fig. 2. A sheep glomerulus with a peripolar cell (arrow) within Bowman's space at the vascular pole. Note the prominent intracytoplasmic granules. MSB thrichrome stain.

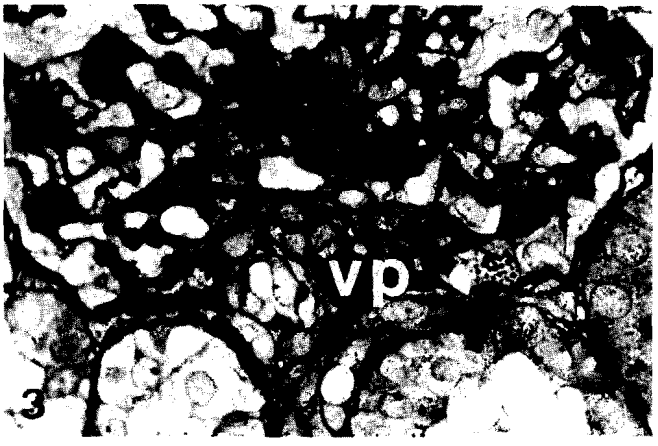

Fig. 3. Resin-embedded section of human kidney, with a peripolar cell (arrow) resting on the basement membrane of Bowman's capsule, adjacent to the vascular pole (VP). Toluidine blue stain.

occurs following birth but their significance is unknown.

Conclusions from morphological studies

Peripolar cells can be recognised by light microscopy by their position at the vascular pole and by the presence of intracytoplasmic granules. Transmission electron microscopy has demonstrated secretory-type granules which undergo exocytosis into the urinary space. The paracrystalline substructure of the granules in some species suggests that they contain a protein which has been synthesised and packaged. In rats, SEM has revealed a large population of peripolar cells. We suggest that, at least in rats, there is a population of non-granulated peripolar cells which can be identified by their SEM appearance but not as yet by conventional microscopy.

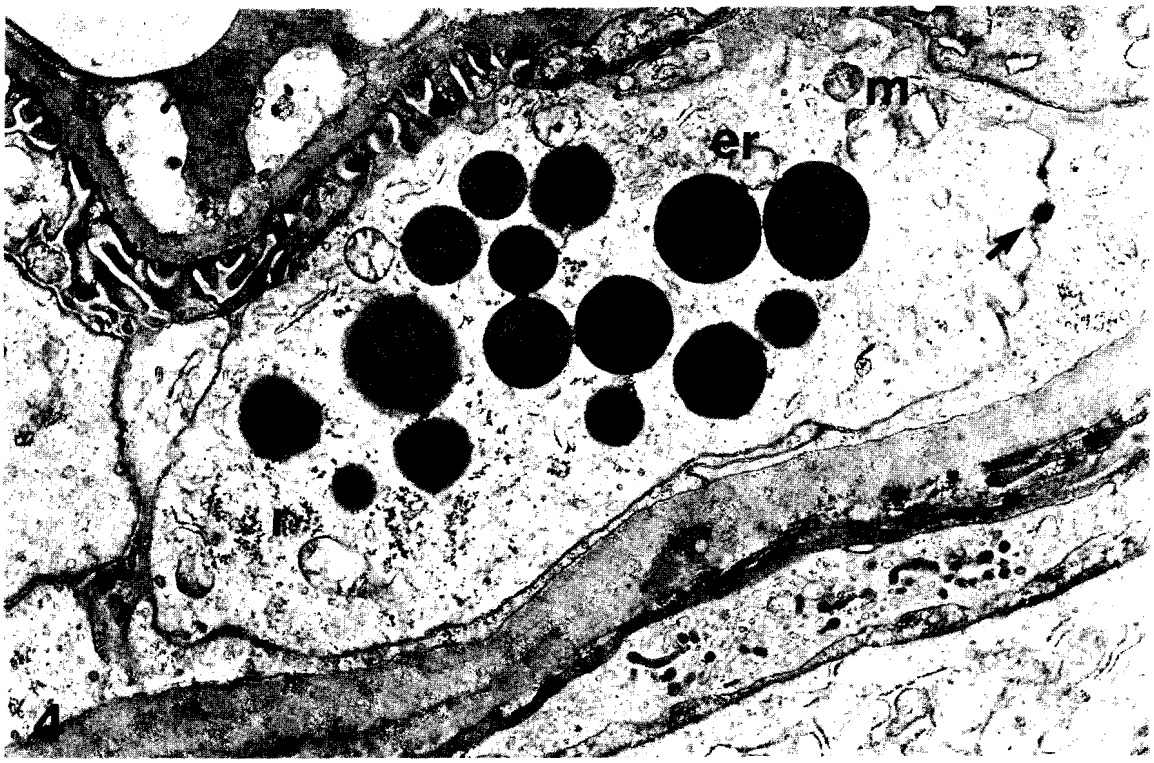

Fig. 4. Transmission electron micrograph of a human peripolar cell. There are multiple membrane-bound granules which show some heterogeneity of substructure. The cell partly overlies processes from adjacent parietal epithelial cells, with which it forms junctional complexes (arrow). Endoplasmic reticulum (er), mitochondria (m) and free ribosomes (r) are also present. × 13,500. Reproduced with permission from Gardiner et al. (1986).

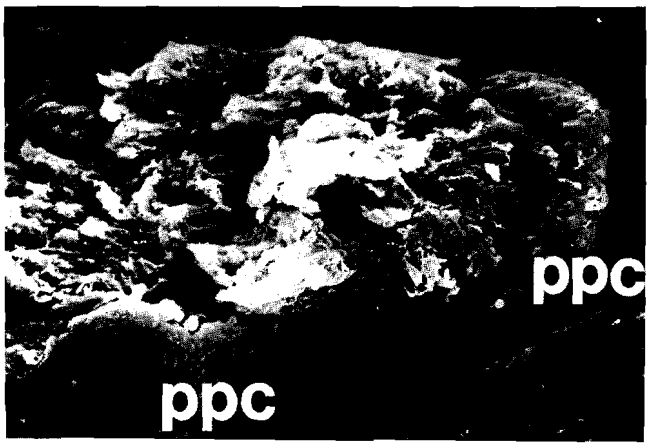

Fig. 5. Scanning electron micrograph of two sheep peripolar cells (ppc) surrounding the vascular pole. The glomerular tuft has been removed by microdissection. The peripolar cells have a bossellated surface due to the intracytoplasmic granules. × 3,000

Fig. 7. Scanning electron micrograph of a guinea pig peripolar cell with a microvillous-covered cell body and thin processes which surround the arteriole (A). × 5,000

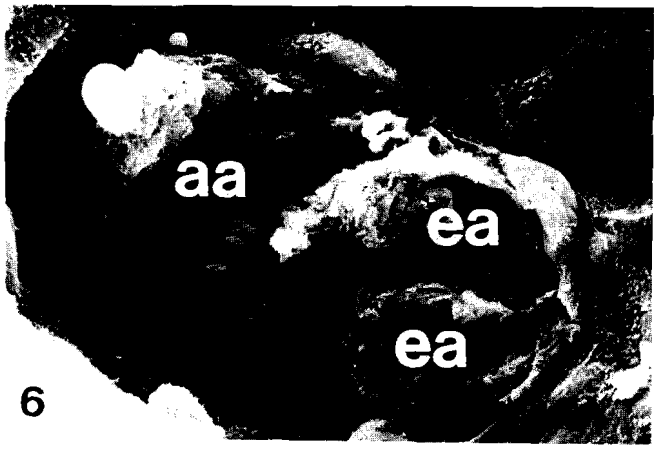

Fig. 6. Scanning electron micrograph of a rat vascular pole, consisting of one afferent arteriole (aa) and two efferent arterioles (ea). Three peripolar cells (arrows) surround the vascular pole and send cytoplasmic processes around the arterioles. × 2,500

Fig. 8. Scanning electron micrograph of a human peripolar cell adjacent to the glomerular arteriole (a). × 5,000

Table 1. Lysosomal enzymes in granules of peripolar cells, other glomerular epithelial cells and tubular epithelial cells.

	Peripolar cells	Glomerular epithelial cells	Tubular epithelial cells
cathepsin B	–	+/–	+
cathepsin D	–	NK	+
cathepsin H	–	NK	+
cathepsin L	–	NK	+
acid phosphatase	–	–	+
ß glucuronidase	NK	NK	+
ribonuclease	NK	NK	+

Function of the peripolar cell

Animal Experiments

Sodium and water depletion increase peripolar cell numbers in chickens (Morild et al., 1988), but not in sheep (Hill et al., 1983, 1984); however granule exocytosis into the urinary space was observed only in sodium depleted animals (Hill et al., 1983). The role of the peripolar cell and its secretory product in sodium metabolism remains to be established.

Granules occur in both podocytes and parietal epithelial cells in some models of experimental hypertension (Kincaid-Smith et al., 1958; Morild et al., 1988). In Goldblatt hypertension, this occurs in the unclipped kidney but not in the clipped kidney (Szokol et al., 1979). In DOC/salt hypertension in chickens the numbers of peripolar cells are unchanged, however many podocytes and parietal epithelial cells acquire granules which resemble those of peripolar cells (Morild et al., 1988).

The peripolar cell in human disease

Parietal epithelial cells and podocytes become granulated in several pathological states, for example malignant hypertension (Fahr, 1919; Heptinstall, 1983) and toxaemia of pregnancy (Sheehan and Lynch, 1973). In a renal biopsy study of pre-eclampsia, peripolar cells and granulated epithelial cells could not be distinguished by light or electron microscopy (Hill et al., 1988). However in the definitive account of the pathology of pre-eclampsia, Sheehan and Lynch described granules in visceral and parietal glomerular epithelial cells usually close to the vascular pole in approximately half of their cases (Sheehan and Lynch, 1973); their incidence diminished rapidly 4-5 days postpartum. The authors concluded that proteinuria per se could not be the only factor in the production of the granules.

Granule content

We have shown that the human peripolar cell contains no immunoreactive renin (Gardiner and Lindop, 1985), a finding which has since been confirmed in other species (Morild et al., 1988; Trahair et al., 1989). Recently, kallikrein mRNA has been localised by in situ hybridisation at the vascular pole of rat glomeruli, although peripolar cells were not specifically identified (Xiong et al., 1989). However, neither kallikrein nor kallikrein mRNA could be identified in sheep peripolar cells by other workers (Trahair et al., 1989). Peripolar cell granules also contain immunoreactive albumin, immunoglobulins, IgG $(Fab)_2$ and fibrinogen suggesting that peripolar cells absorb protein, from the glomerular filtrate (Trahair et al., 1988, 1989).

If peripolar cell granules do contain absorbed protein, are they related to proteinuria? Glomerular epithelial cells become granulated in most models of proteinuria. The prominence of these granules usually correlates with the degree of proteinuria (Davies et al., 1978; Lawrence and Brewer, 1982; Furness and Turner, 1987), although not always (Messina et al., 1987; Andrews, 1977). Podocytes take up filtered protein by micropinocytosis (Lawrence and Brewer, 1982; Furness and Turner, 1987). The absorbed protein is then incorporated into phagolysosomes which are either digested or extruded into the urinary space (Davies et al., 1978).

Epithelial cell granules or "hyaline droplets" are also found in the tubular epithelium. Albumin is taken up readily by both glomerular and tubular epithelial cells (Lawrence and Brewer, 1982, 1983). Nakajima et al. have recently shown zonal differences in the distribution of proteins whithin individual granules of glomerular but not tubular epithelial cells (Nakajima et al., 1989). Also many proteins, including horseradish peroxidase, myoglobin, bovine lactoperoxidase, haemoglobin, tyrosinase, lysozyme and Fab fragments which are readily absorbed by the proximal tubular epithelium are rarely taken up by the glomerular epithelium (Straus, 1956; Ericson, 1968; Graham and Kellermeyer, 1968; Anderson, 1972; Christensen and Mannsbach, 1974; Druet et al., 1978; Oliver and Essner, 1978). Tubular epithelial granules contain a variety of lysosomal enzymes including acid phosphatase, ß glucoronidase, ribonuclease and cathepsin (Taugner et al., 1985a) (Table 1). Cathepsin B is present in podocytes (Taugner et al., 1985b) but no lysosomal enzymes have been demonstrated in peripolar cells (Morild et al., 1988; Trahair et al., 1989) (Table 1). There is evidence then, that hyaline droplets differ in several respects from glomerular epithelial cell granules and that podocytes differ from peripolar cells in their enzyme content.

The evidence for absorptive activity by peripolar cells does not preclude a secretory function. Cathepsin and other lysosomal enzymes are found in the renin-containing granules of juxtaglomerular myoepithelioid cells and these cells take up exogenous tracers which then appear in the granules (Smith and Farquhar, 1966; Taugner et al., 1985b). Acid phosphatase and proteases are also common in a

variety of secretory granules (Holtzman, 1976; Orci et al., 1978; Chertow, 1981), which may be derived from lysosomes (Smith and Farquhar, 1966). Therefore there is some evidence that the granules in podocytes may behave as lysosomes but there is no compelling evidence that peripolar cell granules are simply lysosomal in nature.

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