ULTRASTRUCTURE OF THE CONTRACTILE SYSTEM OF RENAL PODOCYTES IN VERTEBRATE PHYLOGENY

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Contractility of cells of the visceral epithelium (podocytes) of Bowman's capsule is known to be due to the presence of a highly developed system of microfilaments in their cytoplasm [2]. Comparative aspects of the structure of the microfilament system of podocytes in the kidneys of lower and higher vertebrates are examined in this paper.

EXPERIMENTAL METHOD

Kidneys from adults of both sexes from two families of marine bony fishes were studied: Pleuronectidae – the plaice *Pleuronectes platessa* L. and the long rough dab *Hippoglossoides platessoides limandoides* Bloch (caught in the Barenz and Norwegian Seas) and the Exocoetidae – the tropical two-winged flying fish *Exocoetus volitans* L. (caught in the Indian Ocean) – and these were compared with the kidneys of mongrel dogs. Pieces of kidney tissue (the caudal region of the kidneys in fishes and the renal cortex in dogs) for electron-microscopic study were fixed in a 3% solution of glutaraledhyde in phosphate buffer and postfixed in a 1% solution of OsO_4. Material was embedded in Araldite, ultrathin sections were cut on Reichert and UMTP-2 ultramicrotomes, stained with lead citrate, and examined in JEM-100B and UÉMV-100B electron microscopes.

EXPERIMENTAL RESULTS

The general principle of structure of the epithelial cells of the visceral layer of the glomerular capsule (podocytes) is identical for the nephron of all the species studied and corresponds to that described in the literature [9]. Podocytes (Figs. 1, 2, and 3) faced the lumen of the glomerular capsule and were raised above the basement membrane of the glomeruli on large processes or trabeculae, which broke up in the distal direction into small processes or pedicles, in contact with the basement membrane. Narrow spaces, enclosed by thin bridges, were presented between neighboring pedicles. Consequently, a special feature of the structure of the podocytes of vertebrates is the formation of unique cytoplasmic arcades by their processes, which form a subpodocytic space in the lumen of the glomeruli.

A well developed system of microfilaments was observed in the cytoplasm of podocytes of the kidneys of marine bony fishes (Figs. 1 and 2). These microfilaments, 8–10 nm thick, formed dense bundles consisting of 200 or more separate units. In transverse and tangential sections the microfilaments had a pale matrix. In the region of the perikaryon, bundles of microfilaments surrounded the nucleus concentrically and were in close contact with the outer nuclear membrane. Zones of transition from the body of the podocytes to the trabecular and pedicular processes, where they lay in the surface regions of the cytoplasm, beneath the plasmalemma, could be clearly distinguished. Along the course of the bundles of microfilaments, they formed tight junctions with mitochondria.

Microfilaments in the renal podocytes of dogs were only 4–7 nm thick, they did not form bundles, but were distributed diffusely all over the cell and essentially constituted the matrix of the cytoplasm of the body (Fig. 3a) and processes (Fig. 3a, c) of the podocytes.

In the modern view microfilaments resemble actin, the structural protein of muscle cells and one of the components of the contractile system of muscles [10]. Microfilaments also contain myosin, α-actinin, tropomysin, and other proteins [12]. The presence of a well developed system of microfilaments in the renal podo-

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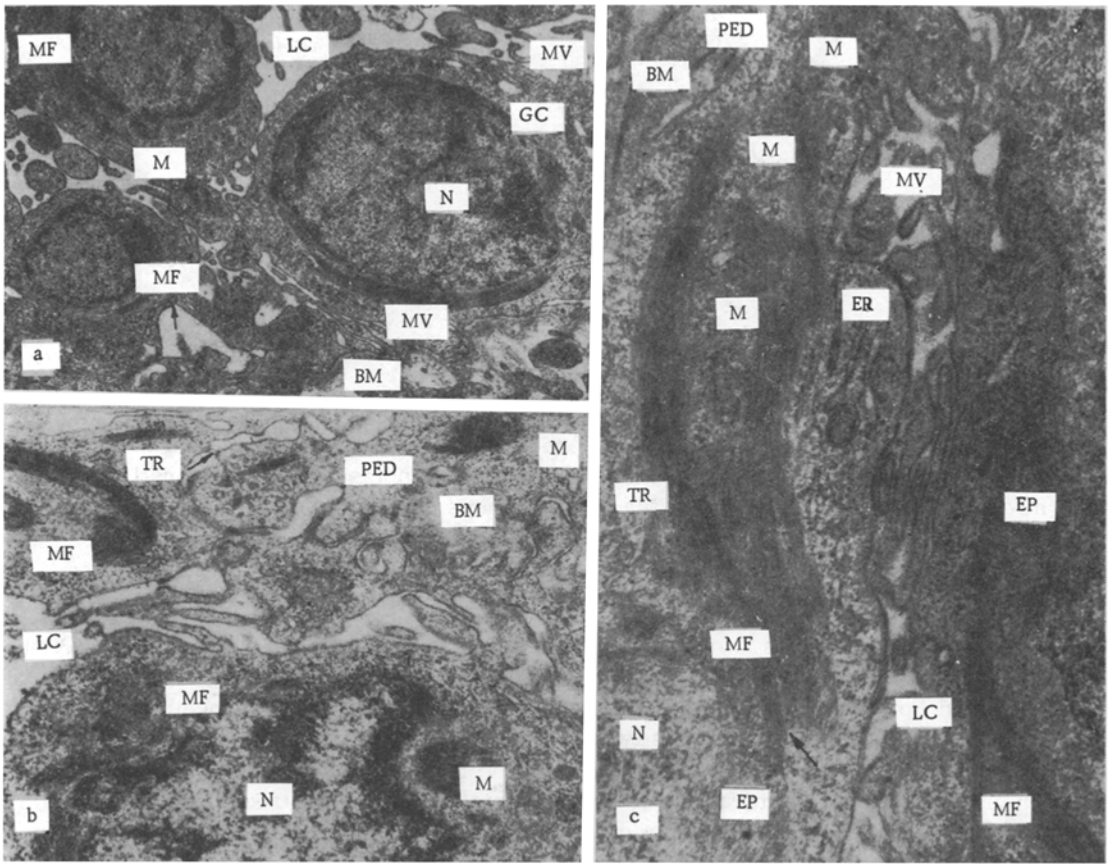

Fig. 1. Fragments of podocytes from renal glomerulus of the plaice. a) Microfilaments in region of perikaryon, b) in region of perikaryon, trabeculae, and pedicles, c) microfilaments in region of trabeculae. MF) Microfilaments, EP) epithelial cells (podocytes), LC) lumen of Bowman's capsule, BM) basement membrane, TR) trabeculae, PED) pedicles, MV) microvilli, N) nucleus, M) mitochondria, ER) endoplasmic reticulum, GC) Golgi complex. Arrows indicate crossing of bundles of microfilaments into trabeculae and pedicles from region of perikaryon; arrows with semicircle denote interpedicular bridges. Magnification: a) 9000, b, c) 18,000.

cytes of the fishes investigated, which differ sharply in their mode of life (bottom and epipelagic fish) indicates a possible morphological and functional universality of this system for the nephron of marine bony fishes, irrespective of their different ecologies. As the writer pointed out previously [2], the podocyte system of microfilaments causes rhythmic contractions of the cell body, trabeculae, and pedicles, and in that case the podocytes play the role of a special kind of pump, propelling the ultrafiltrate through the filtration barrier. In the light of this view the necessity for a subpodocytic space, restricting the amplitude of contraction of the podocytes, becomes understandable because, given the usual structure of epithelial cells, in close contact with the basement membrane, each contraction would lead synchronously to constriction of the glomerular capillaries. To establish the energy supply for the contractile system of podocytes, the intracellular arrangement of the bundles of microfilaments must probably be taken into account. Their close topologic connection with mitochondria enable them to utilize the energy of ATP molecules produced by the mitochondria for their own contraction. The existence of mechanisms of energy coupling, leading to accumulation of electron transfer energy in the form of energy "utilizable" for various processes of nuclear activity, in the nuclear membranes of different animals is now known [1, 3, 5]. On the basis of our own observations and considering the extremely close contact between bundles of microfilaments and the nuclear membrane, it can be tentatively suggested that energy for the contractile apparatus of the podocytes is supplied by oxidative phosphorylation processes taking place in the nuclear membranes. In agreement with data obtained by the writer previously in electron-histochemical studies of localization of lactate dehydrogenase (EC 1.1.1.27), one of the principal specific enzymes of glycolysis, in the podocyte plasmalemma [7], close to which the microfilaments are situated, the possibility cannot be ruled out that energy for contraction of podocytes also is supplied by processes of glycolytic phosphorylation.

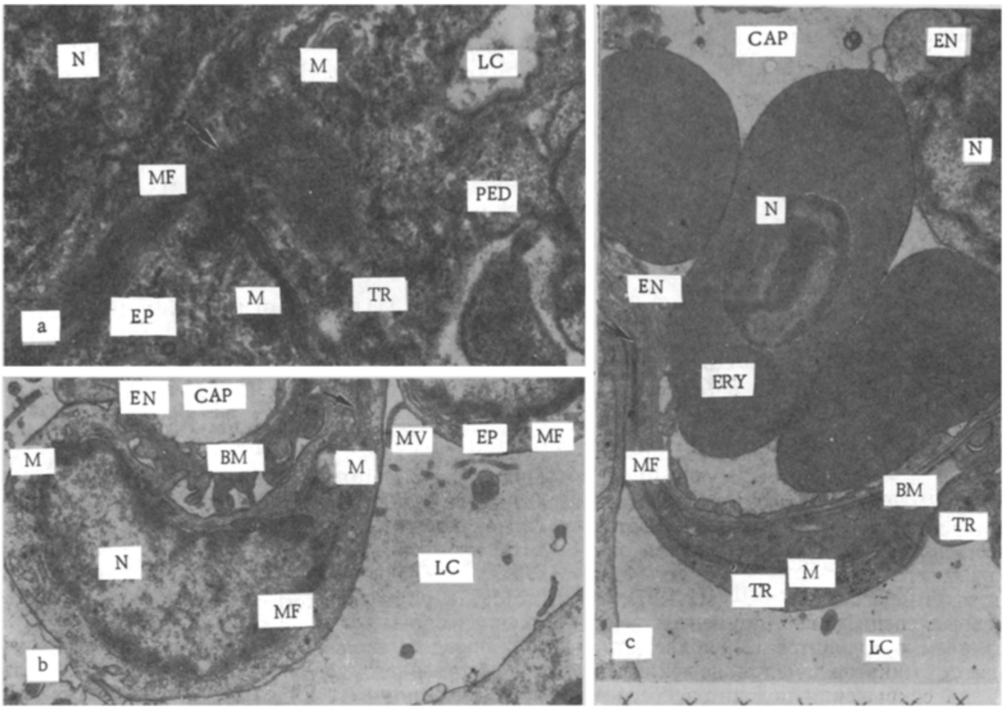

Fig. 2. Fragments of podocytes of renal glomeruli of the long rough dab and flying fish. a) Dab, microfilaments in region of perikaryon and trabecule, 22,000 ×; b) flying fish, microfilaments in region of perikaryon, 8000 ×; c) flying fish, microfilaments in trabeculae, 10,000 ×. CAP) capillary lumen, EN) endothelium, ERY) erythrocyte. Remainder of legend as to Fig. 1.

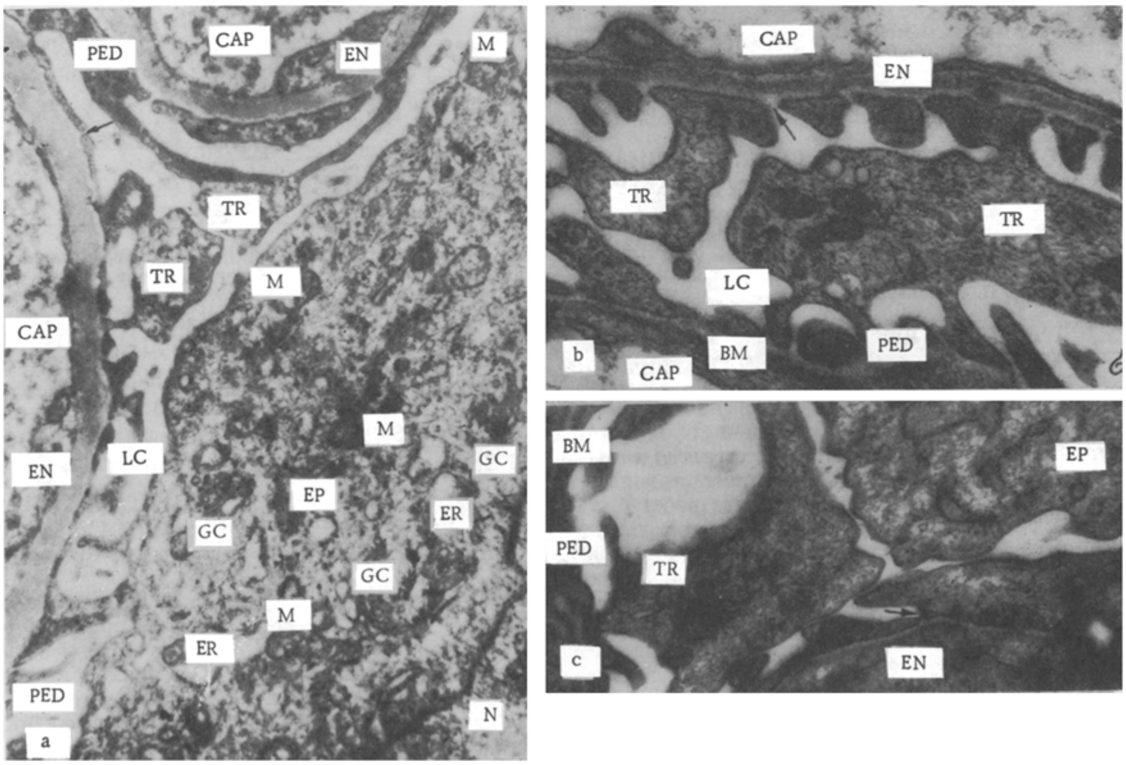

Fig. 3. Fragments of podocytes of dog renal glomerulus. 18,000 ×. a) Zone of perikaryon, b, c) trabeculae and pedicles. Remainder of legend as to Figs. 1 and 2.

The need for a powerful contractile apparatus in podocytes, which perform an active pumping function in the kidneys of marine bony fishes, is evidently explained by the fact that their arterial blood pressure is lower than in mammals, and the relatively small volume of blood ejected by the heart limits the inflow of arterial blood to the kidney [6]. It will be noted that whereas in mammals the weight of the heart is on average 0.59% of body weight, in reptiles 0.51%, and in amphibians 0.46%, in fish it is only 0.2% [11].

In the course of vertebrate evolution (the formation of a four-chambered heart, elevation of the blood pressure, and so on) the system of microfilaments in the renal podocytes undergoes substantial changes. In higher vertebrates (in this case, in dogs) this change is manifested morphologically by depolymerization of bundles of microfilaments, a decrease in their thickness, and their diffuse distribution throughout the cytoplasm of the cells. Consequently, transition from a fascicular type of structure of the microfilament system to a reticular type, determined by evolution, is observed in the cytoplasm of podocytes of the renal glomeruli of lower and higher vertebrates. According to various workers, these two types of systems of microfilaments are most widely represented in the cytoplasm of eukaryote cells [14].

It must be specially emphasized that under pathological conditions, such as in patients with hydronephrosis [4] or a nephrotic syndrome [8], the number of fibrils (microfilaments) in the cytoplasm of the podocytes of the renal glomeruli may be sharply increased. Some investigators [8] quite logically regard this well-defined fibrillary structure of the podocyte cytoplasm in the kidneys of patients with the initial stage of a nephrotic syndrome as an adaptive reaction to proteinuria and a characteristic feature of increased functional activity, due to an increase in their contractile capacity. Unfortunately, this reaction is of short duration and decompensation of the podocytes, with vacuolation and necrosis, develops rapidly [8]. In such situations, to strengthen and stabilize the mechanisms of adaptation, it is evidently advisable to use artificial (drugs, physical agents, and so on) stimulators of microfilament development in the podocytes, for at one stage of evolution of the animal kingdom (marine bony fishes) the podocytes have a well developed system of microfilaments, constituting the basis of their contractile apparatus. This fact also is evidence of the active role of epithelial cells (podocytes) of the glomerulus in urine formation, so that Starling's theory [13], which is still dominant, and which regards ultrafiltration as a process based on a purely physical mechanism of filtration under pressure, can be critically re-evaluated. The principles of that theory are evidently applicable only to higher vertebrates. Their extrapolation to other animals and, in particular, to marine bony fishes, in the light of the results of the present investigation must be done with a due measure of caution and with the introduction of essential corrections.

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