# STRUCTURAL ORGANIZATION OF THE TUBULAR COMPONENT OF THE COUNTERCURRENT SYSTEM OF THE KIDNEY

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UDC 611.611-018-013

KEY WORDS: concentration apparatus; countercurrent system; nephron; ontogeny.

The explanation of the concentrating activity of the kidney by the countercurrent multiplication principle [11] has been developed into the theory of the mechanism of osmotic concentration of urine [1, 2, 4, 6, 9, 10, 14, 15]. The physiological and physicochemical aspects of this process have been studied experimentally [3, 5, 7, 8]. However, the dynamics of formation of tubulovascular relations in the mammalian renal medulla at different stages of ontogeny has been inadequately studied. Data in the literature on spatial relations between components of the osmoregulatory system of the kidney are contradictory [9, 10, 12, 13]. An explanation of this process is possible only after careful analysis of the spatial organization of the tubular systems of the renal medulla, not only at the definitive level, but also, and above all, during their formation.

The object of the present investigation was to study the structure of the tubular component of the concentration apparatus of the dog's kidney during its formation in ontogeny, to trace the dynamics of relations of the nephron loop and collecting tubule from the moment of appearance of their anlagen until the definitive state, and also to establish the time and character of appearance during embryonic life and the nature of formation of the thin segment of the tubular part of the nephron.

## EXPERIMENTAL METHOD

The most adequate method of tackling the problem is through step by step construction of the structures as they are formed. Twelve series of histological sections of kidneys from dog embryos ranging from 9.0 mm in length from the vertex to the tip of the coccyx until birth were studied. After careful study of the histological sections, graphic and plastic reconstructions were made. Series of sections the plane of which passed through the renal medulla were chosen and, under the necessary magnification, each section was drawn successively on a wax slab of appropriate thickness. The outlines of the traced structures (models of the sections) were then cut out of the slabs and a model of the test object was assembled.

## EXPERIMENTAL RESULTS

The established concept of repeated T-wise division of generations of derivatives of the mesonephric duct is not disputed except with respect to spatial relations between neighboring generations of collecting tubules. Quantitatively speaking, each newly formed tubule gives rise to three new equivalent tubules. The anlagen of the budding tubules are arranged at different angles and in different planes relative to the previous generation, and form an angle of about 120° with each other (Fig. 1). This trifurcation of the derivatives of the Wolffian duct is easily traced in the early stages of development of the kidney and it characterizes only the first four or five populations, i.e., it corresponds to anlagen of the collecting tubules of the future juxtamedullary nephrons and the papillary ducts. Subsequent budding of the tubules is accompanied by disturbance of the triple system. In the present writer's view, this was due to inequality in the rates of growth and development of subsequent populations of Wolffian duct derivatives, in connection with the formation of a network of intramural vessels, and also to the fact that as each generation of collecting tubules approached the surface of the organ, the cellular metanephrogenic material was "exhausted" and they gave rise at first to two tubules each, but later they eventually became terminal.

In 22.5 mm embryos,the anlage of the tubular part of the nephron consists of a short looped tubule located near the newly formed renal corpuscle and a blind and slightly dilated end of the collecting tubule with

Department of Human Anatomy and Department of Pharmacology, Chernovtsy Medical Institute. (Presented by Academician of the Academy of Medical Sciences of the USSR V. N. Chernigovskii.) Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 89, No. 6, pp. 739-741, June, 1980. Original article submitted May 15, 1979.

 0007-4888/80/8906-0840$07.50 

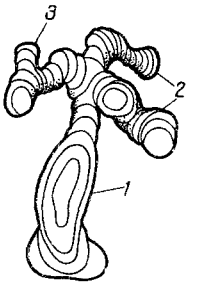


Fig. 1

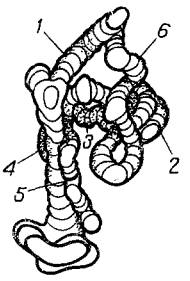


Fig. 2

Fig. 1. Graphic reconstruction of formation of derivatives of the mesonephric duct. 1) Anlage of capillary duct, 2) anlage of first generation collecting tubule, 3) anlage of second generation collecting tubule.

Fig. 2. Graphic reconstruction of formation of nephron. 1) Anlage of collecting tubule, 2) anlage of renal corpuscle, 3) anlage of proximal convoluted tubule, 4) anlage of descending loop of tubule of nephron, 5) anlage of ascending loop of tubule of nephron, 6) anlage of distal convoluted tubule.

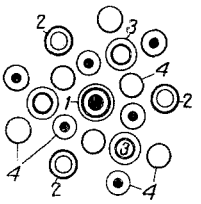


Fig. 3. Scheme of transverse section through conical bundle. 1) Collecting tubule, 2) descending loop of nephron, 3) ascending loop of nephron, 4) blood vessels.

which it forms an anastomosis. Later one loop of the tubule, which lies closest to the newly formed collecting tubule and, consequently, which is buried in a well-marked layer of mesenchyme, increases in length and lies along this, and later the preceding generation of collecting tubules, with their limb directed toward the central part of the kidney (Fig. 2). This loop is the anlage of Henle's loop.

The tubular part of the nephrons of equivalent populations is formed in a similar manner. As a result of the fact that in the initial stage of development the collecting tubules are comparatively short, loops of nephrons of three equivalent populations, "sinking" toward the center of the organ, lie along the collecting tubule of the preceding generation; around each collecting tubule at the level of the anlage of the inner zone of the renal medulla, loops of three nephrons of the corresponding populations are found (Fig. 3).

Functional differences between different segments of the nephron are known to correlate with their morphology. In the definitive state of the ascending and descending portions of Henle's loop there are significant cytological differences. Certain particular features also appear in the ultrastructure of cells in the descending and ascending portions of the thin segment of the loop of the nephron [4]. At the beginning of formation of Henle's loop (20.5 mm) certain distinguishing features can be detected between its descending and ascending portions. For instance, the course of the descending portion is straighter than that of the ascending portion, where more convolutions are found. The ascending portion lies closer to the collecting tubule, it makes contact more frequently with its wall, whereas the descending portion hardly ever makes contact with the tubule. In the early stages of development (20.0-21.0 mm embryo) lengthening of the loop of the nephron

takes place comparatively slowly. Growth of the convoluted part of the tubule takes place more slowly still. From the time of formation of the intramural vessels of the kidney (embryos 24.0-26.0 mm long) the rates of differentiation of all parts of the nephron increase appreciably. As a result of this both limbs of Henle's loop assume a more distinctly straight course, and the bend of the loop reaches the innermost regions of the organ, within the substance of the well-developed layer of mesenchyme.

In the initial period of formation of Henle's loop the lumen of the tubule and the thickness of its wall are comparatively uniform throughout its length. The first signs of appearance of the anlage of the thin segment of the nephron occur at the time of formation of the intramural vessels of the renal medulla (in embryos 28.5-36.0 mm long) and they take the form of separate fragmentary constrictions in the ascending part of the loop. These constrictions lie in places where the tubule comes closest to the wall of the collecting tubule. At this level the lumen of the tubule becomes slit-like in shape, but the thickness of its wall remains unchanged. Later (in embryos 37.0-50.0 mm long and until birth), as a result of an apparent spread of the constricted segments of the tubule along its length, they join together to form a single segment. A change in the shape of the cells of the tubule wall is observed in these same places: from high epithelium they are transformed into cubical, and they then become flattened in shape.

It follows from what has been said that the structural and functional unit of the concentration apparatus of the renal medulla in dogs is a conical bundle, the central axis of which is formed by the collecting tubule. Around this tubule, descending and ascending portions of loops of, in most cases, three nephrons and their accompanying blood vessels are arranged in a definite order. The tubules are arranged so that the ascending portions occupy the central position and the descending portions lie a little externally. The formation of the thin segment of the nephron takes place through fusion of individual fragmentary constrictions of the tubule into a single thin segment of the nephron.

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