

The Structure of the Human Juxtaglomerular Apparatus A Morphometric, Lightmicroscopic Study on Serial Sections * **

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Summary. 49 juxtaglomerular apparatuses were examined using 1.9 μ thick Giemsa-stained serial sections from human renal tissue embedded in plexiglass. In 43 juxtaglomerular apparatus the direct contact areas between the different juxtaglomerular structures and the basal area of the macula densa were calculated. A positive, significant correlation was found between the size of the macula densa and the direct contact area between macula densa and Goormaghtigh's cell field on the one hand, and between the macula densa and the direct contact area between Goormaghtigh's cell field and the afferent arteriole on the other. There was also a significant, positive correlation between the direct contact area of Goormaghtigh's cell field with the macula densa and that of Goormaghtigh's cell field with the afferent arteriole. On the efferent side none of these correlations were significant. Thus a "flow of information" from the macula densa via the Goormaghtigh cells to the afferent arteriole is morphologically possible. The direct contact areas between macula densa and the afferent or the efferent arterioles were not correlated with any of the other parameters. Epithelioid cells were present in the interlobular arteries, prior to and within the juxtaglomerular apparatus in the afferent arterioles, as well as within and beyond the juxtaglomerular apparatus in the efferent arterioles.

Key words: Reconstruction of the juxtaglomerular apparatus — Macula densa basal area — Juxtaglomerular contact areas — Macula densa feedback mechanism — Goormaghtigh's cell field — Epithelioid cells.

The juxtaglomerular apparatus of the mammalian kidney consists of the hilar parts of the afferent and efferent arterioles with their epithelioid cells, the cells between the hilar arterioles known as the cell field of Goormaghtigh, and the macula densa (Barajas and Latta, 1963, 1967; Bing, 1964; Faarup, 1965; Bucher and Riedel, 1966; Hatt, 1966; Meyer, 1971).

The question concerning the function of this apparatus can now be answered insofar as it may be assumed that it plays an important part in the regulation of body fluid and sodium chloride, as well as in renal hypertension (Goormaghtigh, 1939; Tobian, 1960; Vander and Miller, 1964; Skinner *et al.*, 1964; Thurau and Schnermann, 1965; Schnermann *et al.*, 1966; Bohle and Sitte, 1966; Thurau, 1967; Thurau *et al.*, 1967; Tobian, 1967; Vander, 1967; Bohle, 1968; Meyer *et al.*, 1969; Helber *et al.*, 1970; Schnermann *et al.*, 1970; Thurau, 1972; Thurau *et al.*, 1972).

At present the spatial relationships between the structures of the juxtaglomerular apparatus are not clear, because there are contradictory findings and a lack of information about the size of the contact areas between the individual structures forming the juxtaglomerular apparatus (Barajas and Latta, 1963; Faarup, 1965; Barajas, 1970, 1971).

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The present study was undertaken to provide a detailed topographical analysis of the juxtaglomerular apparatus in man and to obtain morphologic measurements as a basis for understanding the function of this portion of the kidney.

Material and Methods

Two morphologically normal kidneys with normal function were surgically removed for transplantation from two patients, 19 and 45 years of age. Immediately after finishing the surgical procedure, small blocks of tissue were prefixed in 4% formaldehyde, refixed in 2% OsO_4 , and embedded in plexiglass. From the kidney of the 19-year-old patient the tissue was deliberately taken from the subcapsular and juxtamedullary renal cortex as well as from Bertini's columns, while the specimens of the other kidney came from various cortical layers without regard to their localization.

Histological examinations were carried out on 1.9 μ thick, Giemsa-stained serial sections, 100 to 105 sections per series. The thickness of the sections was determined by means of transillumination interference microscopy according to Jamine and Lebedeff (Hale, 1958) by measuring the phase deviation with a Sénarmont compensator. The mean thickness was 1.9 μ , with a maximal range of 1.7 to 2.1 μ .

From the first kidney we obtained serial sections from 40 juxtaglomerular apparatuses out of which 37 were measured systematically after taking microphotographs, at a final magnification of 370:1. From the second kidney we took serial sections from 9 juxtaglomerular apparatuses and measured 6 systematically. Seven serially sectioned juxtaglomerular apparatuses were drawn to scale in three dimension by the Norwegian etcher and painter H.Th.A. Bjaerke, the projection method was used starting from two tangents to Bowman's capsule running parallel 90° apart (Fig. 1).

In addition, a series of 100 sections 4 μ thick were made from paraffin embedded and PAS-stained renal tissue from the 19-year-old patient. This tissue had been taken parallel to a sagittal cut through the kidney, thus comprising the entire width of the cortex and the outer medullary zone. From this material we reconstructed 5 randomly selected nephrons from each of the subcapsular, intermediary, and juxtamedullary cortical layers. We followed the tubule from the ascending loop of Henle past the macula densa into the distal convoluted tubule and noted the direction of the hilar arterioles. With these 4 μ thick serial sections we also determined planimetrically the volume of 10 juxtamedullary and 12 subcapsular juxtaglomerular cell complexes composed of Goormaghtigh's cell field and epithelioid cells of the afferent and efferent arterioles (Meyer, 1972).

The structures of the juxtaglomerular apparatus were defined as follows:

The macula densa was considered as that part of the distal tubule adjacent to the glomerular vascular pole which was distinguished from the remaining distal tubule by narrow and tall epithelium with closely arranged nuclei (Zimmermann, 1933; Goormaghtigh, 1937). Goormaghtigh's cells were the poorly delineated cells in the angle of the hilar arterioles. These cells have only a small amount of cytoplasm and chromatin-rich, spindle-shaped nuclei. The region occupied by these cells is called Goormaghtigh's cell field (Goormaghtigh, 1932). This cell field borders on the macula densa, the outer surface of the basal membrane of the parietal layer of Bowman's capsule at its junction with the glomerular capillary tuft, and the hilar arterioles. Its border with the mesangium of the hilar region of the renal corpuscles was arbitrarily assumed to correspond to the transition from the parietal to the visceral layer of Bowman's capsule (Fig. 1a). Where Goormaghtigh's cell field did not border on any of these structures, the transition of the dense arrangement of cell nuclei to a loose arrangement of nuclei of interstitial connective tissue was taken to be its boundary.

In order to clarify how the different structures of the juxtaglomerular apparatus are in contact with each other and how large these contact areas are, measurements were first made in each section of each series of the direct contact lengths between:

1. macula densa and the Goormaghtigh cells,
2. the Goormaghtigh cells and the afferent arteriole,
3. The Goormaghtigh cells and the efferent arteriole,

4. macula densa and the afferent arteriole,
5. macula densa and the efferent arteriole.

The basal area of the macula densa was also measured.

The direct contact areas between the structures of the juxtaglomerular apparatus were calculated from the length of contact, taking into account the number of tissue sections and their mean thickness.

It is not possible to obtain mathematically exact measurements of the contact areas due to the histological and technical factors affecting the structures. Therefore, the values obtained are approximate and are used for the purpose of comparison.

The data was examined statistically. In all the series it fulfilled the statistical requirements for normal distribution, and a collective evaluation of the data of all 43 juxtaglomerular apparatuses seemed justifiable. In order to find statistically significant correlations we used Spearman's rank correlation. For testing whether linear or exponential correlations were present, classical correlations were drawn up if it seemed appropriate on the basis of the measurements. $\alpha=0.05$ was chosen as the level of significance.

In 31 randomly selected nephrons the mean cell number of the macula densa was determined. For this purpose, all macula densa nuclear cuts from each individual macula densa were first determined as well as the number of sections through 10 nuclei of each macula densa. The quotient of these two counts gave the cell number for each macula densa.

Results

Our measurements and reconstructions showed:

1) In all 49 examined juxtaglomerular apparatuses there was always an extensive direct contact between the macula densa and Goormaghtigh's cell field. In addition, the macula densa was in direct contact with the afferent arteriole in 47, and with the efferent arteriole in 46 out of 49 examined juxtaglomerular apparatuses. Both arterioles were always in direct contact with Goormaghtigh's cell field (Fig. 1).

2) The macula densa structure was not limited to the contact areas between the distal tubule and Goormaghtigh's cell field and the hilar arterioles. Related to the transverse section of the tubule, it invariably extended beyond the contact areas with Goormaghtigh's cell field and hilar vessels. Outside these contact areas the macula densa bordered on peritubular capillaries or peritubular interstitial tissue (Fig. 2). In the area of contact between the macula densa and Goormaghtigh's cell field or the hilar arterioles, no peritubular capillaries or interstitial tissue were demonstrable.

3) The mean number of macula densa cells found in 31 randomly selected nephrons was 51. The mean basal surface of a macula densa cell thus worked out at ca. $100 \mu^2$. As a control the edge length of 5 macula densa cells in each of 10 distal tubules was measured. The arithmetrical mean for the edge length of a macula densa cell was 13.5μ .

4) In the region of the macula densa the tubular lumen was found to be wider in 40 out of 49 juxtaglomerular apparatuses examined than in the preceeding and following parts of the distal tubule (Fig. 1). Small, hernia-like protrusions covered with macula densa epithelium were observed in the distal tubule in 14% of the juxtaglomerular apparatuses. This structure enlarged the contact area of the macula densa with Goormaghtigh's cell field. A similar type of protrusion can be found in other parts of the distal tubule (Peter, 1907), covered, however, with normal tubular epithelium.

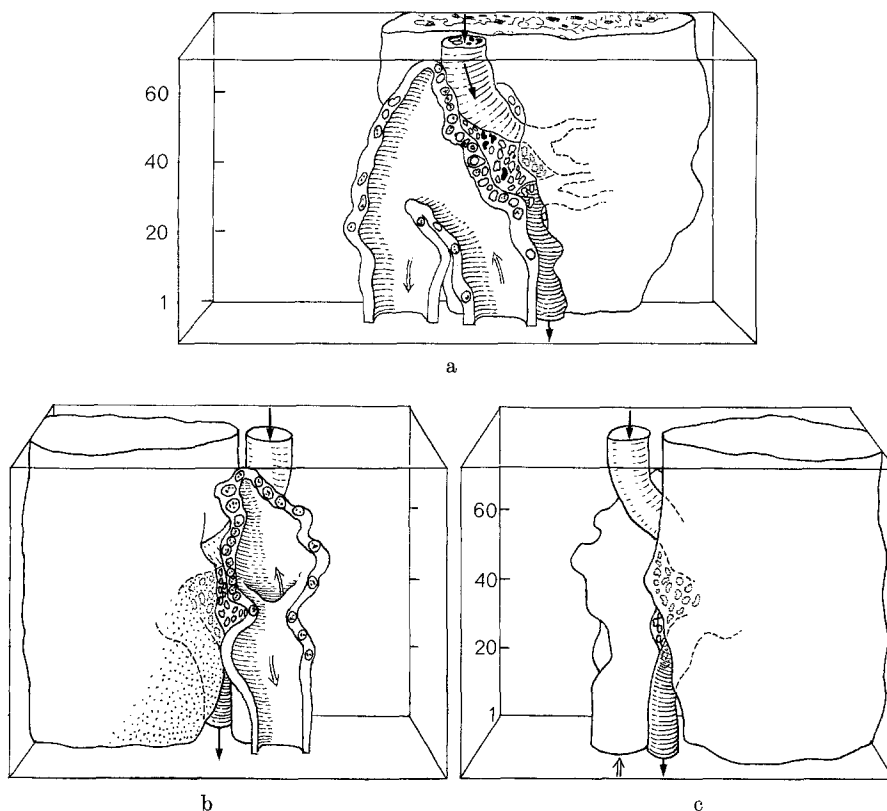


Fig. 1a—c. Scale reconstruction (190:1) of the vascular pole of a glomerulum with juxta-glomerular apparatus from $1.9\ \mu$ thick, Giemsa-stained serial sections. (a) From above, (b) from the left, (c) from the right. The flow direction of blood and urine is marked by arrows. The Goormaghtigh cells in the angle between the two arterioles, the cell nuclei of the macula densa and in the remaining part of the tubule are shown. The epithelioid cells of the hilar arterioles are not shown. In the background (a), left and right (b and c) of the vascular pole the outer surface of Bowman's capsule. The arbitrary border between Goormaghtigh's cell field and the mesangium (drawn lightly) is indicated in Fig. 1a and b by the contour of Bowman's capsule between the hilar arterioles. Note the widening of the distal tubule in the macula densa region

5) The entire basal area of the macula densa averaged about $5300\ \mu^2$, the mean direct contact area between Goormaghtigh's cell field and the macula densa only $2060\ \mu^2$. Thus only 39% of the total basal area of the macula densa was in contact with Goormaghtigh's cell field. Assuming that the normal kidney consists of 10^6 nephrons, the total basal area of all maculae densae of one kidney is equivalent to the size of a square with sides about 7 cm long.

6) There was a positive, linear correlation ($p < 0.0005$) between the size of the basal area of the macula densa and its contact area with Goormaghtigh's cell field. The size of the basal area of the macula densa was, however, not correlated with the size of the direct contact area between the macula

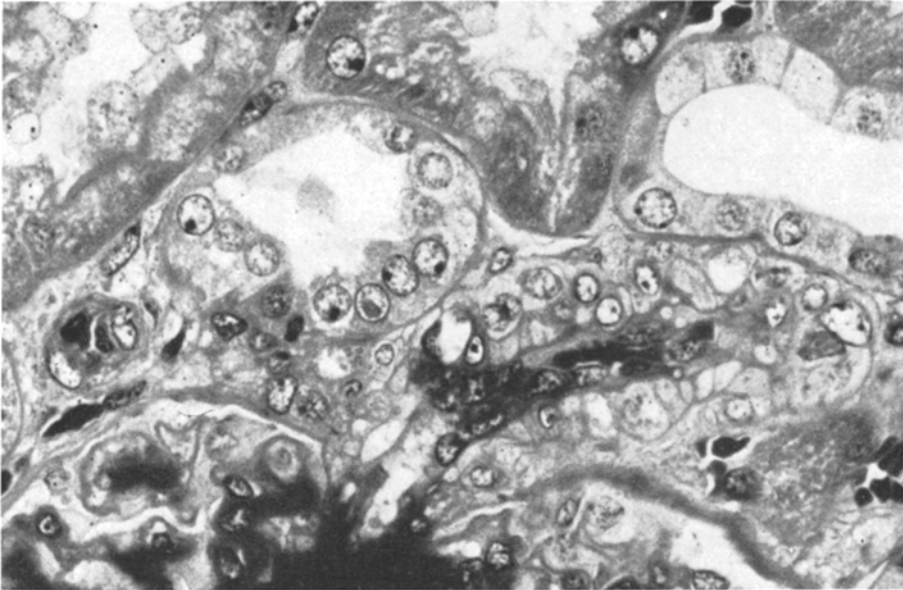


Fig. 2. Juxtaglomerular apparatus with epithelioid cells in the afferent arteriole, Goormaghtigh's cell field, macula densa, and the efferent arteriole. Note: (a) the direct contact between the afferent arteriole and macula densa, (b) a macula densa structure on both sides of the contact zone with the afferent arterioles, (c) the presence of epithelioid cells in the afferent arteriole outside the area of contact with the macula densa, (d) interstitial tissue between the efferent arteriole (left) and macula densa, (e) Goormaghtigh's cell field in contact with the afferent arteriole and macula densa. Section thickness 1.9 μ , Giemsa staining, 695:1

densa and the afferent arteriole ($0.10 > p > 0.05$) or the efferent arteriole ($0.40 > p > 0.30$).

7) The larger the Goormaghtigh's cell field, the more extensive was the area of direct contact with the macula densa and also the direct contact area with the afferent arteriole ($0.005 > p > 0.0025$), but not with the efferent arteriole ($0.10 > p > 0.05$). The direct contact area between the Goormaghtigh cells and the afferent arteriole was on average 1050 μ^2 . It was about twice as large as the contact area between Goormaghtigh's cell field and the efferent arteriole (600 μ^2).

8) The walls of both hilar arterioles may contain epithelioid cells. In both arterioles, within the juxtaglomerular apparatus, they were situated mainly in the contact zone between the arteriole and Goormaghtigh's cell field and less frequently between the arteriole and macula densa. The afferent arterioles contained epithelioid cells more often (in 47 out of 49 juxtaglomerular apparatuses) and in greater number than the efferent arterioles (in 26 out of 49 juxtaglomerular apparatuses). The presence of epithelioid cells in the walls of the hilar arterioles was not confined to the contact of the arteriole with the Goormaghtigh cells or with the macula densa, since they were found also in parts of the arteriole not bordering on either of the two structures. Furthermore, epithelioid cells occurred along the afferent and efferent arterioles beyond the juxtaglomerular apparatus (Fig. 3) and occasionally in the interlobular arteries.

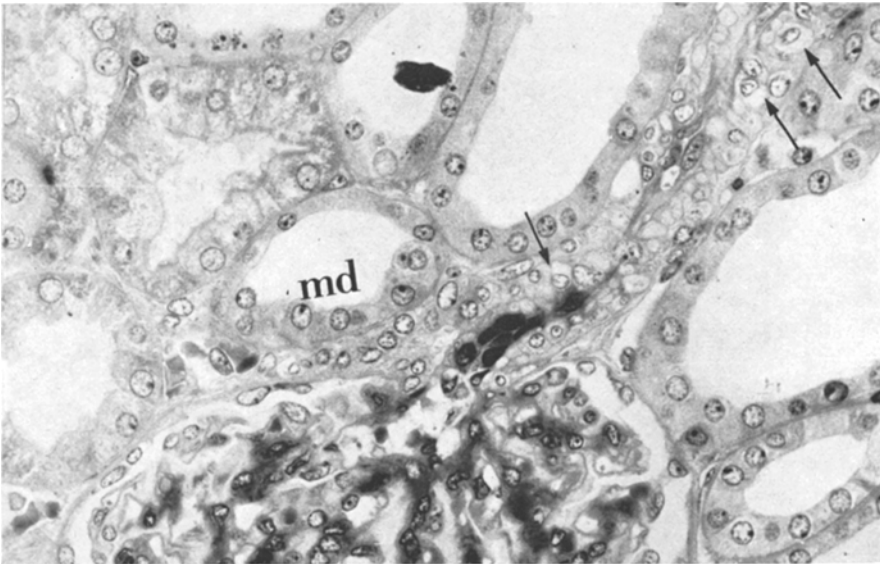


Fig. 3. Juxtaglomerular apparatus with macula densa (*md*), the afferent arteriole and Goormaghtigh's cell field. The afferent arteriole in longitudinal section with numerous epithelioid cells in the wall, up to 120 μ distant from the macula densa (arrows). Goormaghtigh's cell field appears between the afferent arteriole and macula densa. Section thickness 1.9 μ . Giemsa staining, 370:1

9) The mean volume of a single juxtaglomerular cell complex (Goormaghtigh cells and epithelioid cells) planimetrically determined in the kidney of the 19-year-old patient was 29000 μ^3 .

10) There was an inverse flow of blood and urine in the region of the juxtaglomerular apparatus, which could be demonstrated on the 15 nephrons reconstructed from the PAS-stained series.

Discussion

This report presents for the first time morphometrically derived relationships for the structures of the juxtaglomerular apparatus in the normal human kidney. An inverse flow of blood and urine within the juxtaglomerular apparatus has been found both in the human juxtaglomerular apparatus and in the rat (Barajas and Latta, 1963; Faarup, 1965). Whether this observation is of functional importance or merely due to an ontogenetic factor, we cannot say.

We cannot confirm that the findings of Barajas and Latta (1963), and Barajas (1970, 1971), in the rat kidney, which revealed a more extensive contact of the distal tubule with the efferent arteriole than with the afferent arteriole, also apply to the human kidney, if we confine our considerations to the direct contact areas between the macula densa and hilar arterioles. Neither do our results agree with Faarup's (Faarup, 1965), who observed approximately equal contacts between macula densa and both hilar arterioles in the rat kidney.

Our measurements show that in man the direct contact area between macula densa and the afferent arteriole is about twice as large as that between macula

densa and the efferent arteriole. However, we do not think that these relationships are of functional importance. We consider the direct contact between macula densa and the hilar arterioles to be a consequence of the close spatial arrangement of the structures of the juxtaglomerular apparatus. This statement is based on the findings: 1) the size of the contact area between the afferent or efferent arterioles and the macula densa did not correlate with either the size of the basal area of the macula densa or with Goormaghtigh's cell field, and 2) the inconstant presence of a direct contact between macula densa and the hilar arterioles found in the rat (Barajas and Latta, 1963, 1967; Faarup, 1965) and in man (Bohle *et al.* 1970).

If an immediate transmission of information between the macula densa and one or both hilar arterioles is supposed, a direct contact between these structures would be expected to occur without exception. However, since Goormaghtigh's cell field is also according to several other authors (Goormaghtigh, 1937; Oberling and Hatt, 1960; Thoenes, 1961; Bing, 1964; Biava and West, 1966; Faarup, 1965; Bohle and Sitte, 1966; Bohle, 1968; Barajas, 1970, 1971; Bohle *et al.*, 1970) always in contact with the macula densa as well as with the hilar arterioles, it is more likely that information from the macula densa reaches the hilar arterioles via Goormaghtigh's cell field. Our measurements suggest that the flow of information to the afferent arteriole is of decisive importance, because the size of the contact area between Goormaghtigh's cell field and the afferent arteriole correlates with the size of the contact area between Goormaghtigh's cell field and macula densa and with the basal area of the macula densa (Fig. 1). According to our investigations only about half of the basal area of the macula densa borders on the hilar vessels and Goormaghtigh's cell field. In relation to the transverse section of the tubule the macula densa projects mainly laterally beyond Goormaghtigh's cell field, i.e. macula-densa cells are present where neither Goormaghtigh cells nor hilar arterioles are in an immediate spatial relation to the early distal tubule. Whether this morphological behavior of the macula densa is of importance for the maintenance of an osmotic gradient between the content of the urinary tubule and Goormaghtigh's cell field, whose intercellular meshwork of basement membrane-like material according to Gomba and coworkers (1972) may serve to transport sodium, we do not know. On the other hand, the direct contact between the hilar vessels and the distal tubule does not in itself lead to the formation of a macula densa structure, even when the arteriolar walls contain epithelioid cells (Fig. 4).

Our results also show that the presence of epithelioid cells does not depend on the contact between the hilar arterioles and the macula densa or the Goormaghtigh cells, since we observed epithelioid cells outside the juxtaglomerular apparatuses in 33 out of 49 afferent and in 5 out of 49 efferent arterioles examined. The widening of the distal tubule at the macula densa segment indicates that the urinary flow in the region of the juxtaglomerular apparatus should be decreased, thus increasing the time of contact between the urine and the macula densa epithelia. This dilatation of the distal tubule in the macula densa segment has been described in previous observations by Peter (1907) and Biava and West (1966) in agreement with our findings.

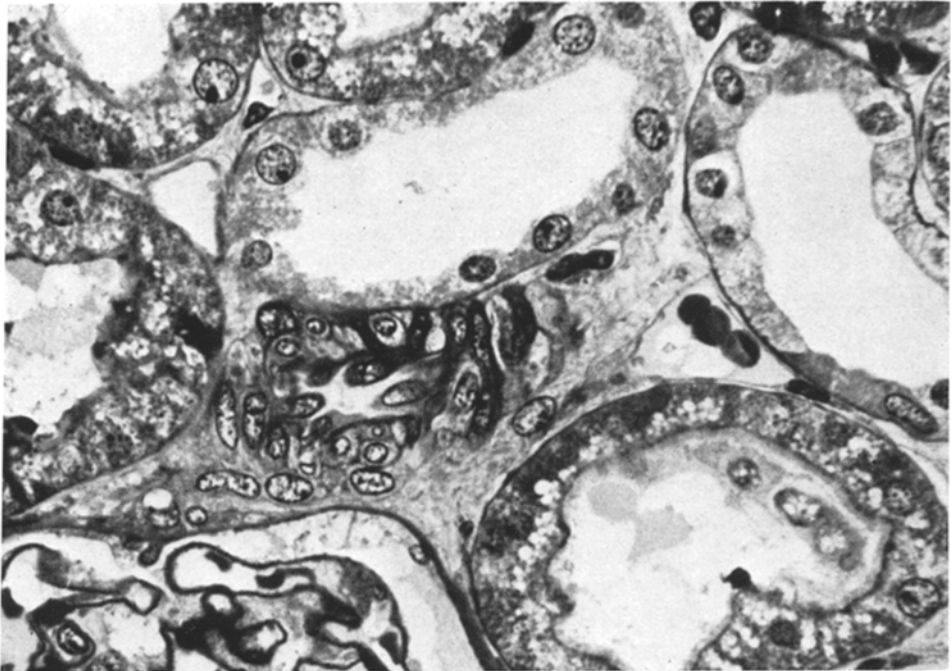


Fig. 4. The afferent arteriole with several epithelioid cells in direct contact with the appertaining distal tubule. Bottom left the glomerulus. Note that the direct contact between arteriole and the distal tubule does not evoke the formation of a macula densa. Section thickness 1.9 μ , Giemsa staining, 695:1

Our measurements derived from the three-dimensional reconstruction of the juxtaglomerular apparatuses provide a more detailed basis for further considerations on the function of the hilar glomerular region in the human kidney.

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