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Research Article

HISTOLOGICAL AND ULTRASTRUCTURAL STUDY ON THE JUXTAGLOMERULAR APPARATUS IN THE KIDNEY OF THE DROMEDARY CAMEL (*CAMELUS DROMEDARIUS*)

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A B S T R A C T

The histology and ultrastructure of the different components of the juxtaglomerular apparatus (JGA) in the kidney of the dromedary camel (*Camelus dromedarius*) were described in the present study. Five samples selected randomly from the renal cortex of eight female adult dromedary camels were used for histology and ultrastructure. Results obtained showed that the macula densa (MD)cells were located at the terminal part of the cortical straight distal tubule and they were present either as single layer of cuboidal to columnar cells or as pseudostratified cells. MD cells rested on an irregular thick basement membrane and were characterized by strong PAS +ve stain, sparse collagen fibres and the lack of underlying reticular fibres. Numerous vesicles were often observed within this basement membrane whichwas characterized by a remarkable irregular arrangement. The most striking feature of the luminal surface of the MD cells was the presence of a single cilium. The MD cells were attached by gap junctions and the lateral surfaces of adjacent cells were separated by irregular intercellular spaces which were more prominent in the columnar type. The cytoplasm of the juxtaglomerular cells (JGCs) showed microfilaments and two types of cytoplasmic granules. The basal laminae of the JGCs, extraglomerular mesangeal cells (EMCs) and of the endothelial cells of the afferent arteriole near the JGCs appeared to have different types of vesicles. The cytoplasm of the EMCs was filled with spherical mitochondria, well developed rough endoplasmic reticulum and homogeneous granules.

INTRODUCTION

The JGA is a specialized contact region between the glomerulus and the cortical thick ascending limb of the loop of Henle thatis believed to be involved in feedback control of renal blood flow and glomerular filtration rate (Reece, 2015). It also plays an active role in the maintenance of ion homeostasis and control of blood pressure (Yao *et al*., 2009). It represents a major structural component of the renin-angiotensin system and is one of the most important regulatory sites of renal salt and water conservation (Peti-Peterdi and Harris, 2010). It accommodates groups of cells in the vascular pole of the renal corpuscle (Moussa, 1982; Al-Baldawi *et al*., 1985; Kurtz *et al*., 2007; Dongmei-Cui, 2011). These groups of cells are MD in the distal tubule, JGCs (also known as granular, granular epitheloid or myoendocrine cells) in the afferent arteriole and specialized interstitial cells are EMCs(also known as Polkissen, Lacis or Goormaghtigh cells) (Briggs and Schnermann, 1996; Bacha and Bacha, 2000; Dongmei-Cui, 2011).

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Although several studies have been conducted on the histology and ultrastructure of the dromedary kidney (Abdalla, 1973; Moussa, 1982; Safer *et al*., 1988; Safer and Abo-Salem, 1991; Safer, and Katchburian, 1991; Beniwal *et al*., 1997; Beniwal *et al*., 1998) little is known about the JGA. Hence the present study was undertaken to describe the fine structure of the JGA components in the kidney of adult dromedary camel by using normal and special stains and transmission electron microscope.

MATERIAL AND METHODS

Animals and tissues

The study was carried out using eight apparently healthy dromedary female camels slaughtered at a local abattoir in Khartoum state, Sudan. A number of samples (about 1 cm^3) were collected from the cortex of right kidney of each female animal. Samples were then processed for histological and ultrastructural techniques.

Histology

Samples were immediately fixed in 10% neutral buffered formalin. Tissues were then processed by the routine histological techniques (Bancroft and Gamble, 2008). Afterwards, sections were then stained with Hematoxylin and Eosin to choose randomly five samples containing several glomeruli with JGA. Chosen sections were then stained with Masson's trichrome, Van Gieson's, Verhoeff's, or Gomori's silver impregnation technique stains for studying the general structure of the JGA. Periodic Acid Schiff's (PAS) stain was used for the demonstration of the basement membrane of the JGA cells and JGCs granules.

Ultrastructure

Samples were sliced into small pieces (about 1 mm^3) and fixed in 2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.4)for 2-4h (Bancroft and Gamble, 2008). Tissues were then washed in 0.13 M Millonig's buffer pH 7.2 for 10 minutes and then post-fixed in 1% osmium tetroxide in Millonig's buffer for one hour. Samples were rinsed in distilled water and then dehydrated in ascending grades of alcohol (50%, 70%, 80%, 90% and 95%) for 10 minutes each. Tissues were then immersed in 100% ethanol (with Molecular sieve added) two times for 10 minutes each. Samples were cleared in propylene oxide two times 10 minutes each, followed by infiltration with 2:1 and then 1:2 epoxy resin for two hours each. Finally, the samples were embedded in fresh resin overnight in an oven (60^oc).

Semi-thin sections, of 1µm thickness, were cut using a microtome fitted with a glass knife and subsequently stained with buffered toluidine blue. Ultra-thin (50-90nm thick) sections of selected areas were cut on a Reichert-Jung Ultracut (C.Reichart AG., Vienna, Austria), using a diamond knife, collected onto copper grids, and stained with Reynold's lead acetate. The sections were counterstained with an aqueous, saturated solution of uranyl citrate. Sections were then examined in a Phillips CM10 transmission electron microscope (Phillips Electron Optical Division, Eindhoven, The Netherlands), operated at 80kV. A megaview III side-mounted digital camera (Olympus Soft Imaging Solutions GmbH, Munster, Germany) was used to capture the images and iTEM software (Olympus Soft Imaging Solutions GmbH, Munster, Germany) was used to adjust the brightness and contrast.

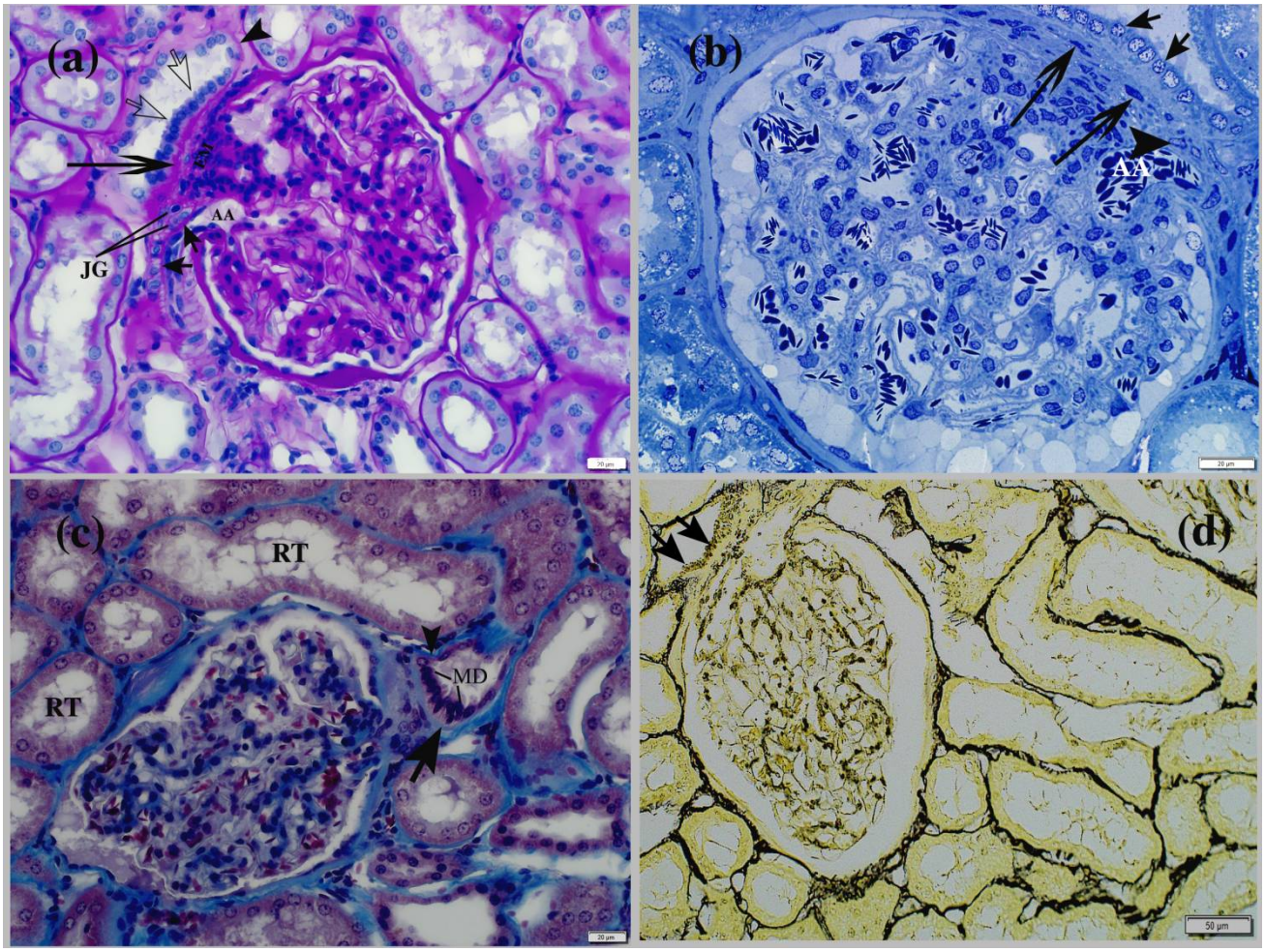

Fig 1 Light photomicrographs of the juxtaglomerular complexin the camel: (a) PAS, (b)Toluidine blue, (c) Masson's trichrome and (d) Gomori's silver impregnation technique.

(a) Transparent arrows: macula densa. JG: juxtaglomerular cells.AA: afferent arterioles.EM: extraglomerular mesangial cells. Short arrows: the basement membrane of the endothelium of the afferent arteriole beside the juxtaglomerular cells. Compare the thickness of the basement membrane (long arrow) of the macula densa and of the normal distal tubule cells (arrowhead).
(b) AA: afferent arteriole.Short arrows:macula densa. Arrowhead: JGCs.Long arrows: extraglomerular mesangial cells.
(c) Arrow: basement membrane of the macula densa.Arrowhead: basement membrane of the normal distal tubule. RT: renal tubules.
(d) Demonstrating the reticular fibres below the different types of the epithelial cells of the nephron except below the macula densa (arrows).

For cytometry, cross sections from the distalstraight tubule where the MD were located,were used to measure the height and width.

RESULTS

Histology

With the light microscope, the MDappeared as a group of cells located at the cortical straight distal tubule just before the junction between the straight and convoluted segments of the distal tubule and facing the vascular pole of the glomerulus (Fig.1.a,b). The MD cells were distinguished readily from the other cells of the distal tubule by being relatively large, tightly packed and showing prominent large dark nuclei (Fig.1.a,c). These nuclei were often located vertical to the basement membrane (Fig.1.a,c) as compared to the nuclei of the cells of other part of the distal tubule which were located horizontally. The MD cells were present as a single layer of cuboidal cells with large spherical nuclei (Fig.1.b) to low columnar cells with large oval nuclei(Fig.1.a). Sometimes the oval nuclei of such cells tended to be arranged in two levels (Fig.1.c).

The basement membrane of the MD cells was strikingly thicker as compared to the other part of the distal tubule and characterized by strong PAS +ve staining (Fig.1.a), sparse collagen fibres (Fig.1.c) and the lack of the underlying reticular fibres (Fig.1.5).

The JGCs were found mainly in the tunica media of arteriole, probably afferent arteriole that was closely related to the glomerulus (Fig.1.a,b). However, these cells could be found far away from the arteriole near one side of the MD and sometimes could be observed in the extraglomerular mesangium.The nucleus was oval or spherical in shape (Fig.1.b). The basement membrane of the endothelium of the afferent arteriole beside the EMCs was thicker than that of the other part of the arteriole and stained stronglywith PAS (Fig.1.a).

The EMCs appeared as group of cells usually confined to the area between the afferent and efferent arterioles and MD cells.However, they were continuous with the intraglomerular mesangial cells. These cells were characterized by flattened dark nuclei and having different sizes arranged in many layers.

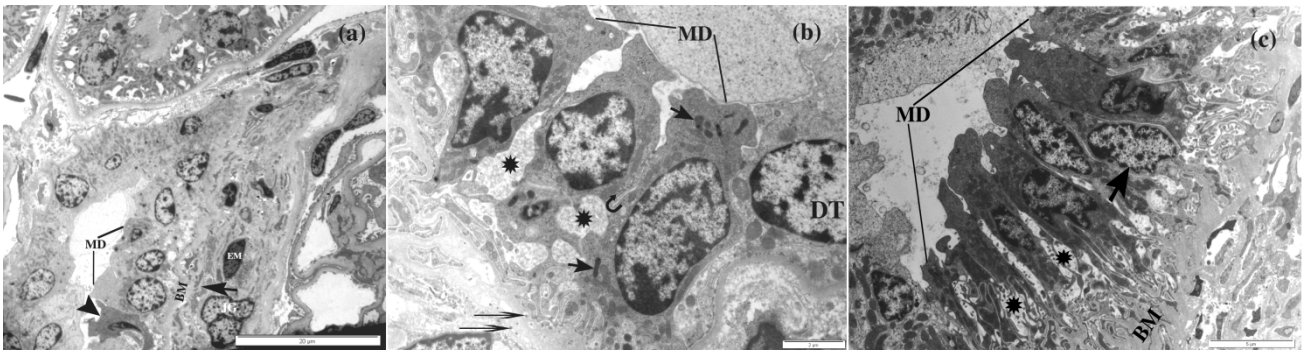

Fig 2 Transmission electron micrographsof the macula densa in the camel.

(a)Demonstrating light macula densa cells (MD) with spherical nuclei and dark one (arrowhead) both resting on irregular basement membrane (BM) with branching processes (arrow). Note juxtaglomerular (JG) and extraglomerular mesangial cells (EM).
(b)High magnification of fig.2.a demonstrating the cytoplasmic communication between two adjacent MD cells (curved arrow), normal distal tubule (DT) cell, wide intercellular space (stars), lysosome (short arrows) in the apical and basilar parts of the MD cells and the basement membrane of the MD containing numerous different types of vesicles (long arrows).
(c)Long macula densa (MD) resting on irregular basement membrane (BM). Note the intercellular space (stars) and surfaces of some cells not reaching the lumen (arrow).

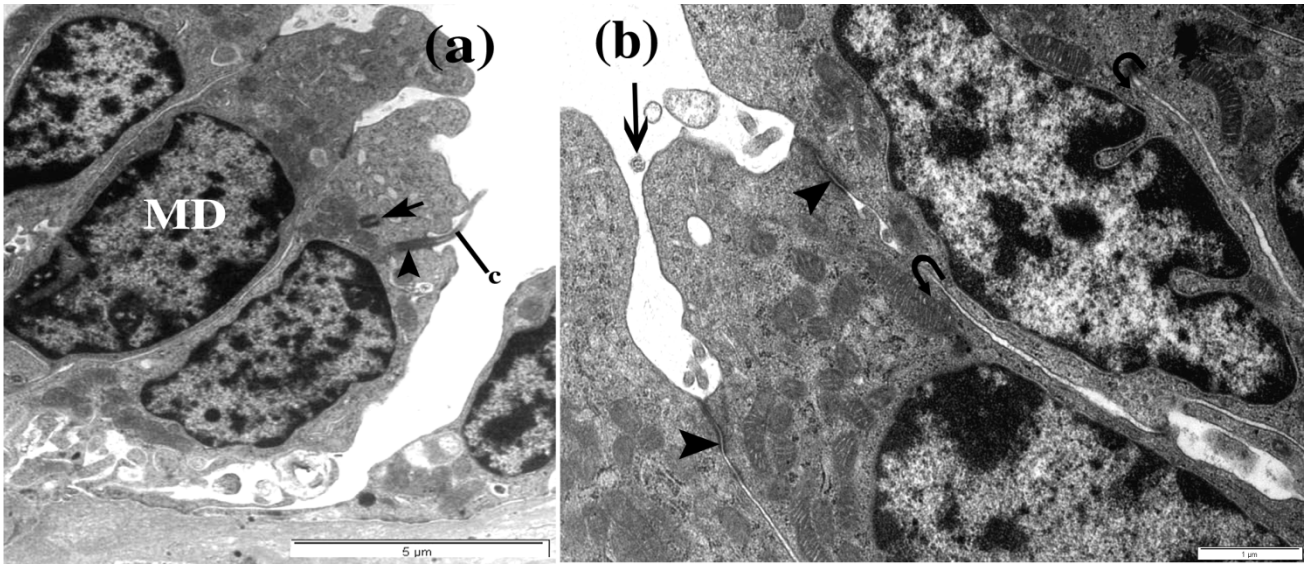

Fig 3 Transmission electron micrographs of the (a) Macula densa cells (MD) with a cilium (C) projecting into the lumen. A centriole (arrow) and the basal body (arrowhead) are also demonstrated. (b) Apical portion of three adjoining MD cells demonstrating their gap junctions (arrowheads), cytoplasmic communication (curved arrows) between two adjacent cells and cross section of cilia (arrow).

Also these cells have thin cytoplasmic processes that were surrounded by a basement membrane or matrix material devoid of any blood or lymphatic vessels (Fig.1.a,b).

Ultrastructure

Ultrastructurally, MD cells were either light cuboidal or dark columnar.The latter were sometimes scattered among the light cuboidal cells (Fig.2.a),but mostly seen aggregated as a group of cells (Fig.2.b,c). So MD cells were present either as a single layer of cuboidal to columnar cellsor had a pseudostratified appearance. The latterwas the most prevalent pattern and characterized by predominant long crowded cells intermingled with relatively shorter cells with their apical surfaces failing to reach the lumen (Fig.2.c). Their nuclei were arranged in two levels and tended to be located quite far from the basement membrane. These nuclei were large oval or irregular in shape, showed prominent indentationsand the heterochromatin was observed mostly aggregated on the periphery (Fig.3.b).

Dark simple columnar cells with large oval nuclei and without any indentation were located vertically not far away from the basement membrane (Figs.2.b). The nuclei of the light cuboidal cells were spherical to oval in shape, approximately centrally located and showed more euchromatin than the dark cells (Fig.2.a). MD cells measured from 10 to 22 µm in their height and from 2 to 7 µm in their width.

The MD cells exhibited electron dense cytoplasm with rough endoplasmic reticulum, clear vesicles and elongated mitochondria in different regions of the cell (Figs.2.b,c and 3.b). Mitochondria were not arranged vertical to the base of the cell and were rarely enclosed within foldings of the basal plasma membrane (Fig.4.a). These mitochondria appeared fewer, smaller and randomly distributed when compared to those of the other normal cells of the straight distal tubule (Fig.2.b). Numerous lysosomes were seen in the apical and basilar parts of the MD cells (Fig.2.b).

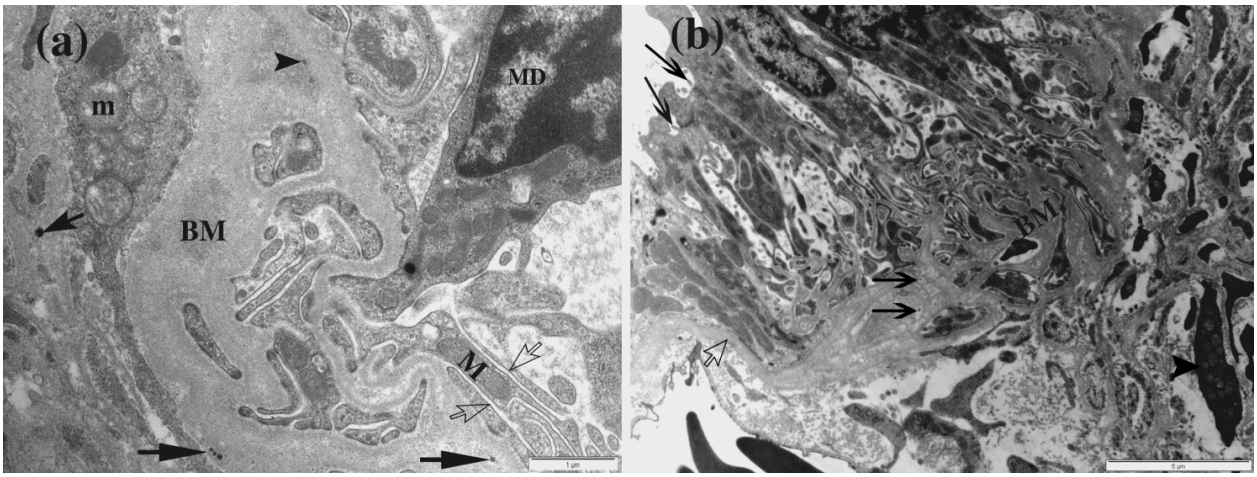

Fig 4 (a) High magnification of Fg.2.c demonstrating the irregular macula densa (MD) basement membrane (BM) containing clear vesicles (arrowhead) and dense-cored vesicles (long arrows), narrow basal part of MD cell and irregular basal infoldings (transparent arrows) containing mitochondria (M). EMCs present spherical mitochondria (m) and dense-cored vesicles (short arrow) in the matrix.
(b)Electron micrograph demonstratingbasal cytoplasmic processes of the MD cells interdigitated with those of the EMCsand the complexity of the basement membrane (BM) of the MD.Note small microvilli at the junctions between the MD cells (long arrows), spherical mitochondria of the EMCs (arrowhead),basement membrane of the MD containing numerous different types of vesicles (short arrows)and thin homogeneous basement membrane of the distal tubule (transparent arrows).

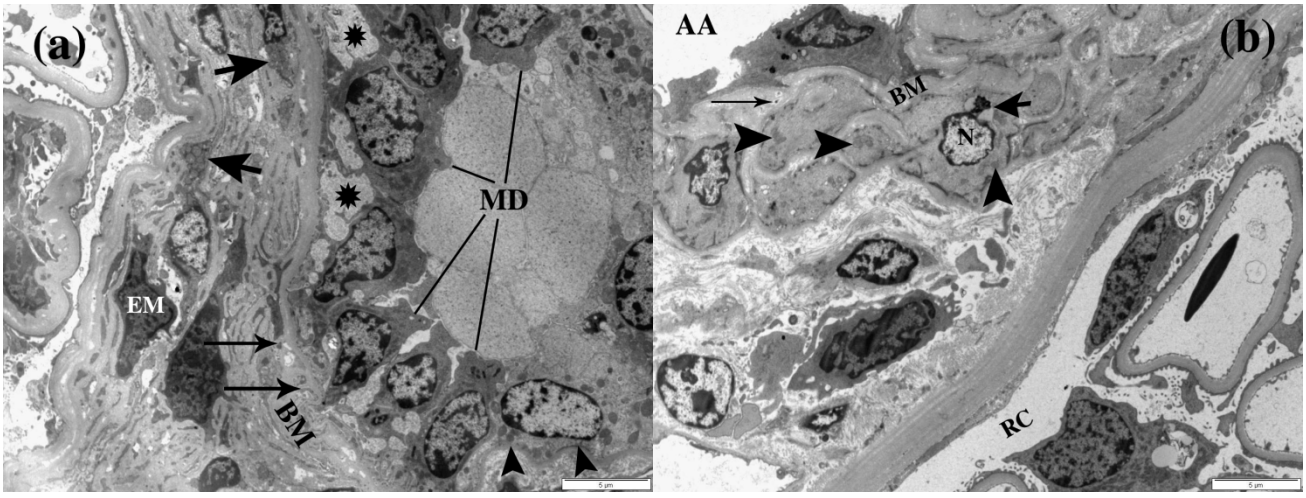

Fig 5 Transmission electron micrographs of the juxtaglomerular apparatus in the camel.
(a)Macula densa (MD) cells presenting oval nuclei and wide intercellular spaces (stars). EM: extraglomerular mesangial cells withspherical mitochondria (short arrows). Note the thickness and arrangement of the basement membrane of the macula densa (BM) with its branching processes (long arrows) and basement membrane of the normal distal tubule cells (arrowheads).
(b) Juxtaglomerular mesangial cells presenting spherical nuclei (N), electron dark bodies (arrowheads) and residual bodies(thick arrows). RC: renal corpuscle. Afferent arteriole (AA) lined by the endothelial cells that rest on a thick basement membrane (BM) contains dense-cored vesicles (thin arrows).

All the MD cells protruded into tubular lumen and sometimes showed short microvilli (Fig. 2.b,c).The most striking feature of the luminal surface of the MD cells was the presence of a single cilium having a centriole which was closely located to the basal body of the cilium and the nucleus (Fig.3.a,b). The cross section through the shaft of the cilia revealed that the outer doublets of the microtubules were 7 to 8 in number (Fig.3.b).

The lateral surfaces of adjacent cells were separated by irregular intercellular spaces. In the columnar type of MD cells, these intercellular spaces were broad and more irregular towards the base (Fig.2.b,c). The MD cells were attached by gap junctions on their lateral aspects and having few microvilli at the apical junctions (Fig.4.b). Cytoplasmic communications between two adjacent cells (Figs.2.b and 3.b) were observed. The basal cytoplasmic processes of the MD cells were invaginated deeply in the basement membrane and interdigitated with those of the EMCs (Fig.4.a,b). The lateral infoldings were generally less developed but more prominent in cuboidal type of MD cells.

The basement membrane of MD was characterized by a remarkable irregular arrangement due to the presence of deep invaginations of the MD basal infolding (Fig. 4.b). It also had branching processes which were often very close to the matrix around the EMCs or were actually continuous (Fig. 5.a). These features of the basement membrane tended to be more pronounced as the length of the MD increased. Numerous vesicles were often observed within this basement membrane at various levels (Figs.2.b and 4.a,b).

The JGCs cytoplasm demonstrated myofilaments and two types of cytoplasmic granules. The first type was light, usually round or oval in shape and comparatively consisting of homogenous contents and appeared to be surrounded by a single membrane. The second type was round and frequently dark containing nonheterogenous contents. The JGCs that were located near to the endothelial cells of the afferent arteriole were surrounded by a basement membrane or matrix material showing electron density similar to that of the basement membrane of the endothelial cells. This layer decreased and fused gradually outward to the matrix of the EMCs. The basal laminae of the endothelial cells of the afferent arteriole near the JGCs and that of the JGCs appeared to contain numerous clear, dense and dense-cored vesicles (Fig.5.b). These cells were attached by gap junctions.

It was confirmed electron microscopically thatEMCs were contacting the base of the MD. This matrix presented electron density similar to that of the MD basement membrane that communicated with its branches and with the matrices of the JGCs and intraglomerular mesangial cells. The EMCs basement membranes appeared having numerous clear, dense and dense-cored vesicles. EMCs appeared irregular in shape due to presence of cytoplasmic processes and were attached by gap junctions. Their nuclei appeared spindle, elongated, oval to irregular in shape having more heterochromatin than that of the other two types of the JGA. The cytoplasm was filled with spherical mitochondria and well developed rough endoplasmic reticulum. Free ribosomes were observed scattered between the mitochondria giving the cytoplasm more dense appearance. Homogeneous cytoplasmic granules similar to those of the JGCs, pair of centrioles and bodies containing vesicles were also observed (Figs.2.a and 5.a).

DISCUSSION

The results of the present investigation complemented earlier histological and ultrastructural observations of the JGA in dromedary camel (Moussa, 1982; Al-Baldawi, 1985; Beniwal*et al*., 1997), but in the available literature the nature and position of the JGA components are still debatable.

The present study showed that the MD cells were located at the terminal cortical straight distal tubule. A similar location of these cells was reported by Kaisslin*et al*. (1977) and Verlander, (1998) in rat, Eurell and Frappier (2006) in domestic animals andBriggs*et al*. (1990), Kriz (1990),Sipos*et al*. (2010) and Zhou *et al*. (2017) in human. Controversially, Bulger *et al*. (1979) in dog stated that MD cells were located at the distal convoluted tubule.Since the MD is considered as a sensor for the concentration of sodium ions (Peti-Peterdi and Harris, 2010; Sipos*et al*., 2010), its position had been suggested to protect them from disturbing influences resulting from the secretory activity of the subsequent tubular portion (Kaisslin*et al*., 1977).

In the present study, histological observations revealed that the MD cells appeared more crowded. A similar finding had been reported by Moussa (1982) in camel, Bacha and Bacha (2000) and Kriz (1990) and Dongmei-Cui (2011) in human. In addition, ultrastructural investigations in this study revealed that most of the MD cells showed a remarkable difference in their length resulting in a pseudostratified appearance. This may explain the stratified arrangement of such cells by using light microscope which has been reported by Dellmann and Brown (1981) in horse and Beniwal*et al*. (1997) in camel.

In the current study, the basement membrane of the MD was very thick and similar observations had been made in the monkey's kidney (Komadinovic*et al*., 1978). Also in this study, the basement membrane of the MD appeared irregular in shape due to presence of irregularly arranged deep invaginations of the MD basal infoldings. Moreover, the branching processes arising from this basement membrane formed extensive and complex contact with the intercellular matrix of EMCs.The special structure of this basement membrane explains the absence of reticular fibres in this area and this may explain the close relationship between the different components of JGA which provide mechanical support and might work as one system. This finding disagreed with Moussa (1982) in dromedary camel and Wheaterand Burlitt(1987), Gartner and Hiatt (2007) and Young *et al*. (2014) in human who reported that MD basement membrane is an indistinct, extremely thin or absent.

Earlier studies demonstrated the presence of various vesicles within the thick basal laminae of the nephron in the desert gerbil (Safer *et al*., 1990) and dromedary camel (Safer and Katchburian, 1991), Bowman's capsule (Mbassa *et al*., 1988) and intraglomerularmesangium (Takami *et al*., 1990) of the rat. Safer and Katchburian (1991) described them as being surrounded by membrane and hence identified them as membrane-bound bodies. Both Safer *et al*. (1990) and Safer and Katchburian (1991) considered these bodies as a unique structure of the desert animals. In the present study, similar structures were also found in the juxtaglomerular apparatus.

They were mainly found in the basal laminae of both MD cells and endothelial cells adjacent to the JGCs, and also in the matrix around the JGCs and EMCs. Due to the increased activity of juxtaglomerular apparatus in animals living in a dry environment (Mbassa, 1988). Consequently, the present study may support the suggestion given by Safer and Katchburian (1991) in that the vesicular bodies could play an important role in the ionic transport mechanism resulting in high osmolarity of the camel urine. The extracellular matrix acts not only to support glomerular/tubular cells but also conveys information to them and modifies their behaviour (Sterzel *et al*., 1992).

The present findings were revealed three types of MD cells; simple cuboidal, simple columnar and pseudostratified columnar cells. The basolateral cell membranes have very rapid regulatory mechanisms which maintain the cell volume during reductions in basolateral osmolarity (Gonzalez *et al*., 1988). It had been noted in the present study that the lateral dilated intercellular spaces, which were previously described by Kriz (1990) in human and Eurell and Frappier (2006) in domestic animals, were more prominent in association with columnar MD cells. Kaissling and Kriz (1982) and Kriz (1990) reported that such spaces varied depending on the functional state of the kidney, and Zhou *et al*. (2017) in human suggested that these spaces were associated with their permeability to water. In the present study, this may suggest the functional differences between the two types of cells observed in this study.

It is known that gap junctions are highly specific membrane structures that contain groups of passages between two adjacent cells (Bruzzone *et al*., 1996). Gap junctional passages were necessary for many physiological actions, including differentiation and cell growth, (Vinken *et al*., 2006), provision of a pathway for signal transduction and organization of multicellular functions (Yao *et al*., 2009). These gap junction passages also provide selective permeability (Goldberg *et al*., 2004) and allow the reciprocity of ions such as Na^+ and K^+ (Mes¸e *et al*., 2007; Cui, 2011). It has been indicated that gap junctions were essential for the correct juxtaglomerular positioning (Kurtz *et al*., 2007) and renal autoregulation (Yao *et al*., 2009). These gap junctions may suggest that they have an important role in the macula densasignaling to renin-producing cells (Kurtz *et al*., 2007). This investigation revealed the presence ofgap junctions between the cells of both EMCs and JGCs and the gap junctions together with their passages were observed between theMD cells.Eurell and Frappier (2006) in domestic animals and Yao *et al*. (2009) in ratobserved the presence of gap junctions between the cells of both EMCs and JGCs. Verlander (1998) in rats suggested that gap junctions between adjacent EMCs and also neighboring intraglomerular mesangial cells may take part in the regulation of nephron filtration rate. Ren *et al*. (2002) added that gap junctions among mesangial cells and between mesangial cells and vascular smooth muscle cells communicate the Tubuloglomerular feedback signal to the afferent arteriole. Controversially, Kirk *et al*. (2010) in human stated that MD cells were having tight junctions.

In the present study, single primary cilia were frequently observed in the MD cells. A similar finding has been reported in other species including human (Sottiurai and Malvin, 1972;Webber and Lee, 1975; Sipos *et al*., 2010; Wang *et al*., 2015). However, unlike the typical pattern of the primary cilium, the present finding revealed a change in the pattern of the cilium microtubule as one or two microtubules located at the centre, resulting in the reduction of the number of the peripheral microtubules. This may be due to the cross sections of the cilia in the present study passed through the shaft. Similarly, Satir *et al*. (2010) stated that the typical pattern of the primary cilium is often lost towards the cilium tip. Unanimously, it was agreed that the major function of primary cilia in kidney wereinvolved in the mechanosensation of urine (Prasad *et al*., 2014). The present study is the first report of the presence of cilium in the MD cells in dromedary camel kidneys and this observation raised an interesting question concerning the significance of cilia in camel JGA which necessitates future investigations.

As noted in the present study, the basement membrane of endothelial cells adjacent to the JGCs was thick and strongly reacted with the PAS stain. At electron microscopic level, this study showed that the basal lamina was in close contact with the basement membranes around the JGCs. This result was similar to that reported in rat (Latta and Maunsbach, 1962) and dog (Bulger *et al*., 1979). This strong structural relationship may suggest that a functional relationship is present between these endothelial cells and JGA components. In the present study, prominent vesicles were located in the extraglomerular mesangium. It has been suggested that the presence of these vesicles in basement membrane might be linked with the ionic transport mechanism (Safer and Katchburian (1991). Moreover, the presence of such vesicles along with massive amount of mitochondria in the present study may indicate for the hyperactivity of EMCs. This may lend support to the accounts given by (Goligorsky *et al*., 1997) and (Zhou *et al*., 2017) who stated that EMCs believed to act as potential transimitters of information between the macula densa, afferent arteriole and intraglomerularmesangium. This eventually leads to regulation of blood flow through the glomerular arterioles which in turn affects the glomerular filtration rate (Verlander, 1998).

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