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Enzyme activity in the kidney of the mudskipper *Periophthalmus koelreuteri* (Pallas)

N. K. EL-SAYED AND A. M. SAFER

Department of Zoology, University of Kuwait, P.O. Box 5969, Kuwait

ABSTRACT

Enzyme histochemical studies were carried out on the head and trunk kidneys of the mudskipper *Periophthalmus koelreuteri*. The enzymes investigated were succinate dehydrogenase (SDH), NAD-linked malate dehydrogenase (MDH), α-glycerophosphate dehydrogenase (α-GPDH), NADP-linked isocitrate dehydrogenase (ICDH), NAD-linked lactate dehydrogenase (LDH), NADP-linked glucose-6-phosphate dehydrogenase (G6PDH), nonspecific esterases and adenosine triphosphatase (ATPase).

Dehydrogenase activities were negligible in renal corpuscles and weak in distal tubules, but were generally high in proximal tubules. Activities of mitochondrial bound enzymes (SDH, MDH and α-GPDH) indicated that more mitochondria were found in the proximal tubules than in the distal tubules, whereas LDH as representative of glycolytic pathway was weakly to moderately reactive in both segments. Non-specific esterases were found in the lysosomal system of PI tubule cells and in the melano-macrophage centres. ATPase activity was found in the renal corpuscle and was more active in the cytoplasm and basement membrane of the proximal tubules than in the distal tubules.

The results imply the importance of the proximal tubule segment in osmoregulation and excretory activities of the kidney of *Periophthalmus* in the hyperosmotic environment of the Arabian Gulf.

INTRODUCTION

The functional glomerular nephrons in the head kidney of the mudskipper *Periophthalmus koelreuteri* resemble those of the typical opisthonephros of marine teleosts (Safer *et al.* 1982), consisting of glomerulus, proximal I, proximal II, distal and collecting tubules.

As the distribution and activities of histochemical components were useful in the characterization of the morphological and functional features of the various segments of the renal tubule of the head kidney of *P. koelreuteri* (Safer *et al.* 1982), it seemed pertinent to extend these investigations to include other enzymes. Moreover, the present information on the distribution and activities of different enzymes in the kidney of fishes is rather scarce, as contrasted to the vast information available on mammalian kidney (Endo & Kimura 1982). Hickman & Trump (1969) presented a histogram of several enzymes characterizing the euryhaline teleost kidney. More

recently the distribution of enzymes has been investigated histochemically, in the course of morphological studies, to differentiate between the various segments of the nephron (Kendall 1972; Oppermann 1973; Hinton *et al.* 1973; Kendall & Hinton 1974; Hackert-Korde 1977; Endo & Kimura 1982; Safer *et al.* 1982). Hentschel & Meyer (1979, 1980, 1982) compared the distribution of oxidative enzymes and some phosphatases in the urinary apparatus of several freshwater and marine fishes. These studies should therefore be of value in elucidating the functional abilities of the euryhaline fish kidney as compared to those of stenohaline freshwater and marine fishes.

MATERIALS AND METHODS

Head and trunk kidneys were dissected from 16 adult *Periophthalmus koelreuteri* (13–18 g fresh weight) collected from the mudflats of Kuwait Bay between October and February.

In the investigation of the activities of dehydrogenases and adenosine triphosphatase unfixed cryostat sections 8–10 μm thick were used. For non-specific esterases the tissue was fixed in formol calcium (1% $CaCl_2$ in 4% formalin) for 4 h at 4°C, washed in sodium cacodylate buffer pH 7.4 for 1 h, then impregnated with gum sucrose solution (Holt 1958) for 1–2 days. Six to eight μm thick cryostat sections were received on gelatine-coated slides and subjected to formaldehyde vapour before incubation.

Bound dehydrogenases (succinate dehydrogenase SDH and α-glycerophosphate dehydrogenase α-GPDH) were incubated in aqueous media according to the method of Nachlas *et al.* (1957) for 15–30 min at 37°C (substrate conc. 0.1 M, nitro blue tetrazolium (NBT) conc. 1 mg/cc). Soluble dehydrogenases (NADP-linked glucose-6-phosphate dehydrogenase G6DPH, NAD-linked lactate dehydrogenase LDH, NAD-linked malate dehydrogenase MDH and NADP-linked isocitrate dehydrogenase ICDH) were demonstrated in unfixed cryostat sections using gel-film media (see Lojda *et al.* 1979, gelatine conc. 12%, substrate conc. 200 mM, co-enzyme conc. 0.5 mg/cc and NBT conc. 1 mg/cc, phenazine methosulphate (PMS) was not added). Incubation time was for 20–30 min at room temperature. Control sections were incubated in media lacking substrates. Gelatine was removed with warm water, sections were post-fixed in 10% formalin and mounted in glycerine jelly.

Non-specific esterases were demonstrated by the method of Holt & Withers (1952). Control sections were incubated in a medium without the substrate. Adenosine triphosphatase (ATPase) activity was visualized by the method of Wachstein & Meisel (1957). Parallel sections were incubated with equimolar concentration of β-glycerophosphate instead of adenosine triphosphate or without substrate. Other sections were incubated in a similar medium lacking magnesium ions. Controls were exposed to heat (90°C for 10 min) and inhibition of alkaline phosphatase by L-cysteine (0.262% for 20 min at 37°C) (Lojda *et al.* 1979). Substrates, NBT and L-cysteine were purchased from Sigma Chemicals Co.

RESULTS

The head and trunk kidneys of the mudskipper are connected by a long strip of renal tissue. They both consist of nephrons supported by haemopoietic tissue of leukocytes,

erythrocytes and malenomacrophage centres, but the amount of haemopoietic tissue is greater in the head kidney. The tubular segment of the glomerular nephron is subdivided into first proximal (PI), second proximal (PII) and distal tubules. PI tubules are composed of low cuboidal or columnar cells which possess centrally or basally placed nuclei and contain many apical inclusions and lysosomes and a prominent brush border. PII tubule cells are more consistently columnar, with centrally placed nuclei, few apical inclusions, lysosomes and a less well formed brush border. The basement membrane of PII cells is folded and conspicuously thicker than in PI. The distal tubules are lined by cuboidal cells with centrally placed nuclei and no inclusions. The brush border is reduced but the basement membrane is well formed. The collecting tubules have a wide lumen lined by cuboidal cells and ensheathed by a layer of collagen fibres. In unfixed frozen section the three segments of nephronic tubules can only be identified by the height of the cells (PII tubules have the highest cells whereas the distal tubule cells are low cuboidal).

ENZYME REACTIONS

All enzymes investigated in this study showed patterns of distribution and activities which were similar in both head and trunk kidneys.

The renal corpuscle showed no activity for all the investigated dehydrogenases (Fig. 1). Mitochondrial bound enzymes (MDH, SDH and GPDH) were most active in the proximal tubules (Figs 1, 2 and 3). In PI, the enzymes were observed mainly in the basal parts of the tubule cells surrounding the basally located nuclei whereas in PII enzyme activities were evenly distributed throughout the cytoplasm. SDH appeared to be more active in PI than in PII while the latter showed more intense reactions for MDH. Distal tubules reacted weakly for all the mitochondrial bound enzymes.

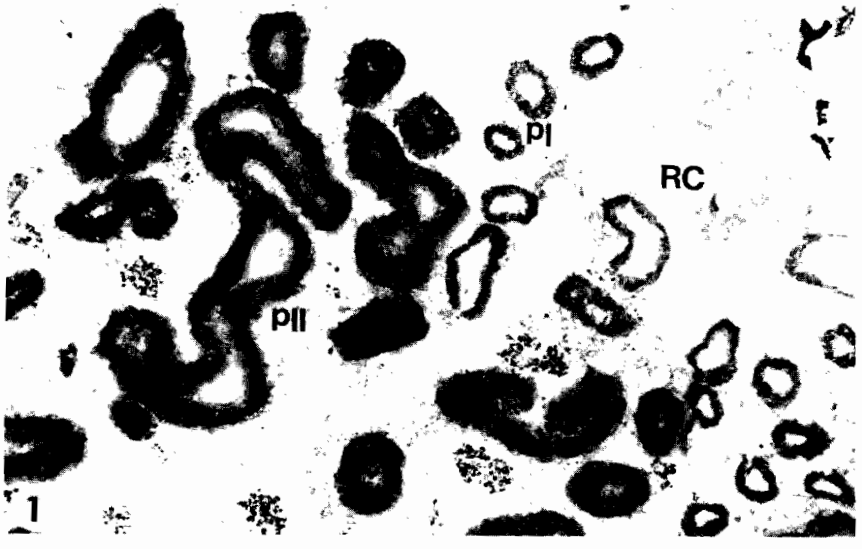

Fig. 1. *Periophthalmus* head kidney, unfixed cryostat section, 8 μm, MDH (NAD-linked) reaction. Intense reaction products occur in the proximal (PI, PII) tubules but none in the renal corpuscle (RC) × 80.

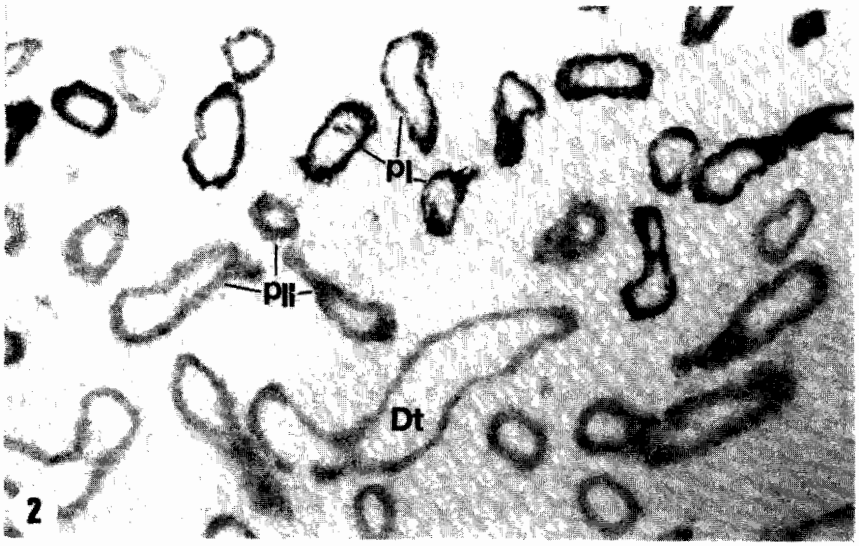

Fig. 2. *Periophthalmus* head kidney, unfixed cryostat section, 8 μm, SDH reaction. More intense reaction products occur in the first proximal (PI) than in the second proximal (PII) tubule cells. Weaker activity occurs in the distal tubule (Dt) × 80.

The strongest ICDH was localized in PII cells (Fig. 4). Moderate activity was exhibited by PI cells but only weak activity for ICDH was observed in the distal tubule cells. A uniform weak to moderate LDH activity was found in all parts of the nephron tubule (Fig. 5) with the exception of the renal corpuscle. In contrast, the level of activity of G6PDH in PI and PII tubules was quite different (Fig. 6). PI tubules did

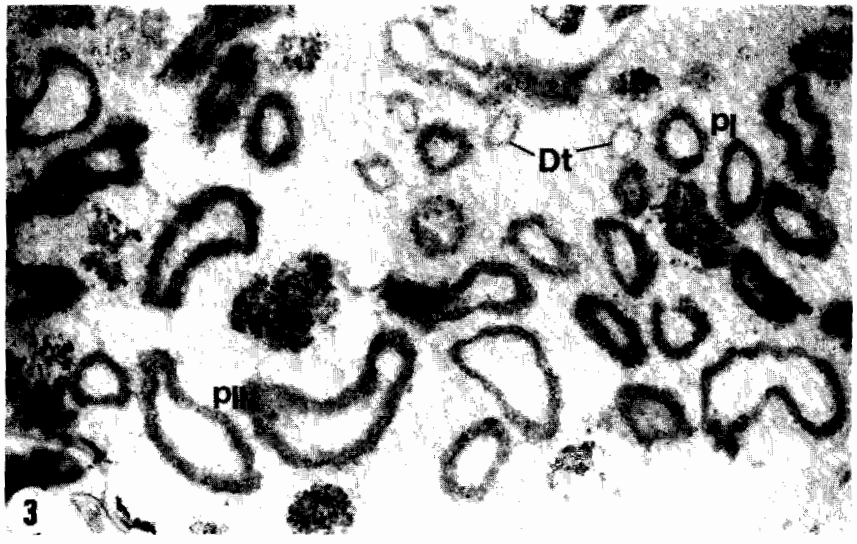

Fig. 3. *Periophthalmus* head kidney, unfixed cryostat section, 8 μm, α-GPDH (NADP-linked) reaction. Moderate to intense activity occurs in the proximal tubules (PI, PII). The distal tubule (Dt) is weakly reactive × 80.

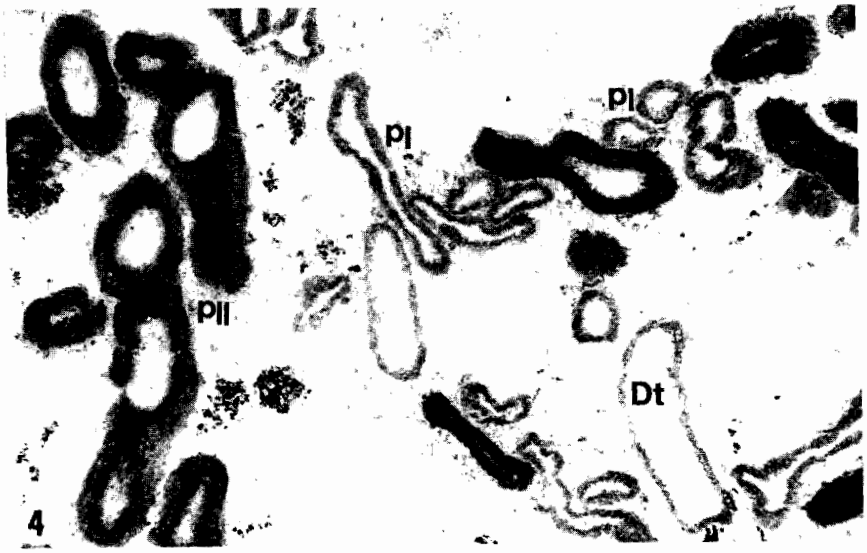

Fig. 4. *Periophthalmus* trunk kidney, unfixed cryostat section, 8 μm, ICDH (NADP-dependent) reaction. Strongest enzyme activity can be observed in the second proximal tubules (PII), moderate activity in the first proximal tubule (PI) and weak to moderate activity in the distal tubule (Dt) × 80.

not respond while PII tubules showed very intense reaction products. Weak to moderate activity was given by the distal tubules. The haemopoietic tissue gave negative results for the investigated dehydrogenases. Control sections showed no formazon deposits.

Non-specific esterase activity was found mainly in the lysosomal system of PI

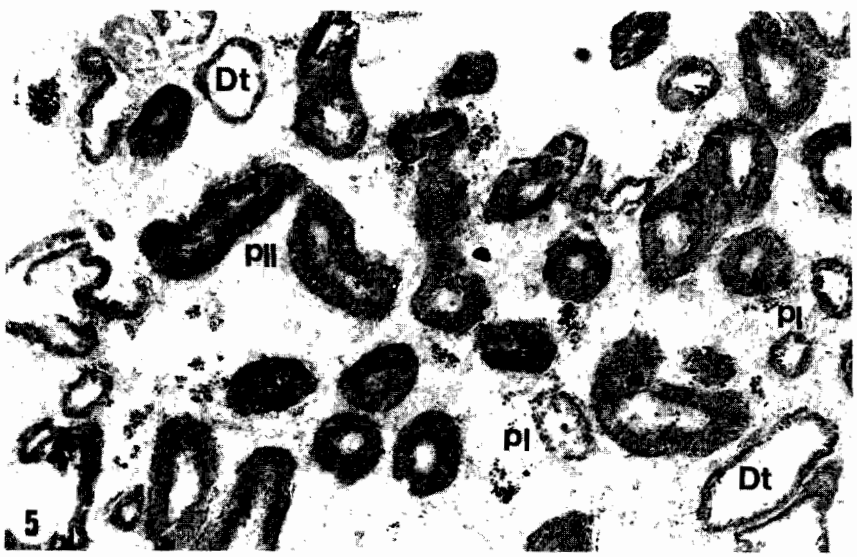

Fig. 5. *Periophthalmus* trunk kidney, unfixed cryostat section, 8 μm, LDH (NAD-linked) reaction. Weak to moderate enzyme activity occurs in all segments of the nephronic tubule × 80.

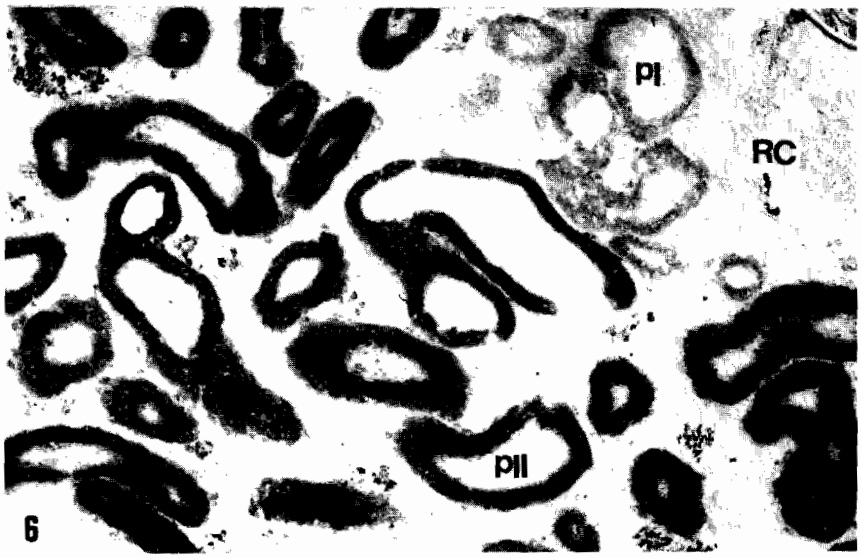

Fig. 6. *Periophthalmus* trunk kidney, unfixed cryostat section, 8 μm, G6PDH reaction. Enzyme activity is mainly located in the second proximal tubules (PII). Note the negative reaction in the renal corpuscle (RC) and weak activity in the first proximal tubule (PI) × 80.

tubule cells, although some activity was also observed in parts of PII tubules, apparently those adjacent to PI segment (Fig. 7). No activity could be found in the renal corpuscle or distal tubule segment. Macrophages were moderately stained for non-specific esterase activity. No reaction products were observed in control sections.

The renal corpuscle showed intense ATPase activity (Figs 8 and 9) which was only

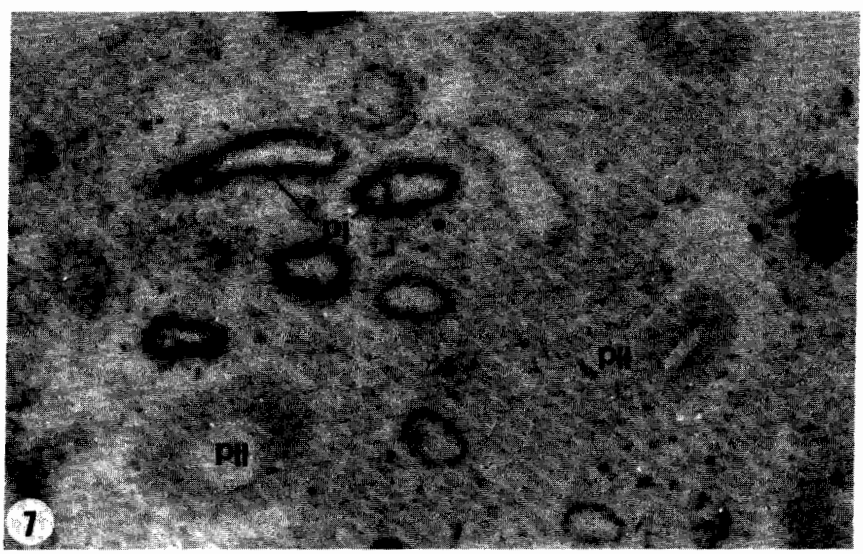

Fig. 7. *Periophthalmus* head kidney, formol-calcium fixed cryostat section, 8 μm, non-specific esterases. Enzyme activity is observed in the lysosomal system of the first proximal tubules (PI) and negative to weak activity in the second proximal tubules (PII) × 80.

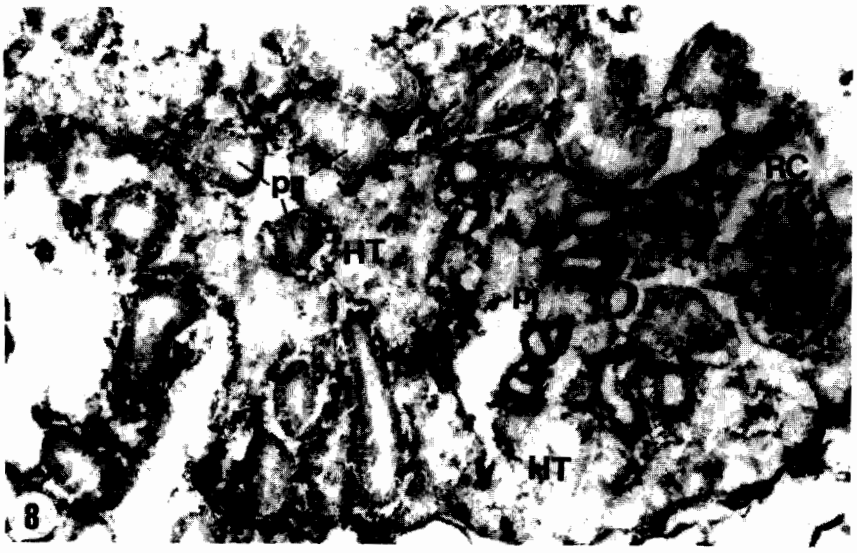

Fig. 8. *Periophthalmus* head kidney, unfixed cryostat section, 8 μm, ATPase reaction. Very intense activity occurs in the renal corpuscle (RC), the first proximal tubules (PI) and the margins of the haemopoietic tissue (HT). Moderate activity takes place in the second proximal tubules (PII). Note the intense activity in some cells of PII tubules (arrows) × 80.

slightly inhibited by L-cysteine. Activity was in Bowman's capsule as well as in the glomerulus. In PI and PII tubules strong ATPase activity was located in the cytoplasm but appeared more intense in PI than in PII (Fig. 8). In PI tubules, this activity was confined to the cytoplasm surrounding the basal nuclei but in PII tubules ATPase activity was observed throughout the cytoplasm although few scattered cells showed

Fig. 9. *Periophthalmus* head kidney, unfixed cryostat section, 8 μm, ATPase reaction. Very intense activity is observed in the renal corpuscle (RC), basal parts of the first proximal tubule (PI) cells and the edges of the adjacent haemopoietic tissue (HT) × 200.

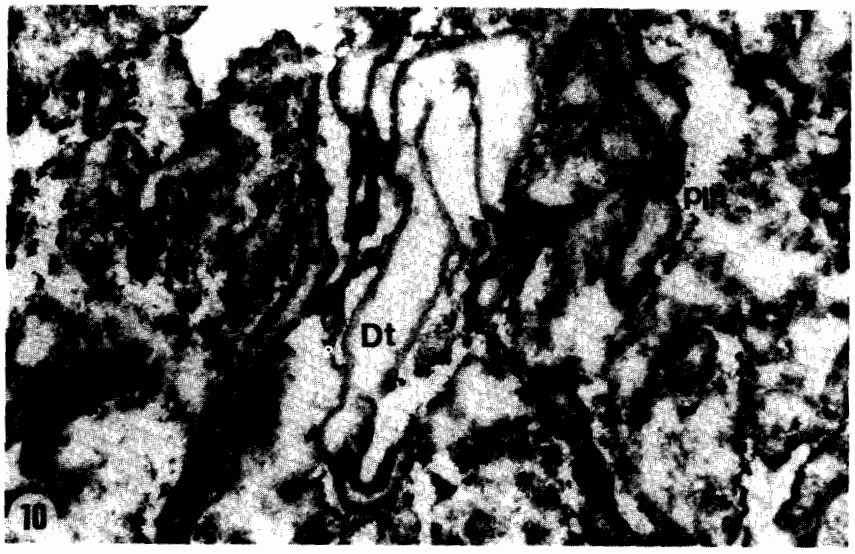

Fig. 10. *Periophthalmus* trunk kidney, unfixed cryostat section, 8 μm, ATPase reaction. Note the weak activity in the distal tubules (Dt) compared to the second proximal tubules (PII) × 80.

activity similar to that in PI cells. The basement membrane of PI and PII tubules was also partially stained, although this activity was not easily distinguished because of the accumulation of intense reaction products in the edges of the haemopoietic tissue adjacent to the tubules. The distal tubules showed enzyme distribution pattern similar to PII except that they were noticeably less intense (Fig. 10). However, few scattered cells of the distal tubule showed intense activity comparable with that of PII.

Control sections incubated in media without substrate or with β-glycerophosphate as substrate were negative (Fig. 11). Heat controls were also negative. L-cysteine slightly inhibited the activity in haemopoietic tissue but not that of the nephron tubule (Fig. 12). Lack of Mg^{2+} in the medium caused reduced ATPase activity in the nephronic tubule.

DISCUSSION

The activities of mitochondrial bound enzymes (SDH, MD and α-GPDH) in the kidney of *P. koelreuteri* indicated that the proximal tubules contain larger numbers of mitochondria involved in aerobic respiration than those in the distal tubules. The distribution of mitochondrial ATPase (Mg^{2+}-dependent) points to the same fact. In PI tubules the mitochondria seem to be localized in the basal parts of the cells but are distributed throughout the cytoplasm in PII and distal tubules, which was confirmed by ultrastructure examinations (unpublished results).

These results are in accordance with the findings of Hentschel & Meyer (1982) on the urinary apparatus of several marine fishes, where the second part of the proximal segment reacted, in general, very strongly to oxidative enzymes as compared to the distal segment. The distinctly positive mitochondrial enzyme activities in the proximal segment of *P. koelreuteri* can be related, as in other marine teleosts (Hickman &

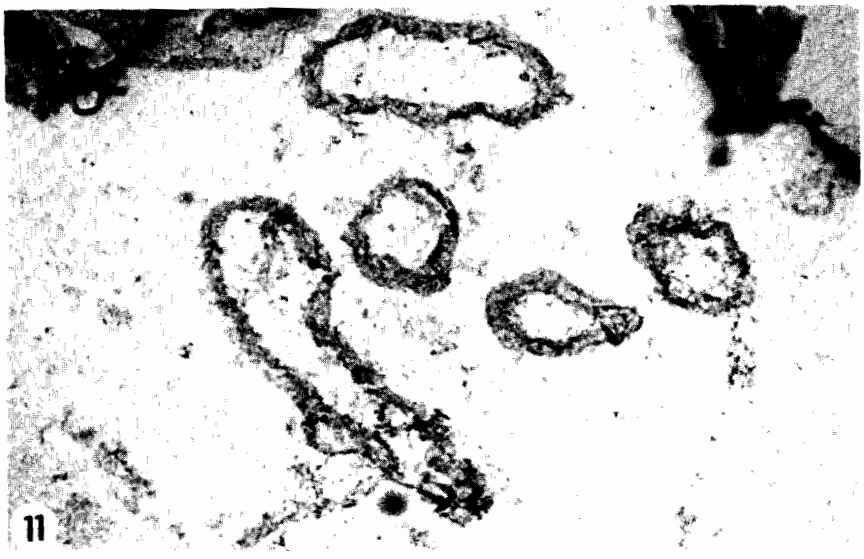

Fig. 11. *Periophthalmus* head kidney, unfixed cryostat section, 8 μm, ATPase reaction medium with β-glycerophosphate as substrate. No activity can be observed in the tubules or the haemopoietic tissue × 130.

Trump 1969; Hentschel & Meyer 1982), to their role in the secretion of divalent ions in adaptation to the hyperosmotic environment.

By contrast to fresh water fish (Hentschel & Meyer 1979, 1982) the distal tubule appears to have no significant active regulatory role in kidney function of marine fishes. The generally weak enzyme activities in the distal tubule of *P. koelreuteri* can

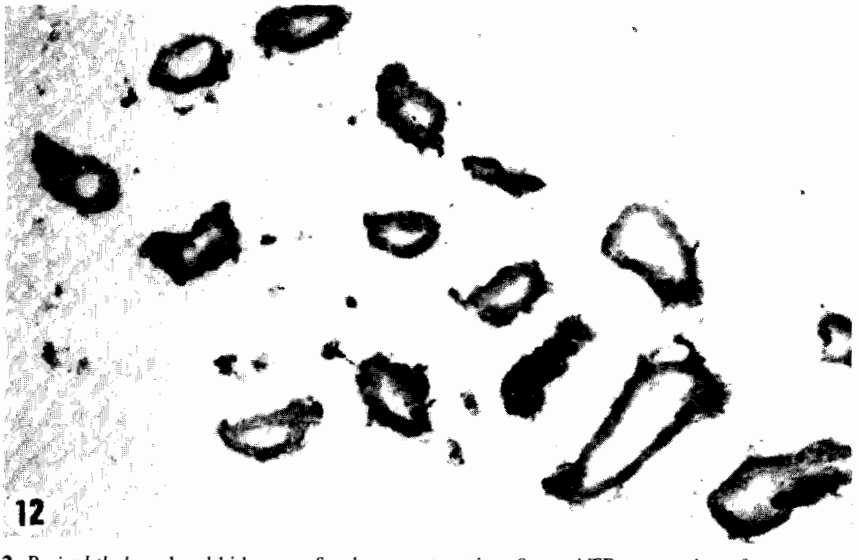

Fig. 12. *Periophthalmus* head kidney, unfixed cryostat section, 8 μm, ATPase reaction after treatment with L-cysteine. Enzyme activity persists in the tubules but not in the haemopoietic tissue × 130.

be attributed to its adaptation to a hyperosmotic environment. In euryhaline fishes, the transfer from fresh to salt water is accompanied by a functional shift of the kidney so that there is more secretion of electrolytes in opposition to the vital process of ion resorption and conservation in fresh water fishes (Hickman & Trump 1969; Forester 1973). The adaptation of the Prussian carp (*Carassius auratus*), a stenohaline fish, to sea water of moderate salinity was reported to be accompanied by weaker activities of some oxidative enzymes in the distal tubule and the collecting duct–archinephric duct systems as a response to weaker energy demands (Hentschel & Meyer 1980). This adaptation was accompanied by fewer and rounded mitochondria (Wendelaar Bonga 1973; Hentschel 1978).

The glycolytic pathway, as indicated by LDH activity, plays a more or less similar role along the nephron, with the exception of the renal corpuscle. Glycolysis, as energy yielder, appears to be secondary to tricarboxylic acid cycle in *P. koelreuteri*. These results confirm the assumptions of Hentschel & Meyer (1979) and agree with those for other lower vertebrates (Himmelhock & Karnovsky 1961; Helmy & Hack 1967). In warm blooded animals energy demands supplied by glycolysis are of considerable significance in proximal and distal tubules while oxidative metabolism dominates in the region of Henle's loop (Schmidt & Guder 1976).

In fish kidneys, changes in environmental conditions may lead to variations in LDH activity in relation to adaptive capability of metabolic processes. Hickman & Trump (1969) have indicated that euryhaline fishes may control the different urine flow rates required for osmoregulation by changes of glomerular filtration rates. This may lead to anaerobic conditions, where energy requirements for active transport can be supplied by the glycolytic pathway (Hentschel & Meyer 1979).

The hexose monophosphate shunt, as marked by G6PDH activity is mainly functional in PII tubule cells of the kidney of *P. koelreuteri*. This activity declines in the distal tubules. Hentschel & Meyer (1979, 1982) have reported that G6PDH was active in proximal and distal tubules of fresh water fish but that in marine fishes weaker activity was observed in the distal tubules. They suggested that strong reaction intensities of G6PDH may be related to the pentosephosphate pathway being involved in the regulation of acid-base metabolism rather than lipid synthesis, basing their assumption on the fact that the tubule cells of the kidneys of the species investigated contain no considerable amount of lipid droplets (Jesperson 1967; Youson & McMillan 1970a, b, 1971; Wendelaar Bonga 1973; Hentschel 1978; Kendall 1972) and that G6PDH activity increases in mammals during acidosis (Dies & Lotspeich 1967). The same assumption may hold true in the case of *P. koelreuteri* as few lipid droplets can be found in PII tubule cells (Safer *et al.* 1982). The role of this enzyme in acid-base regulation may be of great importance in *P. koelreuteri* during air breathing (hypercapnic acidosis) and possibly during submergence in burrows (hypoxic acidosis) at low tide.

Investigations of non-specific esterase activity in fish kidney are lacking. In the mudskipper, non-specific esterase activity was found to be mainly located in the lysosomal system of PI tubules and adjacent parts of PII tubules. This distribution is apparently similar to the esterase activity in the rat kidney (Safer 1978) and coincides with acid phosphatase activity in the nephron of the mudskipper as reported by Safer *et al.* (1982).

ATPase hydrolyzing enzymes were active in the cytoplasm and basement membranes of nephrons of *P. koelreuteri* kidney. In the renal corpuscle very intense

activity was observed which was only slightly inhibited by L-cysteine. Intense alkaline phosphatase was previously reported in the glomerulus of the head kidney of *P. koelreuteri* but not in Bowman's capsule (Safer *et al.* 1982). Otherwise the distribution of alkaline phosphatase in the kidney did not coincide with that of ATPase. ATPase activity was more pronounced in the proximal (PI, PII) than in the distal tubules. Cytoplasmic ATPase was Mg^{2+}-dependent but was not affected by L-cysteine. Besides, its distribution inside the cells was similar to that of mitochondrial bound dehydrogenases. It can therefore be regarded as mitochondrial ATPase and indicates high metabolic activity in the proximal tubule of *P. koelreuteri.*

The activity in the basement membrane was uneven and was greater in the proximal than in the distal tubule cells. Of the few enzyme histochemical reports available on fish kidney, Huntschel & Meyer (1980) and Endo & Kimura (1982) found stronger Na^+-K^+-ATPase activity in the basement membranes of distal than proximal tubules of the fresh water fish *Carassius auratus.* Although the observed ATPase activity in basement membranes of *P. koelreuteri* kidney was not identifed as Na^+-K^+-ATPase (inhibition by ouabain was not used), it would be expected that more of such activity should be found in the segment of the nephron where most of the metabolic activities occur, namely the proximal tubule. The high mitochondrial and membrane bound activities together with aerobic respiration in the proximal tubule presumably indicate active ion transport, possibly divalent ion excretion (Hickman & Trump 1969). This segment apparently plays the major role in osmoregulation and excretory activities of the kidney tubule, at least in the hyperosmotic environment of the Arabian Gulf.

By contrast to fresh water fish (Hentschel & Meyer 1979; Endo & Kimura 1982) the distal tubule showed little enzyme activity denoting that the osmoregulatory function of this segment in fresh water fish is lacking in *P. koelreuteri* adapted to sea water. The possible role of this segment in the adaptation of *P. koelreuteri* to fresh water remains to be determined by further investigations.

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نشاط انزيمات كلية نطاط الوحل
بيريوفثالماس كولريترى (بالاس)

نجلاء كمال السيد وعبدالمجيد علي صفر
قسم علم الحيوان بجامعة الكويت

خلاصة

اجريت دراسة كيميائية نسيجية على نشاط انزيمات كلية نطاط الوحل بيريوفثالماس كولريترى في كل من كلية الرأس وكلية الجذع .

ويشكل هذا البحث دراسة لنشاط انزيمات ديهيدروجينات السكسينات ، ديهيدروجينات الفا جليسيروفوسفات ، وديهيدروجينات ايزوسيترات المرتبطة بالفوسفات نيكوتين اميد ، وديهيدروجينات الفا جليسيروفوسفات ، وديهيدروجينات ايزوسيترات المرتبطة بفوسفات النيكوتين ، وديهيدروجينات اللاكتيت المرتبطة بالنيكوتين ، وديهيدروجينات سداسي فوسفات الجلوكوز المرتبطة بفوسفات النيكوتين الاستريز غير النوعي ، وثلاثي فوسفات الادينوزين .

وتبين ان نشاط الديهيدروجينات شبه معدوم في الكريات الكلوية وضعيف في الانيبيبات البعيدة ، ويشير نشاط انزيمات الميتوكوندريا (ديهيدروجينات السكسينات ، وديهيدروجينات الماليت ، وديهيدروجينات الفا جليسيروفوسفات) إلى أن هناك عددا أكبر من الميتوكوندريا في الانيبيبات البعيدة بينما كان نشاط ديهيدروجينات اللاكتيت ، والذي هو بمثابة مسار جليكوجيني ، ضعيفا او متوسطا في الانيبيبات القريبة والبعيدة . وقد ثبت وجود الاستريزات غير النوعية في لايزوزومات الجزء الأول من خلايا الانيبيبات القريبة وكذلك في مراكز الخلايا البلعمية الضخام ذوات الميلانين . كما تبين وجود تفاعلات ثلاثي فوسفات الادينوزين في الكرية الكلوية ، وكانت أكثر حدة في السيتوبلازم والغشاء القاعدي للانيبيبات القريبة منها في الانيبيبات البعيدة .

وتشير هذه النتائج إلى أهمية الانيبيبات البعيدة في عملية التنظيم الاوزموزى والافراز في كلية نطاط الوحل في بيئة مياه الخليج العربي ذات المجال الاوزموزى العالي .