Function of the excretory system of the crocodile (*Crocodylus acutus*)[1]

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SCHMIDT-NIELSEN, BODIL, AND ERIK SKADHAUGE. *Function of the excretory system of the crocodile (Crocodylus acutus)* Am. J. Physiol. 212(5): 973–980. 1967.—Glomerular filtration rate (GFR), tubular and cloacal functions were studied, during normal conditions, water loading, salt loading, and isosmotic expansion of the extracellular fluid volume. Na^+, K^+, Cl^-, NH_4^+, and osmolality were determined in ureteral and cloacal urine. GFR varied little compared to that of other amphibious reptiles. It increased about 20% after a water load corresponding to 10% body wt, and showed no increase after an isosmotic load. It decreased only 40% after dehydration (10% of body wt). The tubules have little or no capacity for regulating the osmolality or electrolyte composition of the urine. Ureteral urine osmolality remained around 80% of the plasma osmolality under all conditions. The electrolyte concentration of the ureteral urine varied only slightly with the variations in salt load. Cloacal absorption appeared to be more regulated. Under normal conditions Na^+ and Cl^- were almost completely resorbed in the cloaca leaving NH_4^+ and probably HCO_3^- behind. After salt load Na^+ and Cl^- resorption in the cloaca was less complete. The kidney function of the crocodile resembles that of terrestrial reptiles more than that of other amphibious reptiles. The lack of regulation of glomerular filtration rate and the tubular osmolality may be characteristic for uricotelic reptiles. It may also reflect the ancestry, since the crocodile is a descendant of the terrestrial ruling reptiles.

excretion in reptiles; glomerular filtration rate; tubular function; urine osmolality; cloacal function; dehydration; water load; salt load

RECENT STUDIES ON TURTLES, tortoises, and lizards have indicated that the regulation of the rate of flow and osmolality of urine takes place at different levels in the different species investigated (5, 15). It is well known that vertebrates, which cannot produce a urine that is hyperosmotic to the blood, can regulate their excretion through changes in *1*) glomerular filtration rate, *2*) distal tubular salt and water resorption, and *3*) bladder or cloacal resorption of salt and water. However, it is not so well known that the degree to which these different mechanisms are used by different forms varies significantly.

The fresh-water turtle (*Pseudemys scripta*) (5) and the frog (*Rana clamitans*) (19) regulate urine flow and osmolality mostly by wide changes in filtration rate and by changes in distal tubular permeability to water. The desert tortoise (*Gopherus agassizii*) (5), on the other hand, shows much less regulation of the filtration rate and little or no regulation of tubular permeability to water. The ureteral urine is always hypoosmotic to the blood, even when the animal is severely dehydrated or salt loaded. The tropical gecko (*Hemodactylus sp.*) has much the same type of kidney function as the tortoise, while two species of desert lizards, the horned toad (*Phrynosoma cornutum*) and the Galapagos lizard (*Tropidurus sp.*) have no ability to dilute the urine, i.e., the urine is always isosmotic to the blood and the filtration rate is almost constant regardless of the state of hydration (15). In forms that show little or no regulation on the glomerular or tubular level, the urine flow and electrolyte concentrations are primarily determined by the bladder or cloaca.

Since the fresh-water turtle and the frog both lead an amphibious life, whereas the other forms are strictly terrestrial, it seemed possible that their mode of renal regulation is an adaptation to their habitat, i.e., an amphibious animal shows wide variations of glomerular filtration rate and distal tubular water permeability, whereas a terrestrial animal shows little or no regulation on the glomerular and tublar level. Another possibility was that the renal function is adapted to the type of nitrogenous end product that the animal excretes. The frog excretes more than 80 % of its nitrogen in the form of urea, and the fresh-water turtle is also predominantly ureotelic, excreting 45–95 % of its waste nitrogen in the form of urea, the remainder in the form of ammonia and uric acid. The desert tortoise also excretes some urea

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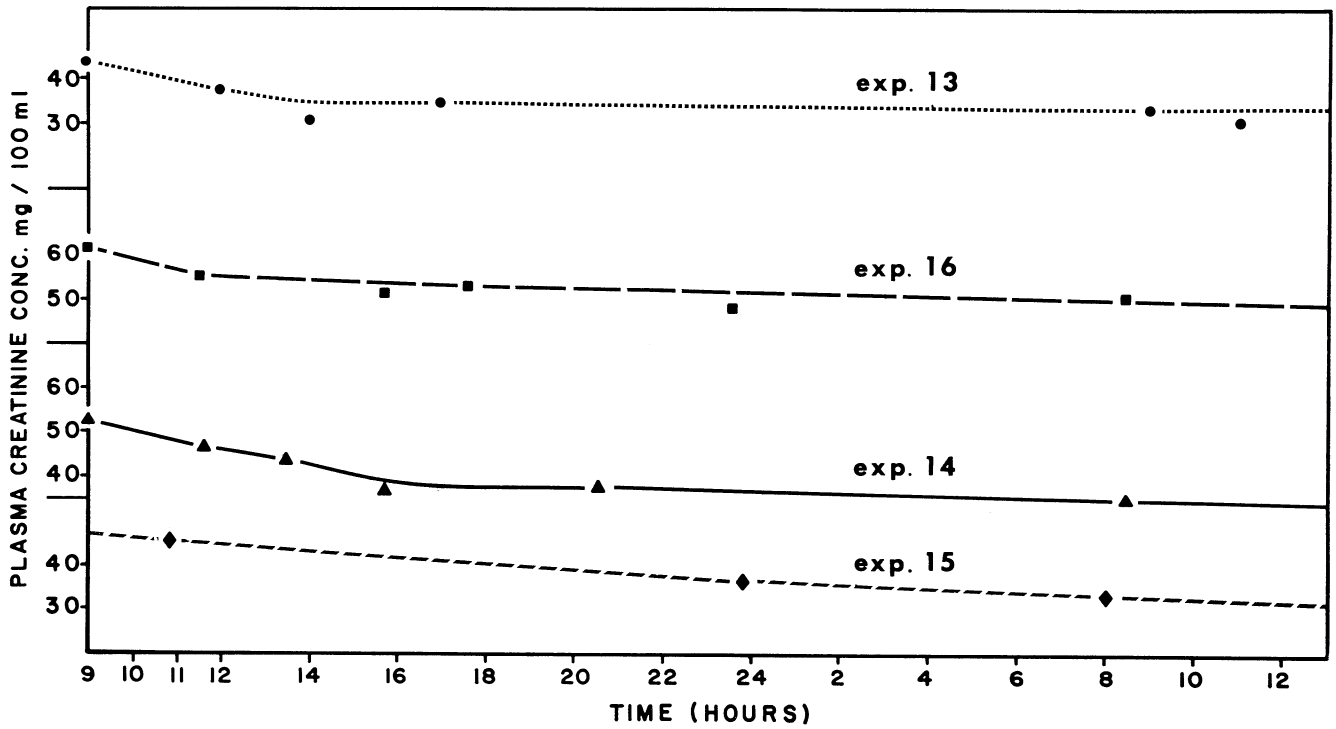

FIG. 1. Typical curves showing the change in plasma creatinine concentration during the experimental period. *Abscissa:* time of day.

but it is predominantly uricotelic (20–50 % of its waste nitrogen is excreted as uric acid) and the lizards are completely uricotelic (over 90 % excreted as uric acid).

In the ureotelic frog and turtle, the glomerular filtration rate is reduced almost to zero with moderate dehydration (5, 19). This seems to be an advantageous adaptation since the urine that might be formed during dehydration would be completely resorbed in the bladder anyway. The permeability of the bladder wall of amphibians to both water and urea (11, 17) is increased during dehydration due to release of arginine vasotocin. Active sodium transport across the toad bladder has been found to be increased by mammalian neurohypophyseal hormones (13, 14). The bladder wall of the turtle is always somewhat permeable both to urea and water, and salt is actively resorbed (1, 5, 10). Thus, when the urine flow is decreased the smaller amount of urine in the bladder will be resorbed. In the forms that excrete uric acid, this is not the case. In the desert tortoise (5), and in the three species of lizards (15) the glomerular filtration rate is only slightly reduced even after severe dehydration. The uric acid or urates accumulate as a crystalline mass in the bladder of the tortoise or in the coprodeum of the lizards where salt is actively and water is passively resorbed. This crystalline mass is then excreted. Thus, a continued urine production during dehydration is advantageous for an animal producing uric acid, since it is enabled to excrete waste nitrogen.

In the present investigation the crocodile was studied. The crocodile lives an amphibious life similar to that of frog and fresh-water turtle. However, the crocodile is ammono-uricotelic. About 70 % of its nitrogenous waste is excreted in the form of uric acid and about 25 % as ammonia (4, 9). Therefore, it was of considerable interest to see whether its renal function is regulated similarly to that of other amphibious vertebrates or whether it is regulated like that of the terrestrial uricotelic reptiles.

To investigate this, the glomerular filtration rate, the tubular function and the cloacal function were studied in crocodiles (*Crocodylus acutus*), during normal conditions, water loading, salt loading, and during isosmotic expansion of the extracellular fluid volume.

The results showed that the excretory system of the crocodile in many respects functions similarly to that of terrestrial uricotelic reptiles, and unlike that of the fresh-water turtle.

METHODS

Animals. Seven crocodiles (*Crocodylus acutus*) caught locally were used. Their body weights ranged from 1 to 4 kg. They were kept in a small crocodile pool that we had constructed outside the laboratory. A platform above the water line permitted the animals to be in or out of water, at will. They were fed fresh fish about once a week.

Renal clearance studies. The glomerular filtration rate was measured as the creatinine clearance. In some animals a modest secretion of creatinine has been found when the creatinine clearance was compared with inulin clearance. However, in all reptiles (5, 8) and amphibians (7) in which the two clearances have been compared, no difference greater than 5–10 % has been found when

TABLE 1. *Ureteral urine*

	Osmolality, milliosmols/kg H_2O		Osmolal U/P	GFR, ml/kg per hr	Creatinine U/P	Urine Concn, mEq/liter			
	Urine	Plasma				NH_4^+	Cl^-	Na^+	K^+
Normal (13)*	234±4	294±3	0.80±0.01	9.6±1.0	7.8±0.6	53.2±1.0	45.0±6.9	61	6.0
SD	18	11	0.06	4.3	2.6	4.9	29.0	(5)†	
5% H_2O load (10)*	225±6	290±5	0.77±0.02	13.2±1.9	6.2±0.3	60.6±6.7	26.3±5.2		
SD	20	12	0.07	5.9	0.8	21.0	22.0		
P			>0.05	>0.05	<0.02	>0.05	<0.05		
10% H_2O load (18)*	199±6	287±4	0.67±0.02	15.2±2.0	4.2±0.5	53.8±2.6	25.6±3.5		
SD	26	10	0.10	8.4	2.0	11.0	15.0		
P			<0.02	<0.02	<0.01	>0.05	<0.05		
10% Isosmotic load (11)*	233±7	310±4	0.77±0.02	7.6±0.6	7.3±0.7	51.0±3.0	53.0±4.5	58	4.4
SD	24	10	0.07	2.1	2.2	10.0	15.0	(5)†	
P			>0.05	>0.05	>0.05	>0.05	>0.05		
Hyperosmotic load (13)*	268±7	330±4	0.82±0.02	7.3±0.8	13.3±1.2	69.0±5.4	68.0±6.3	43	10
SD	25	10	0.07	2.7	4.2	18.0	22.0	(7)†	
P			>0.05	>0.05	<0.01	<0.01	<0.02		
Dehydration (13)*	267±6	318±6	0.84±0.01	6.1±0.6	7.7±1.3	46.4±5.2	58.3±5.7	71	10.5
SD	22	22	0.05	2.1	4.3	19.0	20.6	(3)†	
P			>0.05	<0.05	>0.05	>0.05	>0.05		

Means ± SE of means are presented, as well as standard deviation (SD). *P* values represent significance levels for tests of differences between mean values of experimental state and mean of "normal" values. Sodium and potassium were only determined in a few of the experiments, and were not determined during water diuresis. Because of the small number of determinations no statistical analysis has been made on these values. The normal variations encountered in any one experiment are shown in Table 4. * These parenthetical numbers are the number of collection periods that have been averaged. In some cases two animals, in most cases three, were used. † These parenthetical numbers are the number of collection periods averaged for sodium and potassium.

high plasma concentrations of creatinine such as in these experiments were used. Due to limited facilities caused by working away from our own laboratory we could not compare creatinine with inulin clearances. This, of course, is a disadvantage, but it is highly unlikely that any error due to a difference between the creatinine and inulin clearance could influence our findings significantly.

The night before, or 2–3 hr prior to the experiment, a subcutaneous injection of creatinine in saline was given in the forelimbs (500 mg/kg body wt). This gave plasma creatinine concentrations of 40–60 mg/100 ml. The change in plasma creatinine concentration with time in several different experiments is shown in Fig. 1. The reason for working with such high plasma concentrations is that the error due to tubular creatinine secretion is then negligible. When the experiment started the crocodile was strapped to a wooden board with an opening under the cloaca. Ureteral urine samples were collected directly from the openings of the ureter by means of a 7-cm-long polyethylene catheter (o.d. 1.2 cm, i.d. 0.9 cm), which was inserted into the cloaca to about the middle of the coprodeum. The catheter was closed in the end that was inserted into the cloaca but had two large openings (1.5 cm long, 0.5 cm wide) on each side which covered the urinary papillae in the urodeum. (The catheter was constructed after we had sacrificed a crocodile and studied the anatomy of the cloaca and the position of the urinary papillae). The catheter was held in place by means of adhesive tape around the catheter and around the base of the tail of the crocodile. The urine flowed continuously out of the catheter and collected in a graduated tube taped to the opening of the catheter. To insure that no urine was retained in the cloaca and that the catheter did not become clogged by uric acid, the catheter was gently moved up and down in the cloaca at the end of each urine collection period and was then removed, washed and reinserted. Ureteral urine collection periods lasted from 45 min to 2 hr depending on the rate of urine flow. Eight to twelve urine samples were collected in each experiment. When cloacal urine samples were collected, the crocodile was left for 2–12 hr in a wire cage or an empty aquarium and the cloaca was emptied by means of the catheter before and at the end of each collection period. In a few instances spontaneously voided urine samples were col-

TABLE 2. *Ureteral urine*

	Osmolality	GFR	Creat. U/P	NH_4^+	Cl^-
5% H_2O load	95	137	80*	114	59*
10% H_2O load	84*	158*	54†	101	57*
10% Isosmotic	95	79	94	96	118
Hyperosmotic	102	76	171†	130†	150*
Dehydration	105	64*	99	87	130

Values found in the various experimental states are expressed in percent of normal values. * Difference from normal significant at the 5% level. † Difference from normal significant at the 1% level (based on means).

lected by placing the crocodile in a wire cage over a slanting parafilm-covered board. The urine was made to run directly into a beaker containing oil.

Blood was collected every 2–3 hr from the caudal tail vein using a heparinized hypodermic needle, size 18–20. Since the entire procedure involved no surgery and no traumatic or painful procedures, the crocodile needed no anesthesia. Each crocodile was used two to four times

TABLE 3. *Cloacal urine*

	Osmolality, milliosmols/kg H_2O		Osmolal U/P	GFR, ml/kg per hr	Creatinine U/P	Urine Concn, mEq/liter			
	Urine	Plasma				NH_4^+	Cl^-	Na^+	K^+
Normal (5)*	251	294	0.86			118	16.5	5.9	2.7
Range	(238–269)	(289–296)	(0.84–0.91)			(103–142)	(1.5–30.1)	(1)*	
H_2O load (4)*	184	278	0.66	15.7	5.3	58.7	10.2		
Range	(160–210)	(276–281)	(0.58–0.75)	(15.2–16.3)	(4.7–6.8)	(46.7–61.3)	(7.5–16.2)		
Isosmotic load (6)*	225	304	0.74	7.4	10.0	57.9	37.6	36.4	4.6
Range	(192–245)	(291–320)	(0.61–0.80)	(4.1–12.0)	(5.09–12.0)	(45.2–68.6)	(17.0–62.2)	(21.2–80.0) (3)†	(2.8–6.0)
Hyperosmotic load (2)*	310	346	0.91	8.3	16.8	73.6	76.7	38.0	35.0
Range	(307–313)	(346)	(0.90–0.92)	(7.6–9.0)	(15.8–17.2)	(71.2 76.2)	(76.7)	(35.0–40.0) (2)†	(30.0–40.0)
Dehydration (12)*	217	315	0.70	5.3	9.3	54.4	35.9	21.4	4.0
Range	(144–263)	(283–345)	(0.44–0.87)	(3.7–8.0)	(7.1–13.7)	(15.6–120.4)	(3.9–84.2)	(5.9–34.0) (3)†	(2.7–4.8)

Because of the small number of determinations only the range of values are given. Sodium and potassium concentrations were not determined in cloacal urine during H_2O load and only in a few samples during the other conditions. * These parenthetical numbers are the number of collection periods that have been averaged. In some cases two animals, in most cases three, were used. † These parenthetical numbers are the number of collection periods averaged for sodium and potassium.

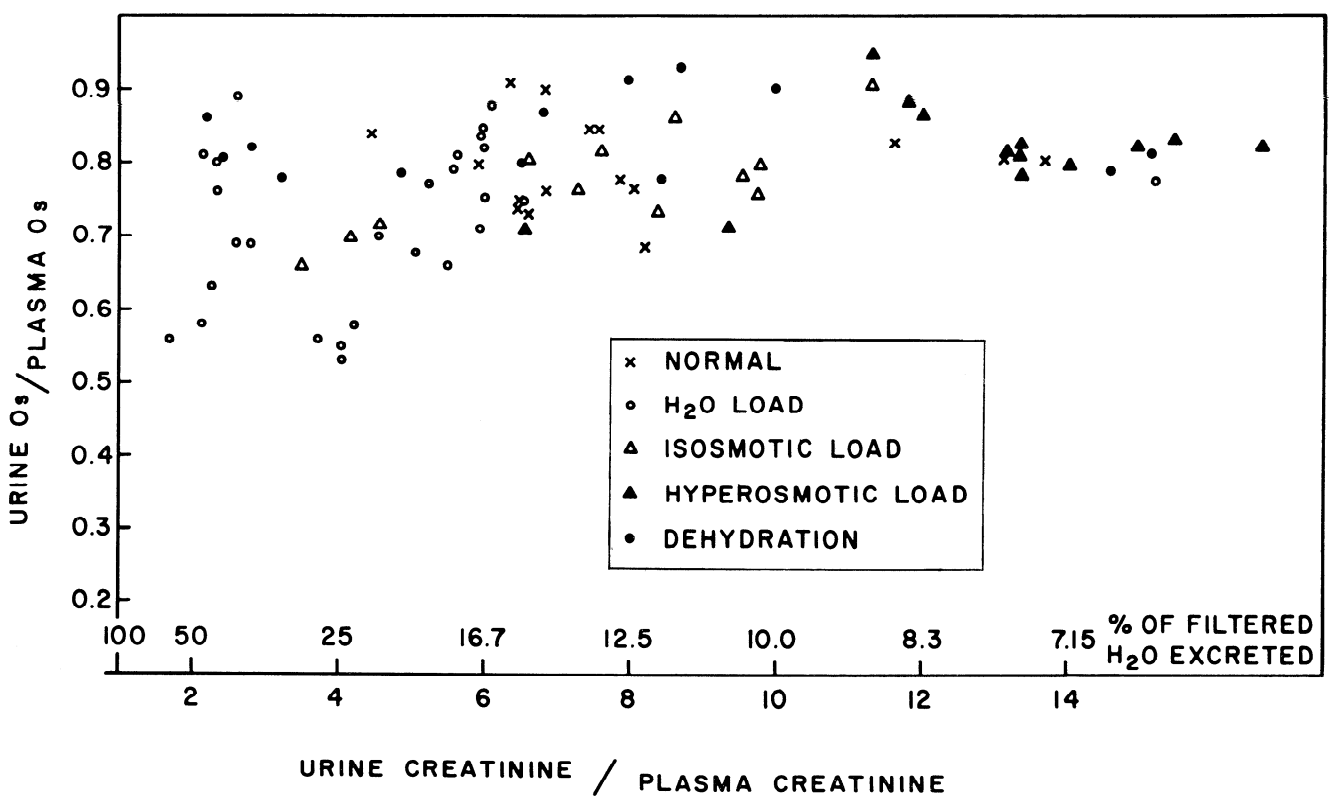

FIG. 2. Osmolality of the ureteral urine divided by the plasma osmolality given as a function of the tubular resorption of water (expressed as creatinine U/P). The urine osmolality varies only little with the tubular resorption of water and the state of hydration of the animals.

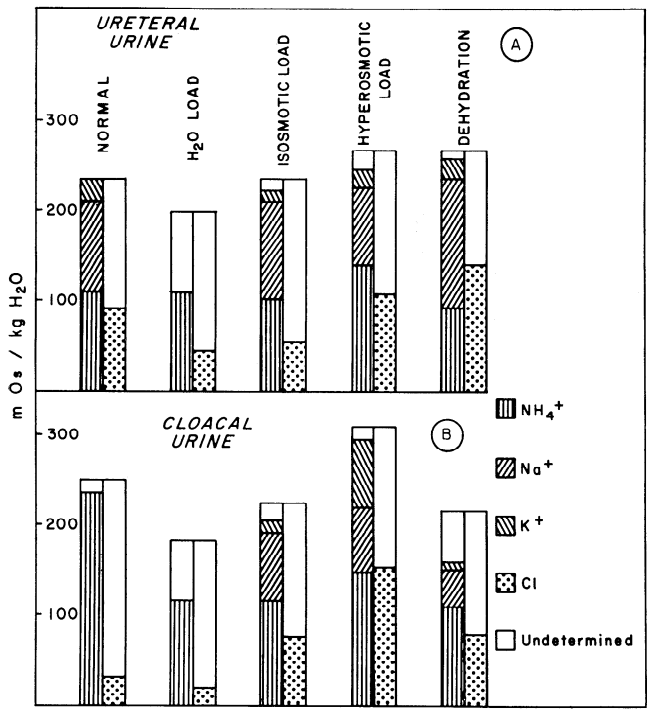

FIG. 3. Composition of ureteral urine (*A*) and cloacal urine (*B*) during the various experimental conditions. It should be noted that Na^+ and K^+ were not determined in the water-load experiments. The fact that they are not presented does not indicate that these ions were absent.

in the various experiments. The crocodiles remained healthy during the entire 7-week period that we worked on them.

For dehydration experiments the crocodiles were removed from water and placed in a dry aquarium for 1–2 days prior to the experiment. Room temperature was 80–85 F, relative humidity about 50%. This resulted in a 5–10% loss of body wt. For water loading, tap water was given by stomach tube in an amount corresponding to 5–10% of body wt. For isosmotic expansion of extracellular fluid they were given 0.9% saline subcutaneously, 5–10% of body wt. For salt loading a 9% salt solution was given subcutaneously in amounts calculated to raise the blood osmolality 25 and 50 milliosmols/kg H_2O, respectively. All subcutaneous injections were given in the loose skin around the forelimbs or neck region. It is very important not to give the injections in the hindlimbs or tail because the renal portal vein carries the solution to the renal capillary net before it is distributed in the general body fluid. In an early experiment when we gave hyperosmotic saline subcutaneously in the hindlimbs the urine osmolality reached twice the osmolality of the blood. This never happened when the salt load was given in the front region of the animal, and was obviously due to the hyperosmotic perfusion through the renal portal system.

Blood samples were centrifuged and the plasma separated from the red cells. Plasma samples and urine

TABLE 4. *Consecutive samples of ureteral and cloacal urine*

Urine Sample	Sample	Time	Urine Flow, ml/kg per hr	GFR	Creat. U/P	Osmolality, milliosmols/kg H_2O	NH_4^+	Cl^-	Na^+	K^+
				Experiment 15: dehydration						
1	Cloacal	2045				138	58.1	7.1	6	2.7
2	Ureteral	2045–2230	0.50	4.2	8.5	234	36.5	51.2	68	6.0
3	Cloacal	2230–0940	0.28	4.0	13.1	166	15.6	14.2	24	4.6
4	Ureteral	1000–1200	0.30	4.3	14.5	251	22.5	47.9	70	8.0
5	Cloacal	1200–1600	0.41	5.6	17.7	172	27.0	21.9	34	4.8
6	Ureteral	1600–1800	0.30	4.5	15.2	258	24.3	56.7	76	18.0
				Experiment 16: isosmotic load given at 0940						
4	Ureteral	1030–1130	1.33	11.2	8.4	234	52.3	33.5	48	4.0
5	Cloacal	1130–1530	0.90	9.0	10.0	192	56.3	17.0	21	2.8
6	Ureteral	1530–1630	0.67	6.3	9.5	247	64.2	38.8	47	4.0
7	Ureteral	1630–1730	0.77	7.5	9.8	240	58.0	46.2	52	7.0
8	Cloacal	1730–2330	0.64	7.0	10.9	208	51.4	41.0	38	5.0
9	Cloacal	2330–0830	0.37	4.1	11.1	235	45.2	62.2	50	6.0
10	Ureteral	0830–0930	0.56	4.9	8.6	277	51.1	84.5	75	10.0
11	Ureteral	0930–1030	0.62	6.0	9.7	254	59.2	75.2	68	10.0
				Experiment 14: hyperosmotic load given at 1125						
9	Ureteral	1530–1630	0.62	9.3	14.9	269	84.6	42.6	36	8.0
10	Ureteral	1630–1730	0.52	8.0	15.5	270	83.4	43.0	35	7.0
11	Ureteral	1730–2030	0.48	7.9	16.6	271	87.8	97.4	38	6.0
12	Cloacal	2030–0820	0.43	7.6	17.8	313	76.2	76.7	40	30
13	Ureteral	0820–0930	0.60	7.1	11.8	306	63.4	98.8	52	38
14	Cloacal	0930–1200	0.57	9.0	15.8	307	71.2	76.7	35	40

Three experiments are presented to show the differences between cloacal and ureteral urine samples and the effect of isosmotic and hyperosmotic salt loading. The first sample (*no. 1*, dehydrated crocodile) represents the cloacal content before the start of the experiment. It is possible that the constant sampling from the cloaca interferes with normal function of the cloaca since the highest ammonia concentrations were never found except in the first sample taken at the start of the experiment. The sodium and chloride concentrations and the osmolality in the dehydrated crocodile were consistently lower in cloacal urine than in ureteral urine. This difference, although much smaller, can still be seen in the salt-loaded crocodiles. In the salt-loaded crocodile the potassium concentration in ureteral and cloacal urine increased 5- to 8-fold 12–24 hr after the salt administration.

TABLE 5. *Cloacal resorption (μM/kg body wt per hr)*

H_2O, ml/kg per hr	NH_4^+	Na^+	K^+	Cl^-	
0.116	8.1	20.7	1.4	15.6	Exp. 15, dehy-
−0.107	−4.0	7.9	1.9	6.8	dration
0.176	5.0			17.4	Exp. 13, isos- motic load
0.102	13.5	23.4	1.0	19.9	Exp. 16, isos-
0.116	12.0	19.8	2.75	16.8	motic load
0.109	7.9	7.6		20.2	Exp. 14, hyper-
0.027	10.0	11.5		16.5	osmotic load

Calculations are based on urine flow and urine concentrations in alternate ureteral and cloacal collection periods. The assumptions were made that the ureteral flow and composition of urine during the cloacal collection equaled the average values determined directly before and after the cloacal collection.

samples were covered with parafilm and refrigerated immediately after they were taken. Osmolality, ammonia, creatinine, and chloride were always determined within 2–24 hr of the time of sampling. Because we did not have a flame photometer in Jamaica the samples for Na^+ and K^+ determination were frozen in Beckman/Spinco polyethylene tubes and transferred frozen to Cleveland for analyses. Sodium and potassium analyses were not made on all samples and this is the reason that we do not have electrolyte determinations during water-load experiments.

Analytical methods. Osmolality of blood and urine samples was determined with a Fiske osmometer, model G-62, on 0.2-ml samples; ammonia by the Conway method (3); chloride with a Buchler-Cotlove chloridometer; and creatinine by the Beckman/Spinco adaptation of the Folin-Wu method. The analytical accuracy of each determination was within 1–2%. Sodium and potassium were determined with a Baird flame photometer, model KY-2.

RESULTS

Role of kidney in regulating composition of urine. The average values of all ureteral urine collections obtained during the various experimental conditions are presented in Table 1, and the percentage change in Table 2. The most remarkable finding is that in spite of the administration of high water loads and osmotic loads the flow and the composition of the urine as it left the kidney (ureteral urine) varied only little. The glomerular filtration rate was reduced during dehydration to 64% and slightly elevated to 158% during extreme water loading. (The absorption of water from the stomach of the crocodile was slow, and consequently the effect on plasma osmolality was not as pronounced as one would expect). These changes, although statistically significant, are small compared to changes found in turtles (5) and frogs (19) under similar conditions where glomerular filtration rate increases 200–300% during water load and decreases to zero during dehydration.

Furthermore, in the crocodiles an isosmotic expansion of the extracellular fluid volume corresponding to 10% body wt did not increase the filtration rate over the normal value.

The tubular functions likewise remained relatively unchanged during the various experimental conditions. The urine osmolality decreased only slightly after water loading and did not increase significantly as a result of a hyperosmotic load or dehydration (Table 3). Thus, the urine osmolality remained around 80% that of the plasma under all experimental conditions. In Fig. 2 the creatinine U/P (urine/plasma) ratios are plotted against the osmolal U/P ratios. The reciprocal value of the creatinine U/P ratios represent the fraction of filtered water excreted. It is seen that although wide variations were observed in tubular water resorption, the osmolality of the urine remained practically unchanged relative to the blood osmolality. The only lower osmolal U/P ratios were observed during extreme water loading. During these conditions the fraction of filtered water excreted was also relatively large.

The average composition of the ureteral urine was remarkably constant during all experimental conditions (Table 1, Fig. 3). The urine contained precipitated uric acid or urates (the amount was not determined in the present experiments). In addition, the urine always contained a significant amount of ammonia corresponding to one-third to one-half of the total cations in solution in the urine. The rest of the cations were primarily sodium and a small amount of potassium. The potassium concentration remained low under all experimental conditions, with the exception of one experiment with hyperosmotic loading where the potassium concentration in the ureteral urine rose to 30 mEq/liter 10–12 hr after the sodium chloride administration (Table 4). The chloride concentration of the urine also rose in this experiment. During isosmotic load, hyperosmotic load, and dehydration (Table 1), the chloride concentration was higher than during water loading ($P < 0.001$).

Role of cloaca in regulating composition of urine. Inspection of the crocodile cloaca showed that it resembles that of various lizards as described by Seshadri (18). There is no bladder, the openings of the ureters are located laterally in the part of the cloaca called the urodeum. A sphincter separates the urodeum from the proctodeum. The urine flows retrograde from the openings toward the coprodeum, which is separated by a sphincter from the rectum. The urine normally remains in the coprodeum for many hours before it is voided spontaneously. The urine is then still watery but contains large amounts of precipitated urates. (We never found feces in the urine.) When the crocodiles were taken directly from the pool and catheterized the urine found in the cloaca had an ammonia concentration of 120–140 mM and a chloride concentration that frequently was less than 5 mEq/liter. In the various states of dehydration and salt loading the cloacal urine differed in composition from the ureteral urine (Tables 3, 4; Fig. 3). The chloride concentration

was consistently reduced and the ammonia concentration usually increased in cloacal urine.

In several experiments cloacal and ureteral urine samples were collected alternately. The compositions of such urine samples are illustrated in Table 4. From these experiments it is possible to make a rough estimate of the amounts of water and ions resorbed in the cloaca, when we calculate the amounts that entered the cloaca per unit time from the ureteral collections just before and after the cloacal collection. The estimated values of cloacal resorption are presented in Table 5.

The values indicate cloacal resorption of sodium and chloride, but do not indicate secretion of ammonia since the increase in ammonia concentration can be accounted for by water resorption under normal conditions. The resorption of Na^+ and Cl^- leaves NH_4^+ as the predominant cation. HCO_3^- is probably the anion (7). It is interesting to note that the osmolality of the urine frequently was reduced in the cloaca.

TABLE 6. *Species differences under normal and experimental conditions*

	Increase in Plasma Osmolality, milliosmols/kg H_2O	Osmolal U/P	Creatinine U/P	GFR, ml/kg per hr	GFR, ml/m² per hr
		Ureotelic			
Frog (*Rana clamitans*)					
Normal		(0.2)	2.7	34.2	156
H_2O load		(0.1)	1.6	82.0	374
Light dehyd.		(0.8)	6.5	5.1	23.3
Severe dehyd.				0	0
Turtle (*Pseudemys scripta*)					
Normal		0.62	3.4	4.7	56.7
H_2O load		0.60	3.6	10.3	124.0
Light dehyd.	20	0.84	8.5	2.7	32.4
Severe dehyd.	20			0	0
		Ureo-uricotelic			
Desert tortoise (*Gopherus agassizii*)					
Normal		0.36	2.4	4.7	56.7
H_2O load		0.57	3.7	15.1	182.0
Salt load	40–50	0.61	4.4	2.9	35.0
Salt load	100			0	0
		Uricotelic			
Gecko (*Hemidactylus sp.*)					
Normal		0.64	4.3	10.4	17.6
H_2O load		0.74	2.2	24.3	41.2
Dehyd.	100	0.74	2.5	3.3	5.6
Horned toad (*Phrynosoma cornutum*)					
Normal		0.93	1.8	3.5	10.8
H_2O load		0.90	3.1	5.5	15.4
Dehyd.	50	0.97	2.6	2.1	6.5
Galapagos lizard (*Tropidurus sp.*)					
Normal		0.91	2.0	3.6	8.8
H_2O load		0.99	2.3	4.5	10.9
Dehyd.	50	0.97	2.1	1.2	2.9
Crocodile (*Crocodylus acutus*)					
Normal		0.82	8.3	9.6	116
H_2O load		0.72	4.3	13.3	160
Dehyd.	30–40	0.85	6.1	6.0	74

The values for *Rana clamitans* are from Schmidt-Nielsen and Forster (19), for Pseudemys and Gopherus from Dantzler and Schmidt-Nielsen (5), for Hemidactylus, Phrynosoma, and Tropidurus from Roberts and Schmidt-Nielsen (15), and for crocodiles from the present paper. Values from approximately comparable conditions have been selected for the comparison. For Gopherus no data are available on dehydration but only on salt load which caused the plasma osmolality to rise. These values have been used here. In the first column the approximate rise in plasma osmolality is given.

DISCUSSION

A comparison of the renal function of the crocodile with that of other reptiles and frogs show a much closer resemblance to the uricotelic terrestrial reptiles, than to the ureotelic amphibious forms (Table 6).

The glomerular filtration rate varies only little in the crocodile. This animal, which lives in and around water, shows only a 58% increase in filtration rate after a water load and no increase after a 10% isosmotic load. In contrast, the filtration rate doubled or tripled in the frog (19) and the turtle (5) after a water load or an isosmotic load.

The filtration rate in the crocodile, as in the terrestrial reptiles, was only slightly reduced after severe dehydration or increase in plasma osmolality. This again is in contrast to amphibians and turtles in which the filtration rate was reduced to zero by moderate dehydration or a 20 milliosmols/kg H_2O increase in plasma osmolality (5, 20). The distal tubule of the crocodile dilutes the urine even less than that of the gecko (15) and the desert tortoise (5), and the permeability to water seems to remain relatively unchanged in the crocodile. Under all conditions the urine osmolality remained around 80% of the plasma osmolality. This is a very modest dilution of the urine considering the fresh-water habitat.

On the basis of these findings (which admittedly include a rather limited number of species) we may tentatively suggest that the type of regulation of glomerular filtration rate and tubular function found in amphibious and terrestrial vertebrates is determined more by the end product of the nitrogen metabolism than by the habitat.

Adaptations of the crocodile to its habitat. Since the crocodile shows so little renal response to its state of hydration, one would not expect it to be able to excrete a water load well. Furthermore, because of the high osmolality of the urine the renal solute loss should be considerable. Other adaptations, however, make it possible for it to excrete excess water.

1) The filtration rate of the crocodile per m² body surface is much higher than that of the terrestrial reptiles. It is of the same order of magnitude as that of the frog.

2) The excretion of ammonia and bicarbonate in the

urine by the crocodilians (4) may be a compensatory adaptation to the amphibious life. Coulson and Hernandez have shown in a series of studies on the alligator (4) that the major ions in the urine are NH_4^+ and HCO_3^-. These two ions are not excreted together in mammals, where ammonia is excreted when the urine is acid, and bicarbonate when the urine is alkaline. The advantage of excreting these ions together may be that they can be excreted instead of sodium, potassium, and chloride, by a tubule that lacks the capacity for establishing and maintaining a higher osmotic gradient and thus electrolytes can be conserved.

3) The further, and in many cases almost complete, resorption of sodium and chloride in the cloaca serves the same purpose of conserving valuable electrolytes. Furthermore, some capacity for regulating cloacal resorption of these ions may be present. The excretion of urine containing almost exclusively NH_4HCO_3 serves the same purpose as excreting a highly dilute urine, i.e., the excretion of excess water. In addition, the crocodile also has a protective mechanism against swallowing too much water. A valve-like fold of skin in the throat enables it to open the mouth and crush the prey under water. When swallowing the prey it raises the head above water (12).

The curious adaptations of the crocodile to its habitat can perhaps best be explained by its ancestry. The crocodilians are descendants of the stem of ruling reptiles (order Thecodontia), bipedal reptiles completely adapted to a terrestrial life (16). The order Crocodilia is, therefore, secondarily adapted to its amphibious habitat, in contrast to the turtles (order Chelonia) which is an early branch of the primitive stem Reptilia (16). According to Romer (16), early reptiles, descending from amphibians, were probably amphibious in their habitat and the amniote egg was merely an adaptation, which removed the egg from the danger of drought and enemies present in the ancestral waters. It is, therefore, not surprising that all chelonian reptiles have the complete set of urea cycle enzymes in their livers, and that the freshwater turtle is predominantly ureotelic and shows the same type of renal function as amphibians. We may assume that the first truly terrestrial reptiles partly lost the urea cycle enzymes and became predominantly uricotelic like the present-day lizards and snakes. The livers of lizards and snakes do not contain the full complement of urea cycle enzymes (2). The crocodilians, although they have returned to water, are ammonouricotelic (only 2 % of their waste nitrogen is excreted as urea (9)). They probably do not have all the urea cycle enzymes, but no data are available on the occurrence of these enzymes in their livers.

The crocodilians having retained their uricotelic adaptation to land were forced to use other forms of adaptations to their habitat.

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