Kidney structure of a euryhaline mammal, the Cape clawless otter (*Aonyx capensis*)

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The Cape clawless otter (*Aonyx capensis*) is one of the few species of mammals that occur in both freshwater and marine habitats, and it therefore must be able to tolerate the high rates of water flux typical of aquatic animals as well as the desiccating effects of seawater. The clawless otter has paired, discrete multirenculate kidneys (total mass = 172 g) comprised of both unipapillary and bipapillary renculi weighing an average of 2.6 and 3.2 g, respectively. The average thickness of the cortex is 2.3 mm, and thicknesses of the outer and inner medulla are 2.4 and 6.4 mm, respectively. These measurements and the overall structure of the kidney of the Cape clawless otter are intermediate between those of freshwater and marine mammals.

Otters occur in both freshwater and marine environments, but only one species occurs in both. The Cape clawless otter (*Aonyx capensis*, Carnivora) inhabits rivers, streams and lakes in all but the most arid regions of sub-Saharan Africa (Skinner & Smithers 1990), but it is also at home in the sea, occurring in coastal waters and estuaries where a proximal source of fresh water is available (Van der Zee 1982; Arden-Clarke 1986; Verwoerd 1987). It feeds primarily on crabs, frogs, and fishes, which it captures underwater using the dexterous, unwebbed toes of its front feet (Verwoerd 1987; Skinner & Smithers 1990).

Freshwater and marine environments present animals with very different osmoregulatory challenges, and this is reflected in the structure and function of their kidneys (Beuchat 1996). Mammals living in freshwater have high rates of water turnover and may only rarely face a risk of dehydration. Their kidneys, consequently, concentrate the urine poorly and are designed instead for the efficient elimination of copious, dilute urine. Marine species, on the other hand, live in a desiccating environment; the concentration of seawater is more than three times that of mammalian body fluids. For them, the ability to excrete salt while at the same time minimizing urinary water loss by producing a concentrated urine is essential.

Euryhaline mammals, those that are equally at home in both fresh and salt water, are rare. Only the manatee (*Trichechus manatus*) and the Cape clawless otter occur in both freshwater and marine environments and also move with apparent ease between them. Because these two species tolerate an exceptionally broad range of osmoregulatory stresses, the structure and function of their kidneys are of considerable interest. Presented here is the first study of the kidney of one of these, the Cape clawless otter.

A male Cape clawless otter was collected as a road-kill probably less than 12 h old in the Western Cape Province of South Africa. It was found near a river southeast of Cape Town, about 10 km inland from the river's exit to the sea in False Bay. The animal was an adult male with an estimated body mass of 15 kg. The kidneys were removed from the animal, weighed, and transferred to 70% ethanol for fixation. After 2 h, clusters of conjoined renculi were dissected free (7 from one kidney and 5 from the other) and weighed. The number of medullary papillae was determined by removal of the ureter and renal pelvis from each cluster, which revealed the papillae in the pelvic space. The renculi were cut medially to reveal the medullary papillae in cross-section. The thicknesses of the cortex, outer medulla, and inner medulla were measured (± 0.01 mm) under a stereo dissecting microscope. Only those sections through the longest dimension of the medullary papilla were used for quantification of inner and outer medullary thickness. Statistical comparisons were performed using ANOVA or Student's t-test with a significance criterion of $p < 0.05$. Data are reported as means ± 1 SE.

Like both the sea otter (*Enhydra lutris*) and river otter (*Lutra lutra*) (Beuchat 1996), the kidneys of the Cape clawless otter were of the type described by Oliver (1968) as 'discrete' multirenculate (Figure 1). Each consisted of multiple renal organs, or renculi (Sperber 1944), that could be distinguished as individual functional units by the presence of a single ureter and shared arterial and venous vessels. Most of the renculi appeared divided on the cortical surface, but some of these

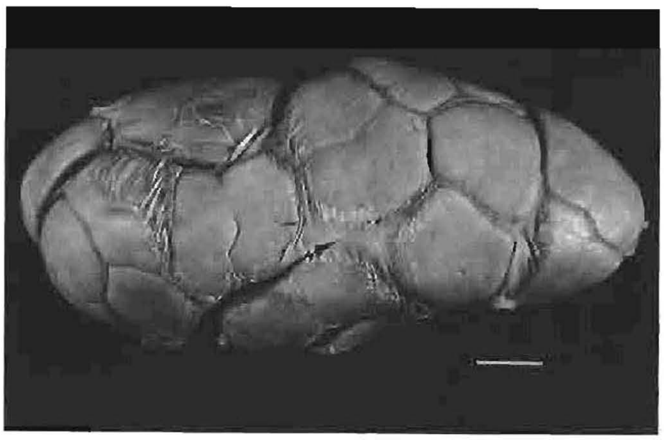

Figure 1 One of the paired kidneys of the Cape clawless otter. Evident on its outer surface are the indentations demarcating some of the renculi. Scale bar = 10 mm.

contained only a single medullary papilla (Figure 2). Others were bipapillary, with the two papillae sharing a common renal pelvis (Figure 3). No renculus contained more than two papillae. Although the cortical tissue of the bipapillate rencular units was continuous (Figure 3), it appeared from the placement and organization of the glomeruli, tubules, and capillary vessels that the individual renculi comprising the unit were functionally separate except for sharing a common pelvis.

The two kidneys weighed a total of 171.7 g. Single and bipapillary renculi weighed an average of 2.61 g (± 0.24, n = 6) and 3.21 g (± 0.35, n = 12), respectively (Table 1); these values were not significantly different (p = 0.189). The thicknesses of the cortex, outer medulla, and inner medulla likewise did not differ significantly between single and bipapillary renculi (Table 1), or between the right and left kidneys; the pooled averages were 2.3 mm, 2.4 mm and 6.1 mm, respectively.

Table 1 Mass and the thicknesses of the cortex, outer medulla, and inner medulla of unipapillary (n = 6) and bipapillary renculi (n = 12) from the Cape clawless otter kidney. Mean (± 1 SE)

	Unipapillary	Bipapillary
Mass (g)	2 61 (0 24)	3.21 (0.35)
Cortex (mm)	2 40 (0 16)	2.20 (0 09)
Outer Medulla (mm)	2.68 (0 17)	2.32 (0 17)
Inner Medulla (mm)	6 90 (0.61)	6.18 (0.27)

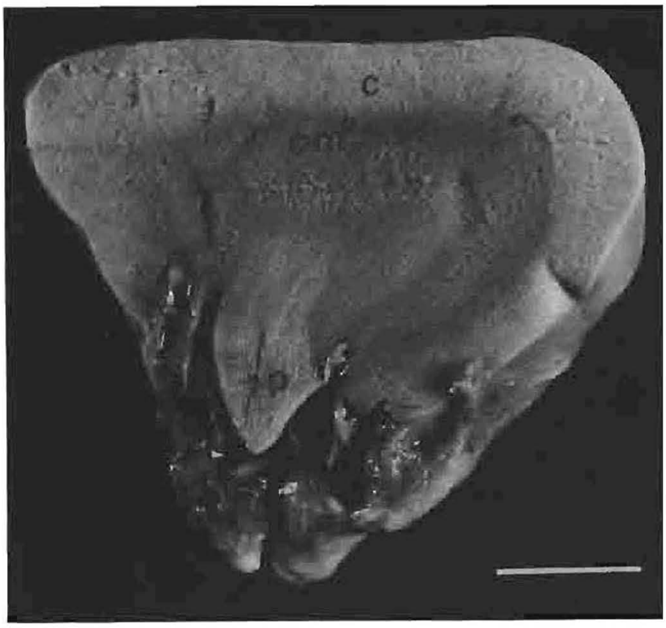

Figure 2 A unipapillary renculus from the kidney of the Cape clawless otter. Indicated are the cortex (*c*), outer medulla (*om*), and the inner medulla that forms the papilla (*p*). Scale bar = 2.5 mm.

Figure 3 A bipapillary renculus from the kidney of the Cape clawless otter. The cortex (*c*) surrounding the two rencular units is continuous, but the outer medulla (*om*) and the inner medullary tissue that forms the two papillae (*p*) are functionally separate. Scale bar = 3 mm.

Before making quantitative comparisons between the kidneys of the Cape clawless otter and those of other mammals, we must first account for the fact that kidney size varies allometrically with body size. Allometric relationships between kidney size and body mass in mammals have been compiled by Beuchat (1996) using data for over 330 species from the literature. These are expressed in the form of a power function ($y = a M^b$, where M is body mass in kg; computed using least-squares linear regression on log-transformed data), which produces a straight line when plotted on log-log axes. Correlations between kidney structure and habitat can be examined by computing the allometric regressions after first separating the species by habitat (Beuchat 1996). Data for a particular species can then be compared with the expected values computed for an animal of equal body mass from a similar habitat using these equations.

There are striking anatomical differences among the kidneys of mammals from different habitats. The kidneys of marine mammals are exclusively of the discrete multirenculate type (Sperber 1944; Beuchat 1996) and, although the total mass of their kidneys tends to be greater than that of a similarly-sized non-marine mammal (Prothero 1984; Beuchat 1996), the renculi are surprisingly small. The predicted cortical thickness for a 15 kg marine mammal is only about 25% that of a similarly-sized species from a mesic habitat, and the thicknesses of the outer and inner medullas are about 30% and 50%, respectively, of those in mesic species (Table 2). Despite the small dimensions of their renculi, marine mammals can concentrate their urine surprisingly well (Beuchat 1996).

The kidneys of freshwater mammals, by contrast, are exclusively of the unipapillary type, and in many species the inner medulla is absent because the loops of Henle lack the thin descending limb. This segment of the nephron is thought to play a major role in the urinary concentrating mechanism and, indeed, much of the interspecific variability in concentrating ability among mammals (after accounting for the effect of body size) can be attributed to differences in the length of the thin descending limb (Beuchat 1996). The urinary concentrating ability of freshwater mammals, especially those lacking the inner medulla, is very modest (Beuchat 1996).

The uniquely broad habitat tolerance of the Cape clawless otter is reflected in the unusual structure of its kidneys, which

Table 2 Total kidney mass and cortical and medullary dimensions for renculi from the Cape clawless otter (unipapillary, bipapillary; from Table 1), as well as the renal dimensions and maximum urine osmolality (U_{osm}, in mmol / kg H_2O) predicted for typical 15 kg mammals from the allometric relationships (in parentheses) for freshwater, mesic, and marine mammals from Beuchat 1996. The allometric equations are in the form of power functions ($y = a M^b$, where M is body mass in kg; see text). There are insufficient data to compute allometric regressions for inner medullary thickness and maximum urine osmolality in freshwater mammals; consequently, these predicted values have been omitted. Urine osmolality of the Cape clawless otter has never been measured

		Predicted		
	Cape otter	Freshwater	Mesic	Marine
Kidney Mass (g)	171.7	59.0	65.3	110.3
		($y = 5.15 M^{0.90}$)	($y = 6.90 M^{0.83}$)	($y = 9.38 M^{0.91}$)
Cortex (mm)	2.4, 2.2	5.5	5.8	1.4
		($y = 2.96 M^{0.23}$)	($y = 3.03 M^{0.24}$)	($y = 1.04 M^{0.12}$)
Outer Medulla (mm)	2.7, 2.3	6.7	5.3	1.8
		($y = 3.42 M^{0.25}$)	($y = 3.10 M^{0.20}$)	($y = 1.11 M^{0.18}$)
Inner Medulla (mm)	6.9, 6.2	–	7.9	4.1
		–	($y = 4.84 M^{0.18}$)	($y = 3.11 M^{0.10}$)
Maximum U_{osm}	–	–	1739	2252
		-	($y = 2280 M^{-0.10}$)	($y = 2649 M^{-0.06}$)

are extraordinarily large for a mammal of its size – nearly three times the size predicted for freshwater or mesic species, and even 70% larger than expected for a marine mammal. Despite this, however, the dimensions of the cortical and medullary regions of individual renculi are modest, falling between those predicted for marine mammals and for species from mesic or freshwater environments (Table 2). Unfortunately, nothing is known about the osmoregulatory physiology of the Cape clawless otter, so the functional implications of these structural features of its kidneys are unknown.

The kidneys of the only other euryhaline mammal, the manatee, provide an interesting comparison to those of the Cape clawless otter. The kidneys of a 925 kg manatee weigh a total of about 2645 g (Beuchat 1996), much less than the prediction for a similarly-sized marine mammal (about 4700 g; from equation in Table 2), but comparable to the size expected of a freshwater species (2400 g). The thickness of the cortex (11 mm) is likewise more similar to that of a freshwater (14 mm) than marine (2 mm) mammal. The outer medulla, however, is much thicker (52 mm) than that of either freshwater (19 mm) or marine species (4 mm). Like some freshwater mammals, the inner medulla is absent in the manatee. Sperber (1944) described the manatee kidney as 'transitional' in structure between those in which the renculi contain divided medullary pyramids but a continuous cortex, and those with completely divided renculi, as is typical of marine mammal kidneys. As for the Cape clawless otter, nothing is known about renal function in the manatee.

Although the manatee and Cape clawless otter share a broad salinity tolerance, the structures of their kidneys suggest that their osmoregulatory capabilities should be very different. Functional studies of both of these unique mammals would be of considerable interest.

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