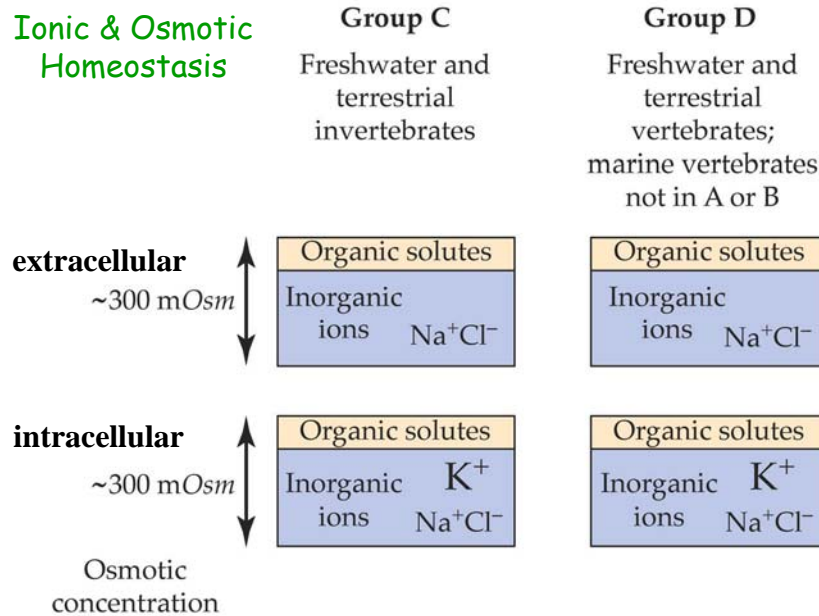


# osmoregulation mechanisms in gills, salt glands, and kidneys

22



ANIMAL PHYSIOLOGY, Figure 25.10 (Part 2) © 2004 Sinauer Associates, Inc.

Salt Secretion:

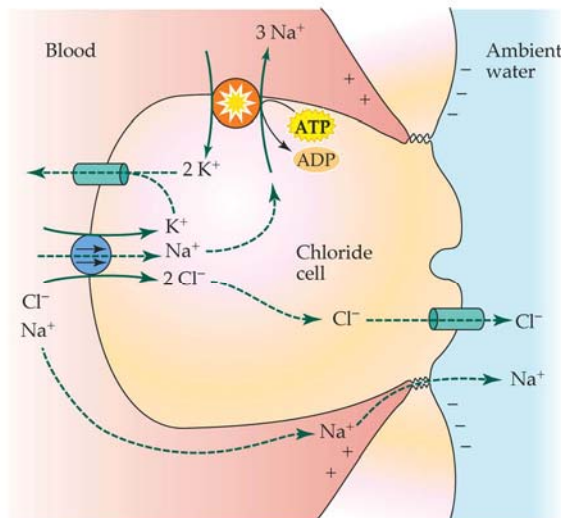
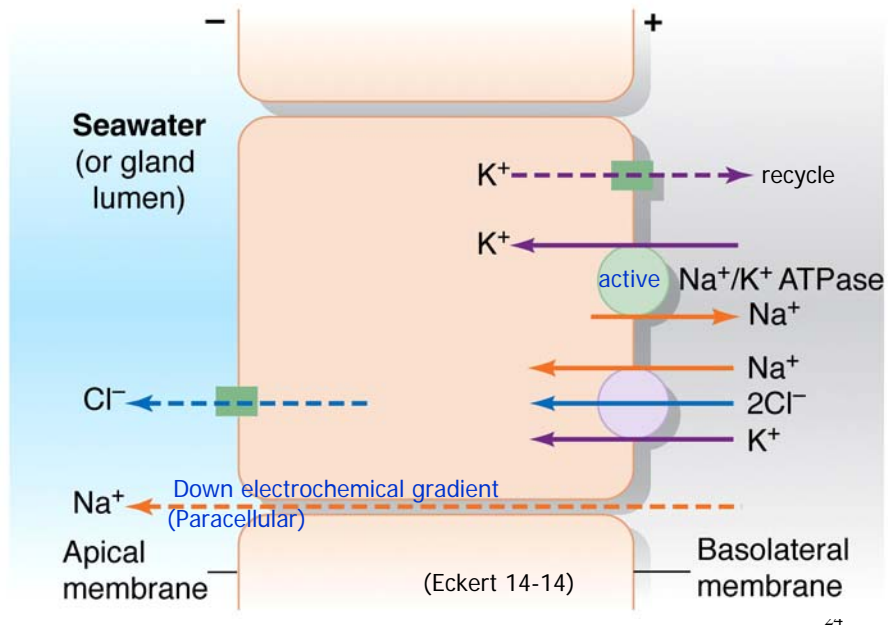


Figure in Box 26.2  
Hill et al. 2004

KEY

	Na <sup>+</sup> -K <sup>+</sup> -ATPase
	Na-K-2Cl cotransporter
	Cl <sup>-</sup> channel or K <sup>+</sup> channel
	Transport against electrochemical gradient
	Transport in direction of electrochemical gradient

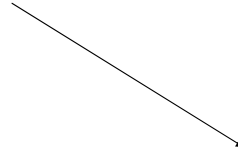
Chloride Cell

ANIMAL PHYSIOLOGY, Box 26.2 © 2004 Sinauer Associates, Inc.

## Salt Glands

Shark **rectal glands** to dispose of excess NaCl

- blood **hyperosmotic** to seawater, but **less salt**
- more **urea** and TMAO (trimethylamine oxide)
- NaCl actively secreted

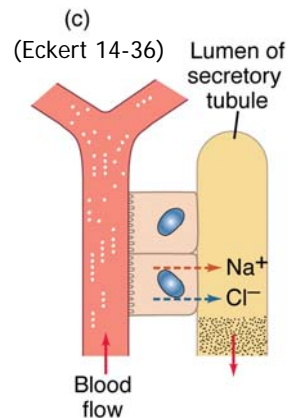


26

## Shark Rectal Salt Glands

### Salt-secreting cells:

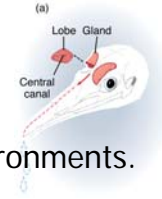
- Na/K-ATPase pump in basolateral membrane
- generates gradient for Na<sup>+</sup> by which Na<sup>+</sup>/2Cl<sup>-</sup>/K<sup>+</sup> cotransporter drives up [Cl<sup>-</sup>] in cell
- Cl<sup>-</sup> across apical membrane
- Na<sup>+</sup> follows paracellularly down electrochemical gradient (and H<sub>2</sub>O)
- apical membrane **impermeable** to urea and TMAO
- therefore **iso-osmotic** secretion with **lots of NaCl**



... slightly different in birds and lizards →

## Salt Glands

(Eckert 14-36)



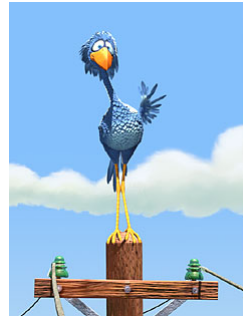
Nasal/orbital salt glands of birds and reptiles  
-especially species in **desert** or **marine** environments.

**Hypertonic NaCl secretions** (2-3x plasma osmolarity)

Allows some birds to **drink salt water** and end up with osmotically free water



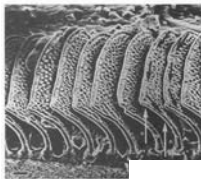
*Amblyrhynchus cristatus*



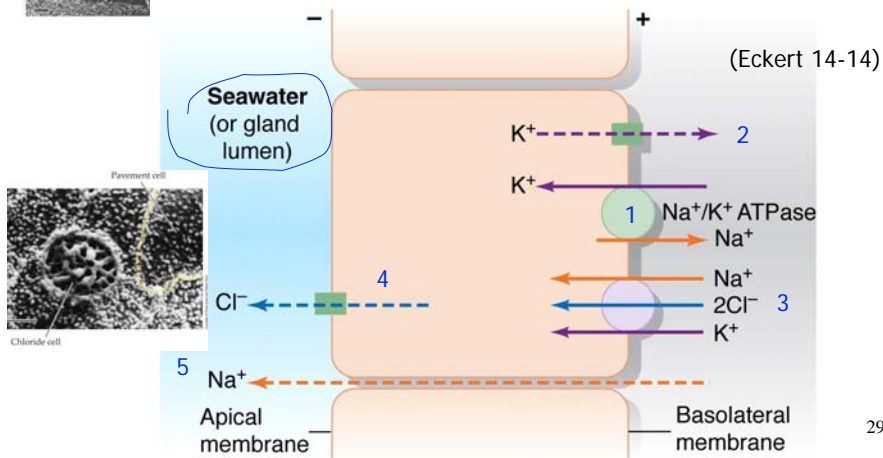
## Fish Gills

**Chloride cells** involved in osmoregulation

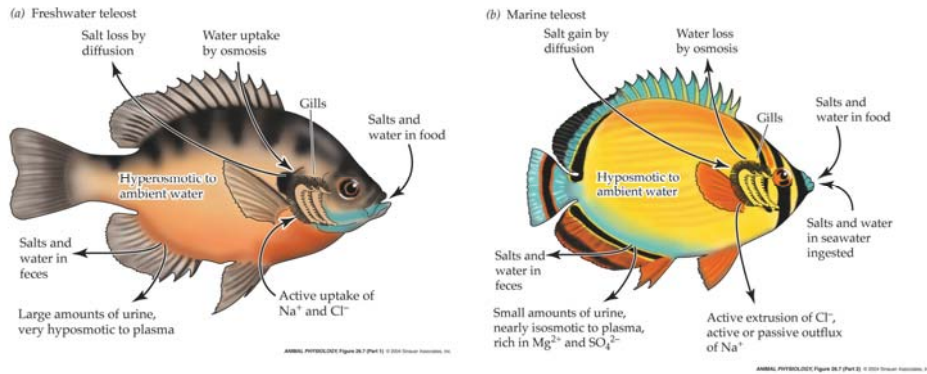
- (recall lab paper on smolting)
- lots of **mitochondria** to power ATPases
- **mechanism similar** in nasal glands (birds and reptiles), and shark rectal gland



Fish skin breathing apparatus consists of gill filaments. The gill filaments are composed of many gill lamellae. The gill lamellae are the site of gas exchange. The gill lamellae are also the site of osmoregulation. The gill lamellae are also the site of ion transport.



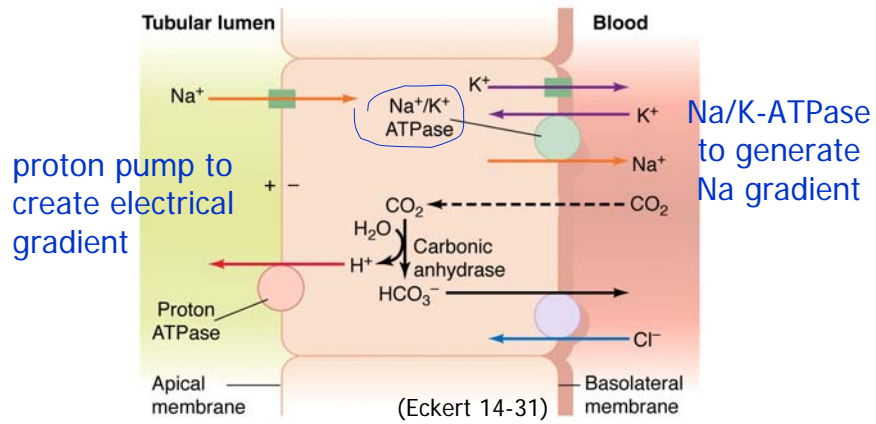
29



Hill et al. 2004, Fig 26.7

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Freshwater fish:  
 The mechanism basically reversed to allow uptake of salt from water against concentration gradient



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(recall lab paper on [smolting](#))

Sea  $\leftrightarrow$  Freshwater

[Switch](#) between getting rid of excess salt in seawater and taking up salt in freshwater



[Growth hormone](#) and [cortisol](#) for  $\rightarrow$  sea  
(more active chloride cells with more Na/K-ATPase activity)

[Prolactin](#) for  $\rightarrow$  freshwater



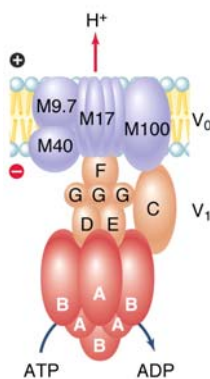
### Osmoregulatory Mechanisms

[Apical](#) surface (faces lumen and outside world)

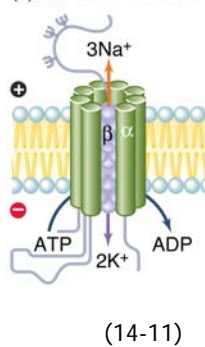
[Basal](#) surface (faces body and extracellular fluid)

- Active movement of ions/salts requires [ATP](#)
- Movement of [water follows](#) movement of ions/salts

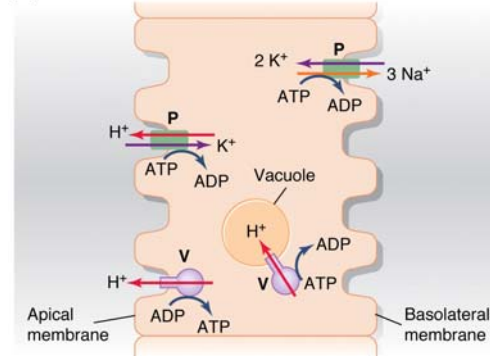
(b)  $H^+$  V-ATPase



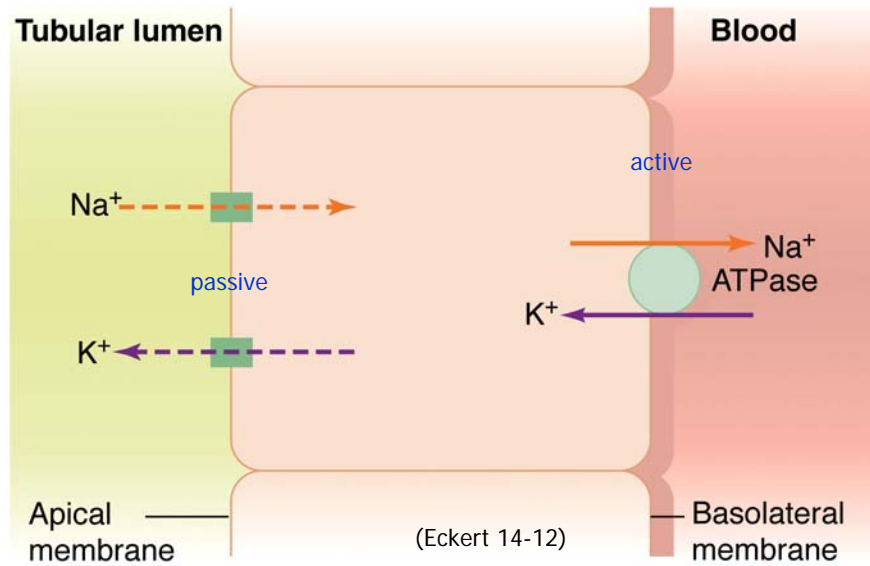
(c)  $Na^+ /K^+ P$ -ATPase



(d)



Gradients established and used...to move ions, water

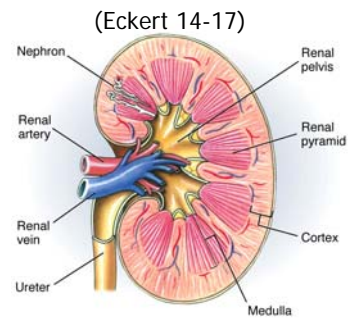


Mammalian Kidney

34

Kidney Functions:

- Osmoregulation
- Blood volume regulation
- Maintain proper ion concentrations
- Dispose of metabolic waste products
- pH regulation (at ~ 7.4)
- Dispose of toxins and foreign substances



How does the kidney accomplish this?

35

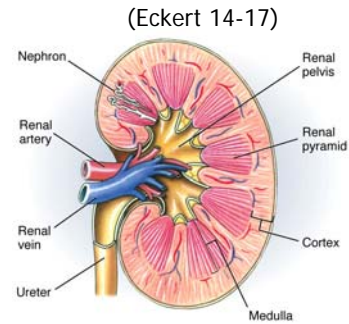


## Mammalian Kidney

- Paired
- 1% body mass
- 20% blood flow

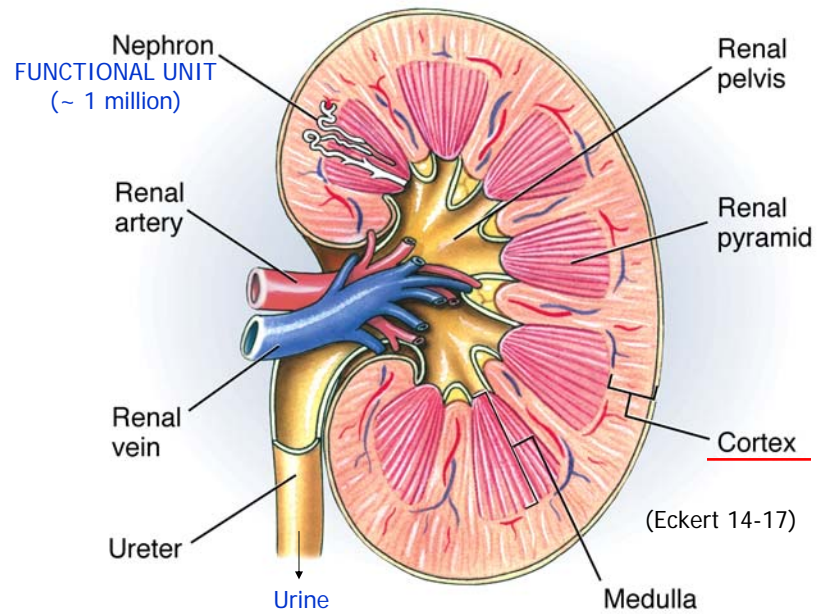
- urine contains:
  - water
  - metabolic byproducts (e.g., urea)
  - excess salts etc.

- from ureter to urinary bladder
  - (smooth muscle, sphincter, inhibition)
- out via **urethra** during **micturition**



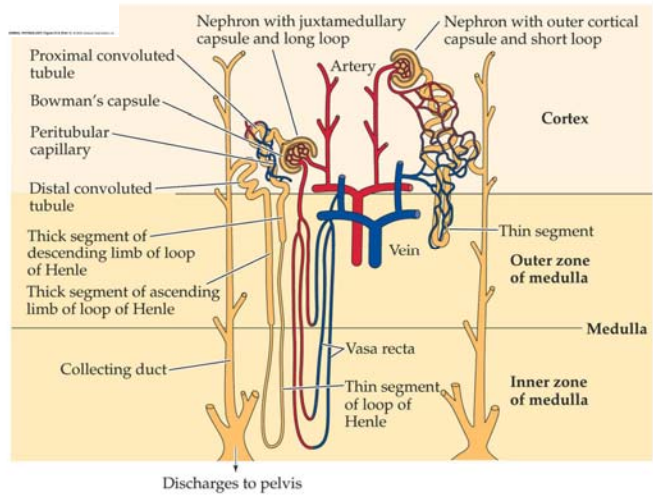
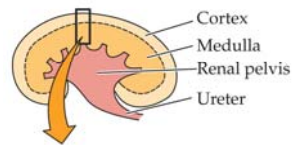
36

## Mammalian Kidney Anatomy





(a) Kidney in cross section



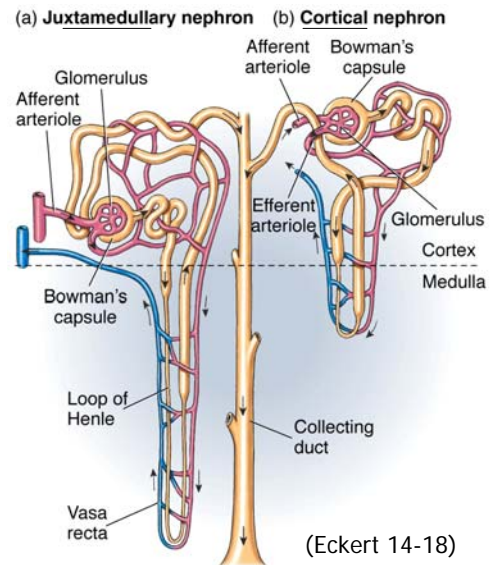
ANIMAL PHYSIOLOGY, Figure 27.6 (Part 2) © 2004 Sinauer Associates, Inc.

## Nephron Anatomy

- 1 -Proximal tubule
- 2 -Loop of Henle
  - descending
  - ascending
- 3 -Distal tubule

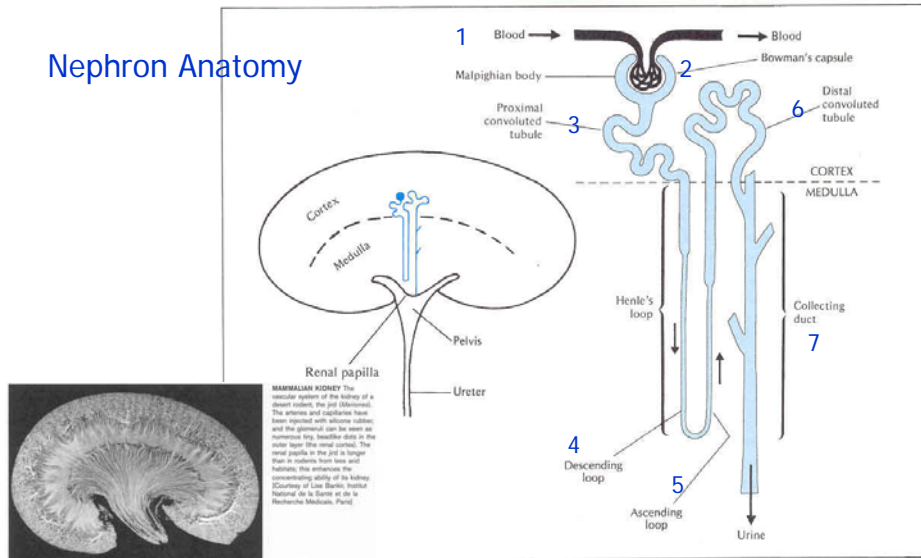
-numerous nephrons empty into **collecting duct**

-collecting ducts empty into **renal pelvis**



(Eckert 14-18)

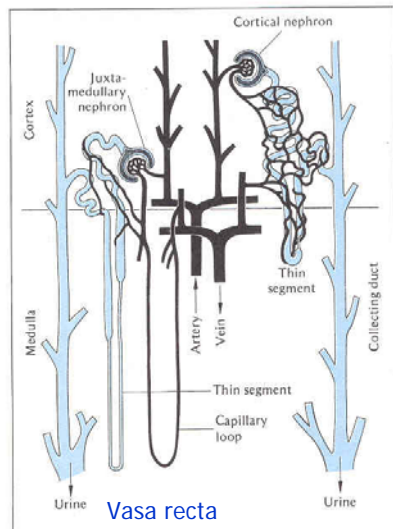
# Nephron Anatomy



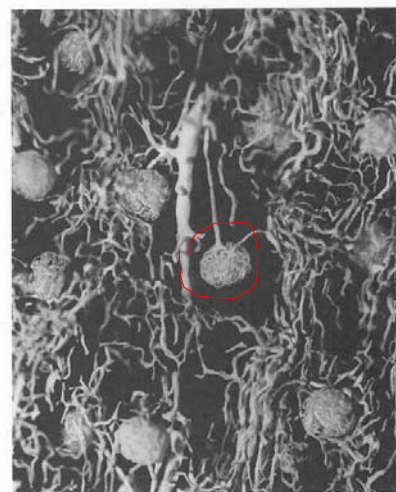
**Figure 9.8** Diagram of a mammalian kidney. The kidney contains a large number, up to several million, of single nephrons. Only one nephron is indicated in this diagram and is shown enlarged to the right. The outer layer of the kidney, the *cortex*, contains the *Malpighian bodies* and the proximal and the distal convoluted tubules. The capillary network within the Malpighian body is known as the *glomerulus*. The inner portion, the *medulla*, contains

*Henle's loops and collecting ducts.*  
The urine is initially formed by ultrafiltration in the Malpighian bodies. The filtered fluid is modified and greatly reduced in volume as it passes down the renal tubules and into the collecting ducts. These empty the urine into the renal pelvis, from where it is conveyed via the *ureter* to the bladder.

Knut Schmidt\_Nielsen 1997



**Figure 9.11** Diagram of countercurrent exchange. The long-looped nephron is surrounded by a capillary network. Most mammalian kidneys contain a mixture of the two types of nephrons, but some species have only one or the other kind. [Smith 1951]



**DOG KIDNEY** Close-up view of glomeruli from a dog kidney after arterial injection of silicone rubber. The glomerulus in the center of the photo shows the slightly thicker vessel leading into the glomerulus and the somewhat thinner vessel leaving it. The diameter of these vessels is about 15 to 20  $\mu\text{m}$ ; the diameter of the glomerulus is about 150  $\mu\text{m}$ . [Courtesy of A. Clifford Barger, Harvard University]

Knut Schmidt\_Nielsen 1997

## Kidney Processes- overview

### 1. FILTRATION

blood --> filtrate

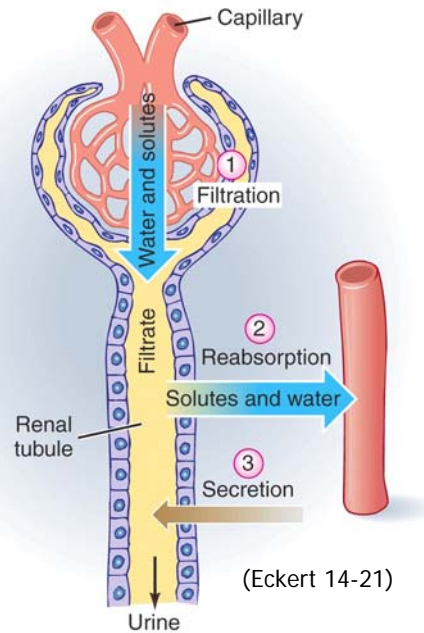
### 2. REABSORPTION

filtrate --> blood

### 3. SECRETION

blood --> filtrate

All 3 involved in final  
Urine Composition



Mosm = x1000

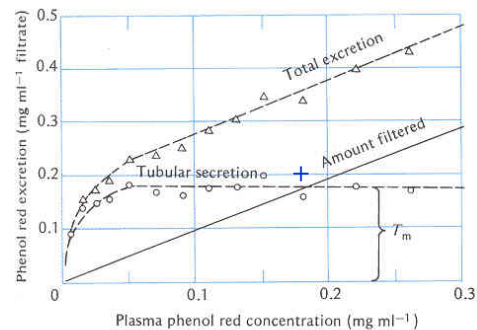
U/P

Animal	Urine maximum osmotic concentration (Osm liter <sup>-1</sup> )	Urine/plasma concentration ratio
Beaver <sup>a</sup>	0.52	2
Pig <sup>a</sup>	1.1	3
Human <sup>b</sup>	1.4	4
White rat <sup>b</sup>	2.9	9
Cat <sup>b</sup>	3.1	10
Kangaroo rat <sup>b</sup>	5.5	14
Sand rat <sup>b</sup>	6.3	17
Hopping mouse <sup>c</sup>	9.4	25

**Table 9.2** The maximum concentrating of various mammals is correlated with the animal, desert animals having the highest concentrations and fresh-water animals



## Filtration plus secretion



**Figure 9.10** Excretion of phenol red by the bullfrog. The amount filtered increases in proportion to the plasma concentration. In addition, phenol red is added to the urine by active tubular transport, increasing the amount in the urine. The amount added by tubular secretion remains constant at plasma concentrations above 0.05 mg per milliliter; this indicates that the tubular maximum for phenol red has been reached. [Forster 1940]

Knut Schmidt-Nielsen 1997

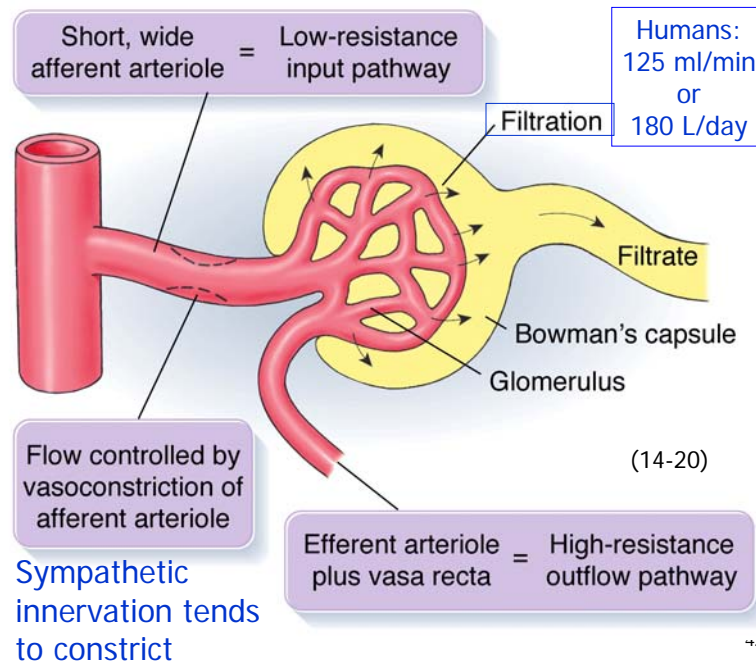
U/P ratio	Implications for excretion		Effects on composition of blood plasma
	Effects on water excretion	Effects on solute excretion	
U/P = 1 (isotonic urine)	Water is excreted in the same relation to solutes as prevails in the blood plasma.	Solutes are excreted in the same relation to water as prevails in the blood plasma.	The formation of urine leaves the ratio of solutes to water in the blood plasma unchanged, thus does not alter the plasma osmotic pressure.
U/P < 1 (hyposmotic urine)	Water is preferentially excreted. Urine contains more water relative to solutes than plasma.	Solutes are preferentially held back from excretion. Urine contains less solutes relative to water than plasma.	The ratio of solutes to water in the plasma is shifted upward. The osmotic pressure of the plasma is raised.
U/P > 1 (hyperosmotic urine)	Water is preferentially held back from excretion. Urine contains less water relative to solutes than plasma.	Solutes are preferentially excreted. Urine contains more solutes relative to water than plasma.	The ratio of solutes to water in the plasma is shifted downward. The osmotic pressure of the plasma is lowered.

ANIMAL PHYSIOLOGY Figure 25.7 (Part 1) © 2010 Sinauer Associates, Inc.

ANIMAL PHYSIOLOGY Figure 25.7 (Part 1) © 2010 Sinauer Associates, Inc.

Hill et al. 2004, Fig 25.7

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Filtration:

Bowman's capsule

3 layers

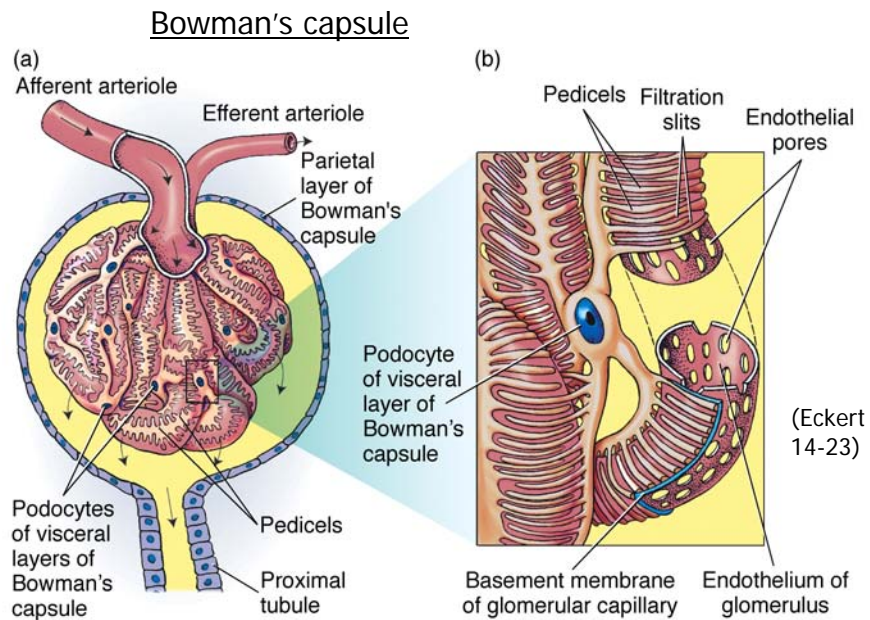
1. **Glomerular endothelial** cells  
-100x leakier than other capillary walls
2. **Basement membrane**  
-negatively charged glycoproteins  
-repel plasma proteins by charge
3. **Epithelial cells**  
-podocytes create slits

Filtrate = protein-free and cell-free plasma

Glomerular Filtration Rate (GFR)

Humans: 125 ml/min or 180 L/day (60x plasma vol.)

46



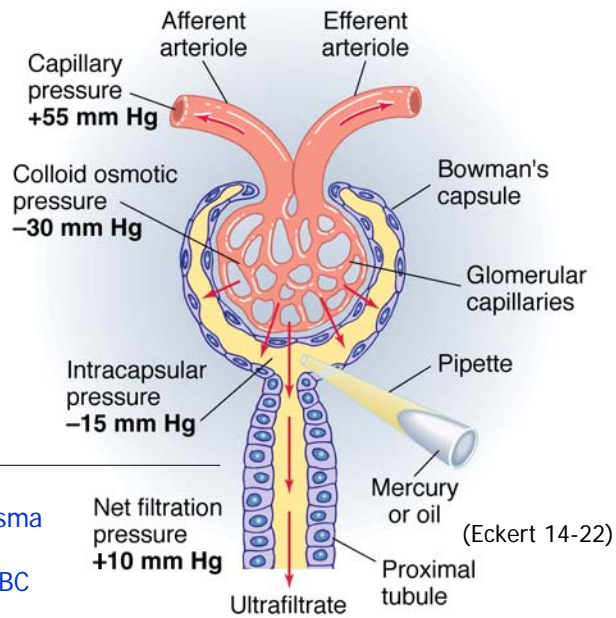
47



## Bowman's capsule

proteins and larger molecules remain

About 20% of the plasma and solutes that enter glomerulus end up in BC

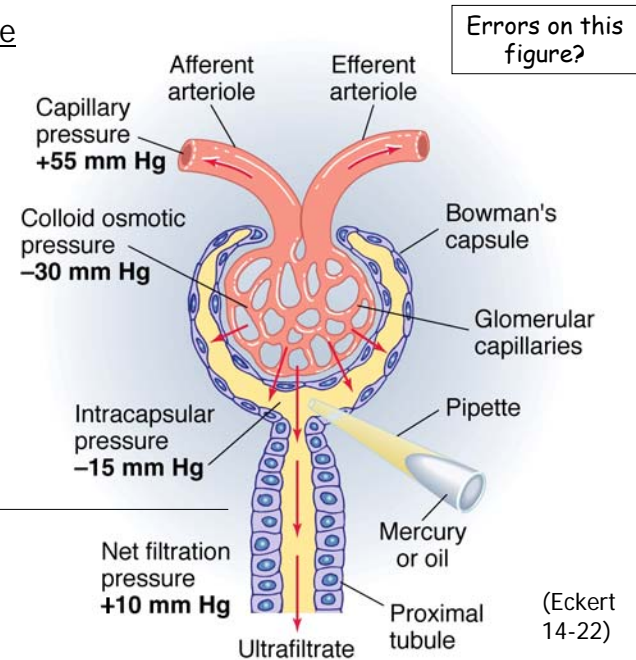


## Bowman's capsule



1. Starvation Implications?

2. Kidney Stone Implications?



## Filtration Regulation:

1. **Myogenic** props. of afferent arteriole resist stretch

2. Secretions from cells of **juxtaglomerular apparatus**  
(where distal tubule passes near bowman's capsule)

-**Macula densa** cells (distal tubule)

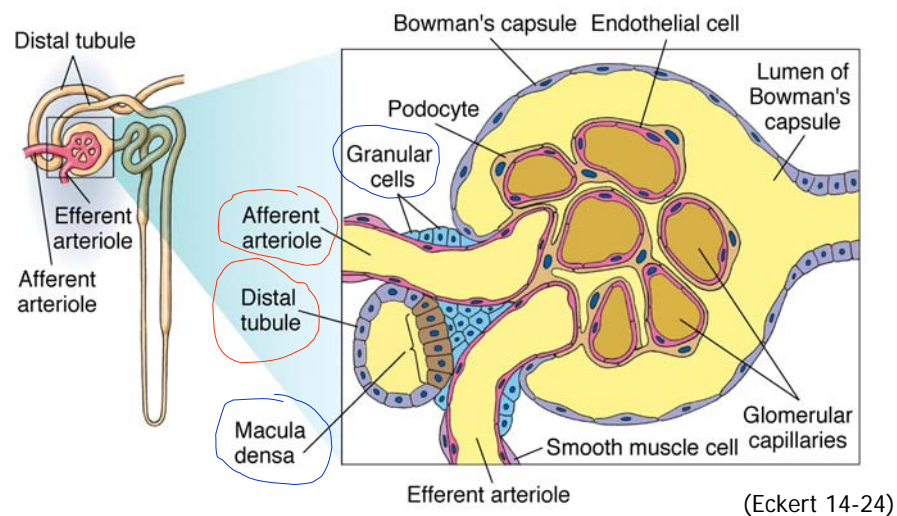
-monitor osmolarity and flow in distal tubule

-paracrine hormonal activity on afferent arteriole

-**Granular or juxtaglomerular** cells (afferent arteriole)

-release **renin** which alters blood pressure...

50



51



## Filtration Regulation:

**Renin** (from granular cells) released in response to  
-low renal BP,  
-low solute [ ] in distal tubule,  
-or sympathetic activation

Renin leads to activation of **Angiotensin II** which  
causes systemic **vasoconstriction to inc. BP**  
stimulates **aldosterone** from adrenal cortex  
**vasopressin (ADH)** from post. pit.  
(these promote salt, water **reabsorption**)

3. **Sympathetic innervation** (reduce GFR)  
-afferent vasoconstriction  
-decreased space between podocytes

52

## Renal Clearance:

Volume of plasma cleared of a substance by the kidney.

(Filtration, Reabsorption, Secretion)

**Inulin (=GFR)** b/c neither reabsorbed nor secreted

If clearance > GFR = secretion

If clearance < GFR = reabsorption

53

### 1. FILTRATION

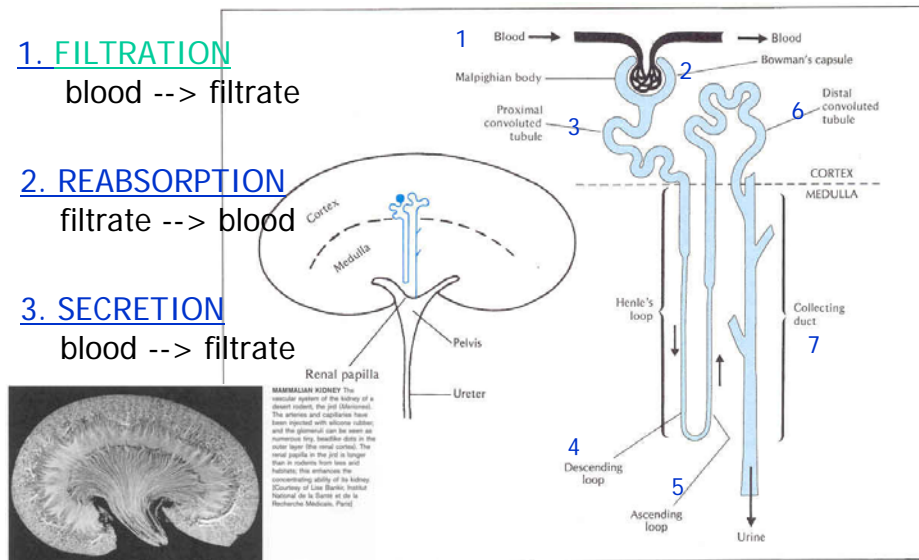
blood --> filtrate

### 2. REABSORPTION

filtrate --> blood

### 3. SECRETION

blood --> filtrate



**Figure 9.8** Diagram of a mammalian kidney. The kidney contains a large number, up to several million, of single nephrons. Only one nephron is indicated in this diagram and is shown enlarged to the right. The outer layer of the kidney, the *cortex*, contains the *Malpighian bodies* and the proximal and the distal convoluted tubules. The capillary network within the Malpighian body is known as the *glomerulus*. The inner portion, the *medulla*, contains

#### *Henle's loops and collecting ducts.*

The urine is initially formed by ultrafiltration in the Malpighian bodies. The filtered fluid is modified and greatly reduced in volume as it passes down the renal tubules and into the collecting ducts. These empty the urine into the renal pelvis, from where it is conveyed via the *ureter* to the bladder.

Knut Schmidt\_Nielsen 1997

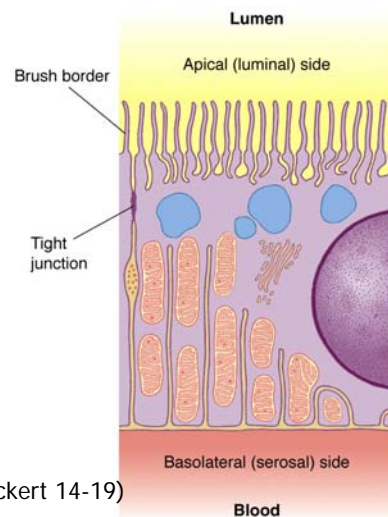
Reabsorption:

of 180 L/day filtered, ~178.5 L reabsorbed in humans

Lots of **active transport of salts** and other substances

Tight junctions not so tight in proximal tubule, so **water can move from filtrate to plasma**

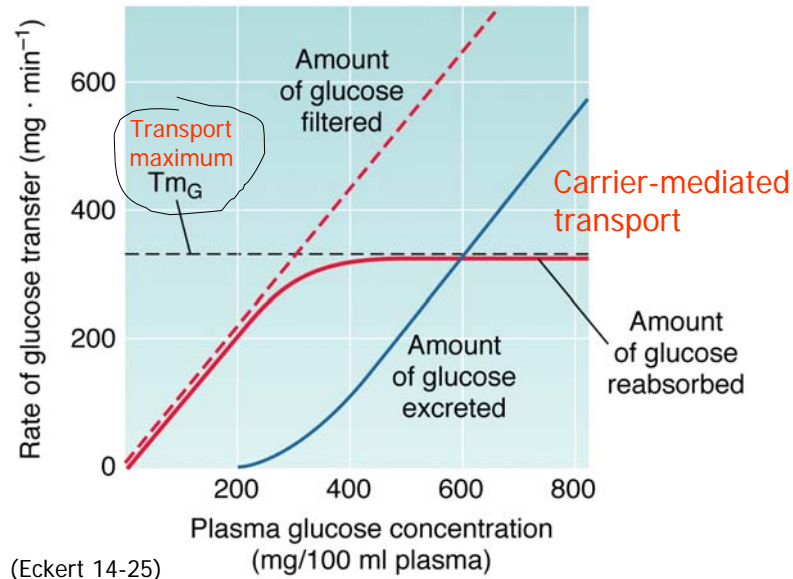
Because of reabsorption (and secretion), **Renal clearance** does NOT often equal GFR



(Eckert 14-19)

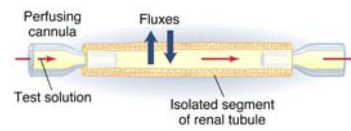
Reabsorption limit –  
Glucose example

$T_m$  at 300 mg/min/100ml plasma



Reabsorption:

(Eckert 14-27)



Proximal Tubule

70% filtered  $\text{Na}^+$  actively reabsorbed

(by  $\text{Na}^+/\text{K}^+$ ATPase pump in basolateral membrane)  
 $\text{Cl}^-$  and water follow

75% of filtrate is reabsorbed

including glucose and amino acids ( $\text{Na}^+$  dependent)  
also, phosphates,  $\text{Ca}^{2+}$ , electrolytes as needed

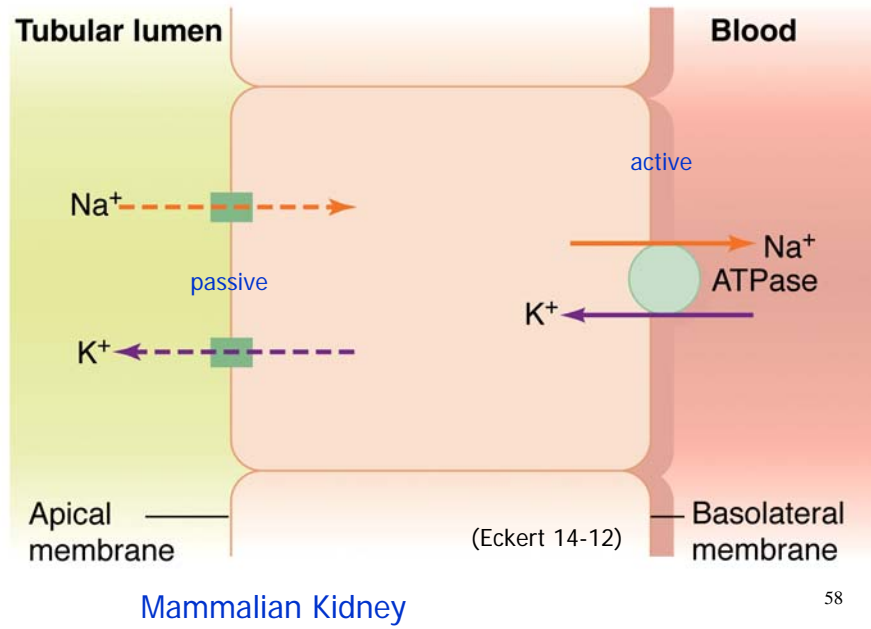
Parathyroid hormone controls phosphate and  $\text{Ca}^{2+}$  reabsorp.  
triggers calcitriol production (Vit. D) for  $\text{Ca}^{2+}$

At end of proximal tubule filtrate is isoosmotic with plasma  
(~300mOsm)

however, remaining substances are 4x concentrated

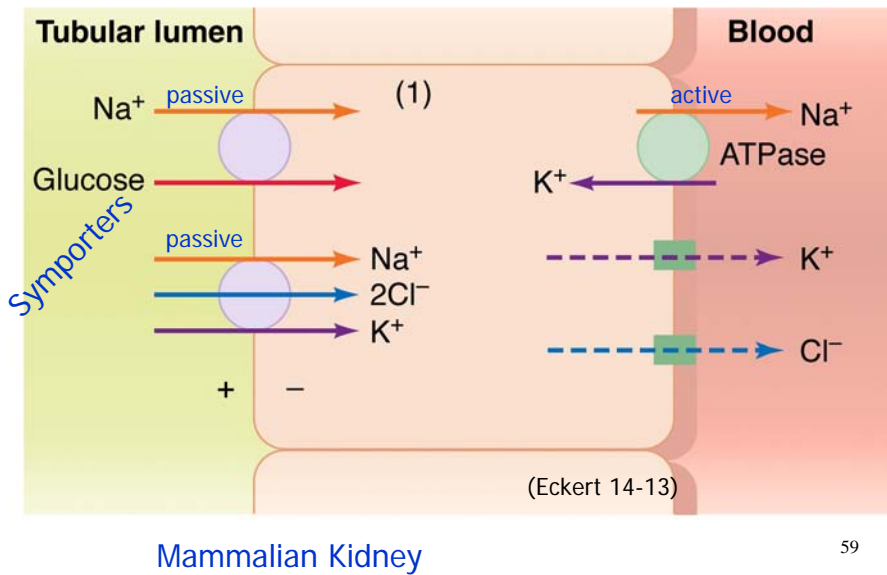
57

Gradients established and used:



Gradients established and used:

(a)



Reabsorption:

Loop of Henle

Descending limb

- no active NaCl transport
- low urea and NaCl permeability
- permeable to water

Ascending thin limb

- no active NaCl transport
- but permeable to NaCl
- low urea permeability
- low water permeability

Ascending thick limb

- NaCl transported out of tubule
- low water permeability

Countercurrent multiplier

One driver of concentrating mechanism of nephron

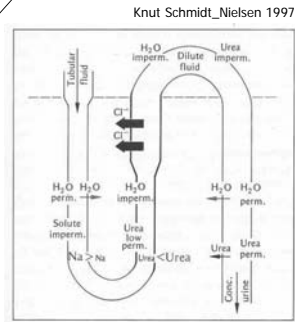
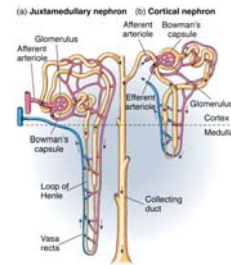


Figure 9.12 Diagram of the concentrating mechanism in the loop of Henle in the mammalian kidney during the formation of concentrated urine. Active transport of chloride ion is indicated by heavy arrows; passive flux of water and urea by light arrows. [Kokko and Tisher 1976]

Reabsorption (and Secretion): (Eckert 14-18)

Distal Tubule

- K<sup>+</sup>, H<sup>+</sup>, NH<sub>3</sub> into tubule
- under endocrine control
- Na<sup>+</sup>, Cl<sup>-</sup>, HCO<sub>3</sub><sup>-</sup> back into body
- water follows
- (Na<sup>+</sup> reabsorption facilitated by aldosterone)



Angiotensinogen  $\xrightarrow{\text{Renin}}$  Ang. I  $\xrightarrow{\text{ACE in lung}}$  Ang. II  $\rightarrow$  aldosterone from adrenal cortex  
 $\rightarrow$  ADH from post. pit.

Collecting Duct

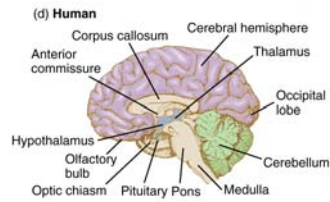
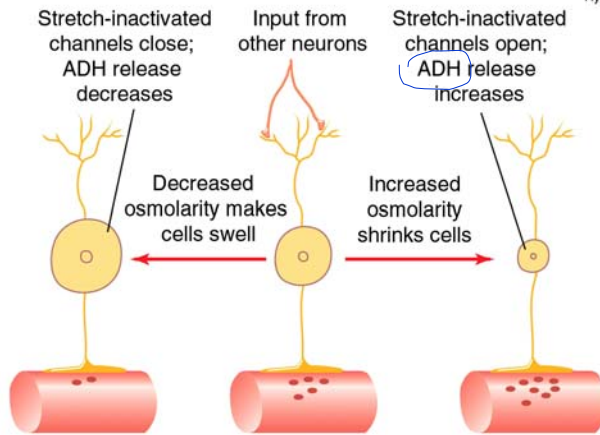
- permeable to water
- hormone control (ADH/vasopressin)
- water (via aquaporins) follows osmotic gradient

-permeable to Urea in inner medulla

Another driver of concentrating mechanism of nephron

-ADH role in water reabsorption/urine concentration

(a) Magnocellular neurons of hypothalamus



-Renin -> Ang. II  
-> ADH

-Baroreceptor input (atrial and arterial)

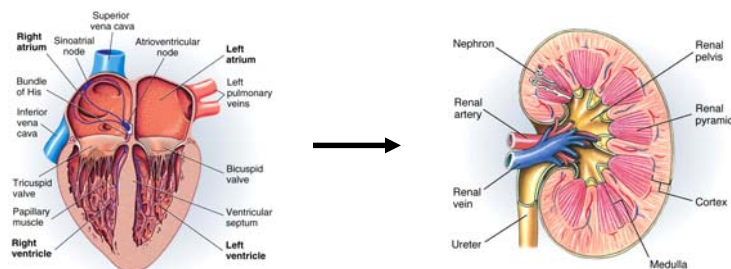
-EtoH inhibits ADH release

62

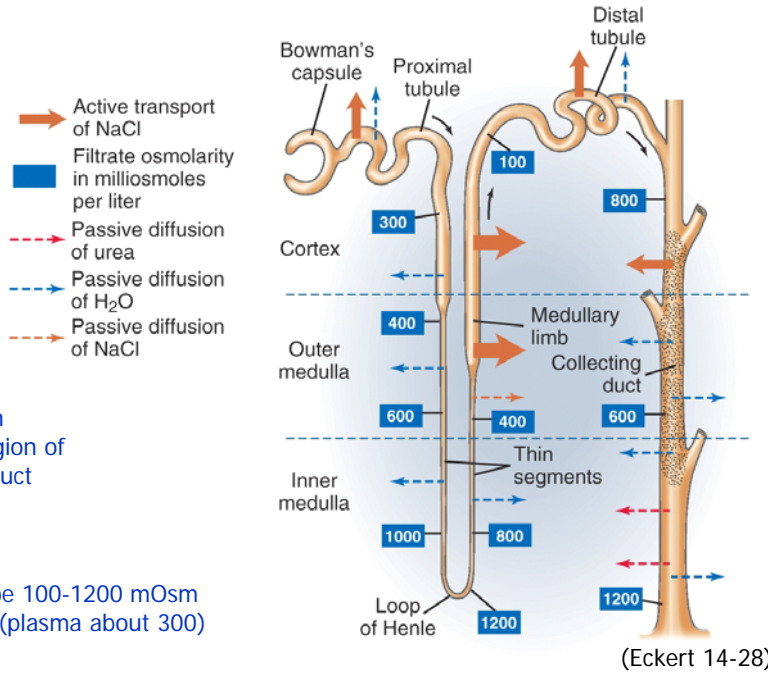
Atrial Natriuretic Peptide (ANP)

-released by atrium cells in response to stretch (elevated BP)

- opposite effect of renin-angiotensin system
- decreases sodium reabsorption
- therefore increased urine production
- ANP inhibits release of ADH, renin, aldosterone



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ADH acts in stippled region of collecting duct

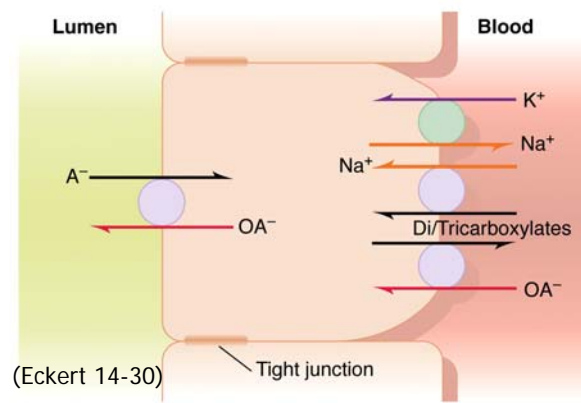
Urine can be 100-1200 mOsm in humans (plasma about 300)

Secretion:

From plasma into tubule of nephron

$K^+$ ,  $H^+$ ,  $NH_3$ , organic acids, organic bases

Organic anions ( $OA^-$ ):



Liver conjugates toxins and waste to glucuronic acid

Secreted into tubule lumen and excreted

Na/K-ATPase  
65



**Table 14-9** Some organic ions secreted by the proximal tubule  
*Eckert*

<b>Anions</b>	<b>Cations</b>
<i>Endogenous</i>	<i>Endogenous</i>
Urates	Dopamine
Hippurates	Epinephrine
Oxalate	Norepinephrine
Prostaglandins	Creatinine
cAMP	
<i>Exogenous</i>	<i>Exogenous</i>
Furosemide	Morphine
Bumetanide	Amiloride
Penicillin	Quinine
Aspirin	Atropine
Chlorothiazides	Isoproterenol

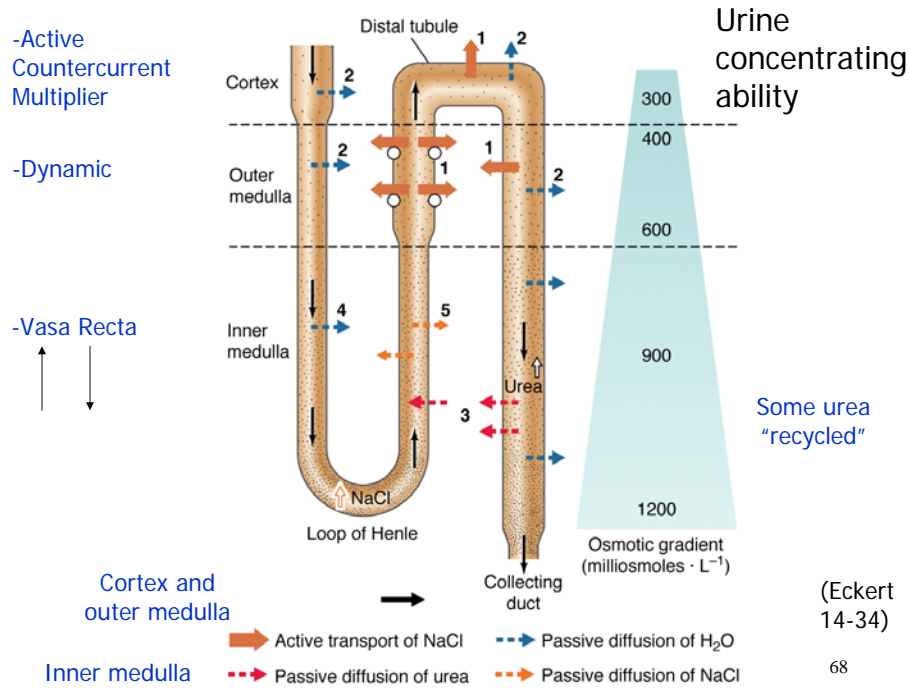
66

**Countercurrent Exchangers (passive)**

**Countercurrent Multipliers (active)**

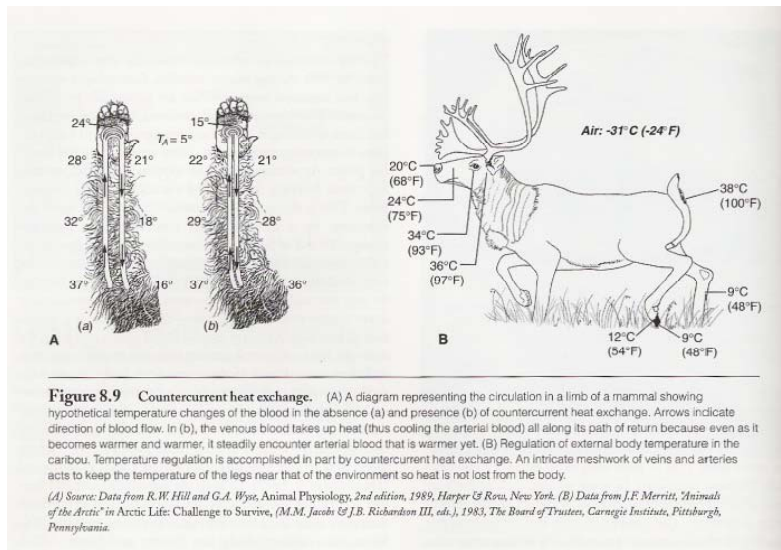
**See p.736 in your text**

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Endotherms in the COLD...

### Countercurrent Heat Exchange

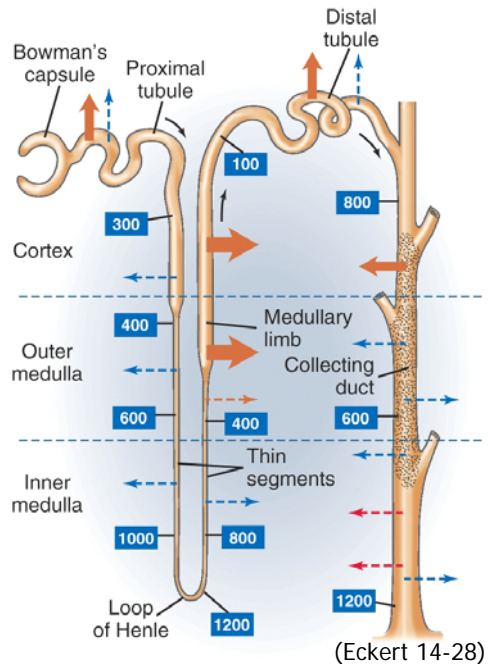


## Urine concentrating ability

-  Active transport of NaCl
-  Filtrate osmolarity in milliosmoles per liter
-  Passive diffusion of urea
-  Passive diffusion of H<sub>2</sub>O
-  Passive diffusion of NaCl

ADH acts in stippled region of collecting duct

Urine can be 100-1200 mOsm in humans (plasma about 300)



(a) The single effect and the end-to-end gradient generated from it by countercurrent multiplication

1. Single Effect
2. End-to-end Gradient

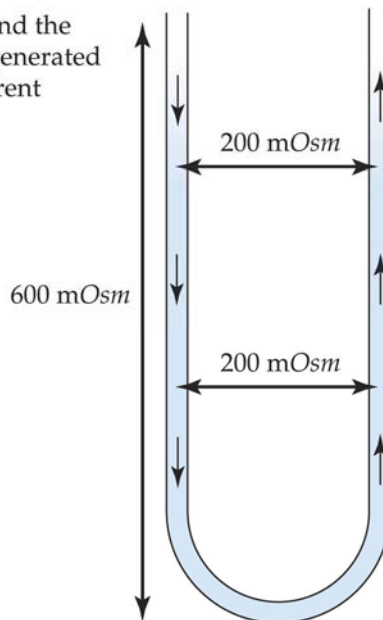
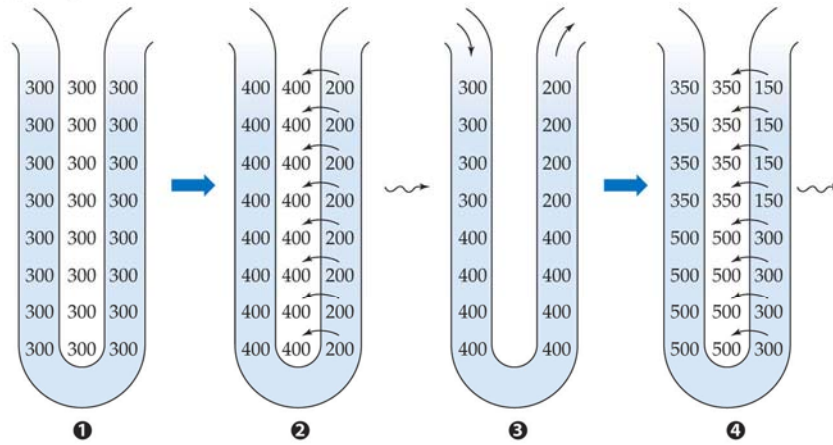


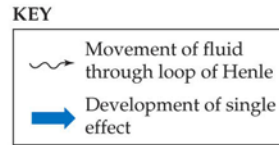
Figure 27.12  
Hill et al. 2004

ANIMAL PHYSIOLOGY, Figure 27.12 (Part 1) © 2004 Sinauer Associates, Inc.

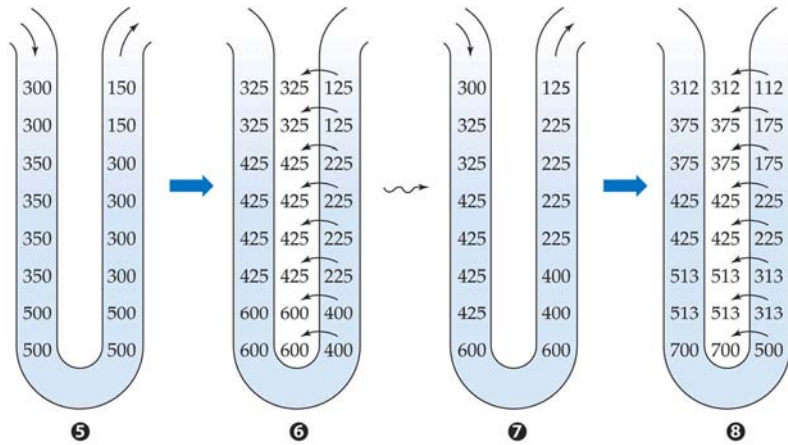
(b) The process of countercurrent multiplication



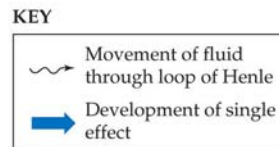
### Countercurrent Multiplication



ANIMAL PHYSIOLOGY, Figure 27.12 (Part 2) © 2004 Sinauer Associates, Inc.

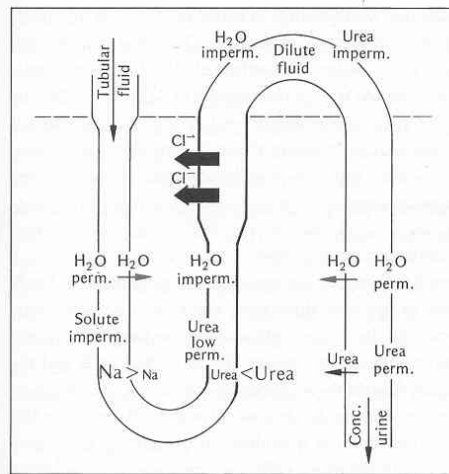


### Countercurrent Multiplication



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Same story,  
different picture



**Figure 9.12** Diagram of the concentrating mechanism in the loop of Henle in the mammalian kidney during the formation of concentrated urine. Active transport of chloride ion is indicated by heavy arrows; passive flux of water and urea by light arrows. [Kokko and Tisher 1976]

Knut Schmidt-Nielsen 1997

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Non-mammalian kidneys:

-Only birds also have **loops of henle**

-**Freshwater** fish with more and larger glomeruli to make lots of **dilute** urine



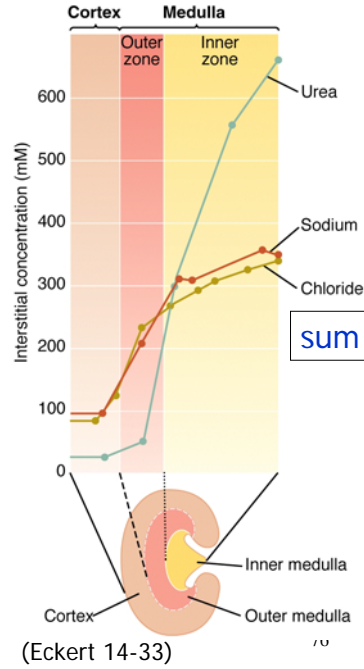
-Some **marine fish without glomeruli** or bowman's capsule – urine formed by secretion, ammonia secreted by gills

-Osmoregulation also via **extrarenal** organs

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## Urine concentrating ability

1200 mOsm in humans  
 9000 mOsm on kangaroo rats  
 9600 mOsm in *Perognathus* (mouse)



- Length of loops of henle
- Corticomedullary concentration gradient

-Active  
 Countercurrent  
 Multiplier

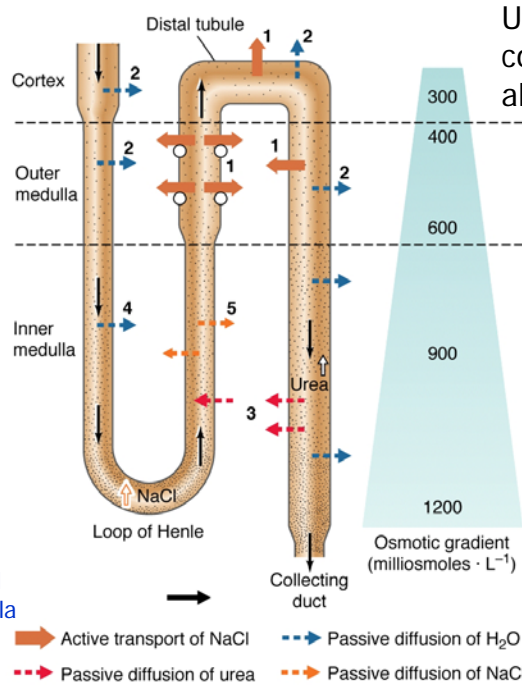
-Dynamic

-Vasa Recta



Cortex and  
 outer medulla

Inner medulla



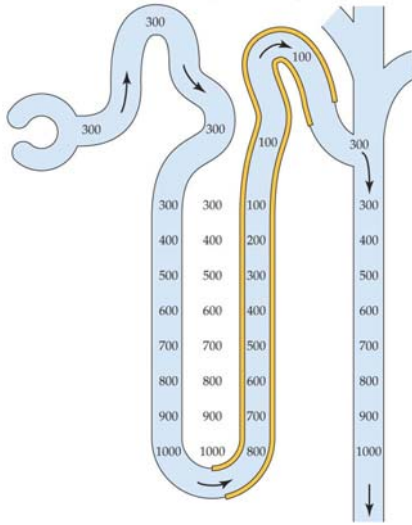
Urine  
 concentrating  
 ability

Some urea  
 "recycled"

(Eckert  
 14-34)

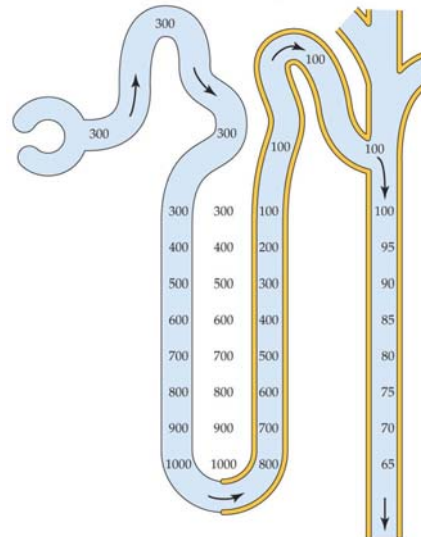
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(a) Antidiuresis: kidney producing concentrated urine



ANIMAL PHYSIOLOGY, Figure 27.14 (Part 1)

(b) Diuresis: kidney producing dilute urine



ANIMAL PHYSIOLOGY, Figure 27.14 (Part 2)

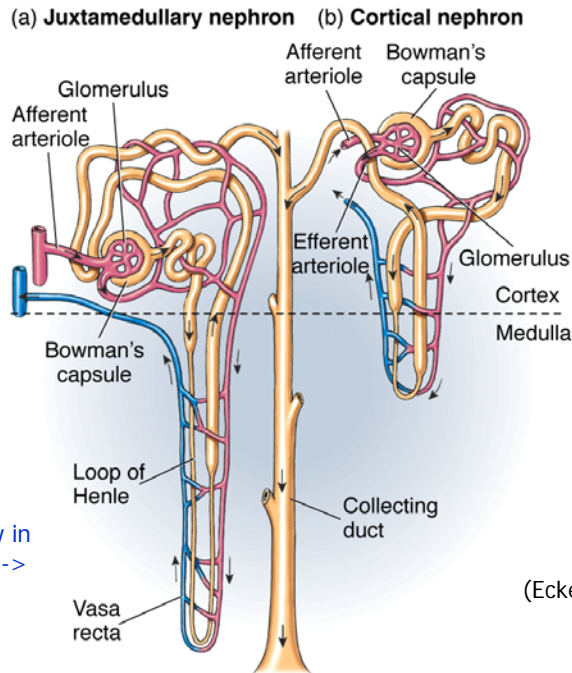
Hill et al. 2004, Fig. 27.14

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Urine  
concentrating  
ability

-Vasa Recta  
↑  
↓

-Loops of Henle only in  
Mammals and Birds ->  
Hyperosmotic Urine

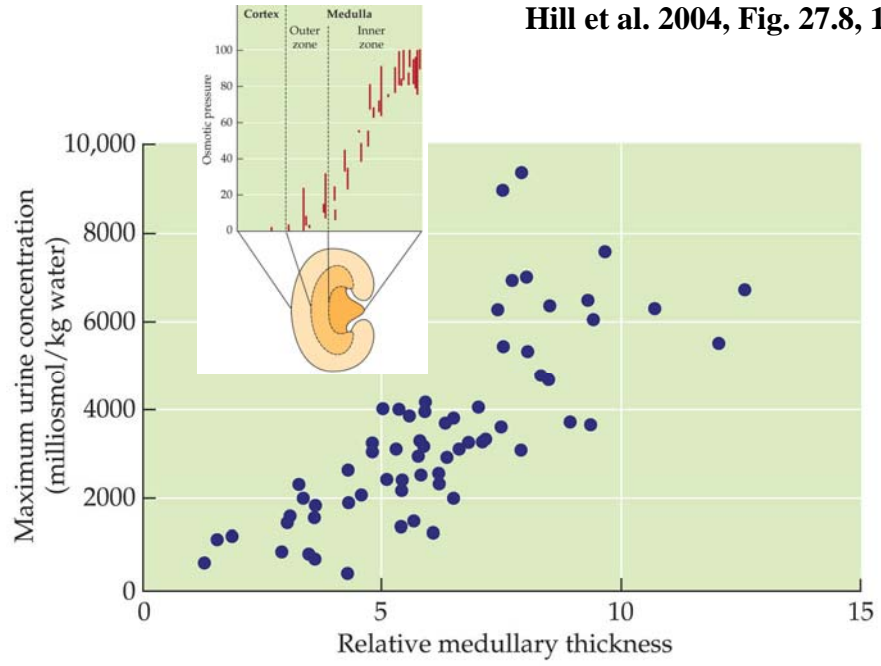


(Eckert 14-18)

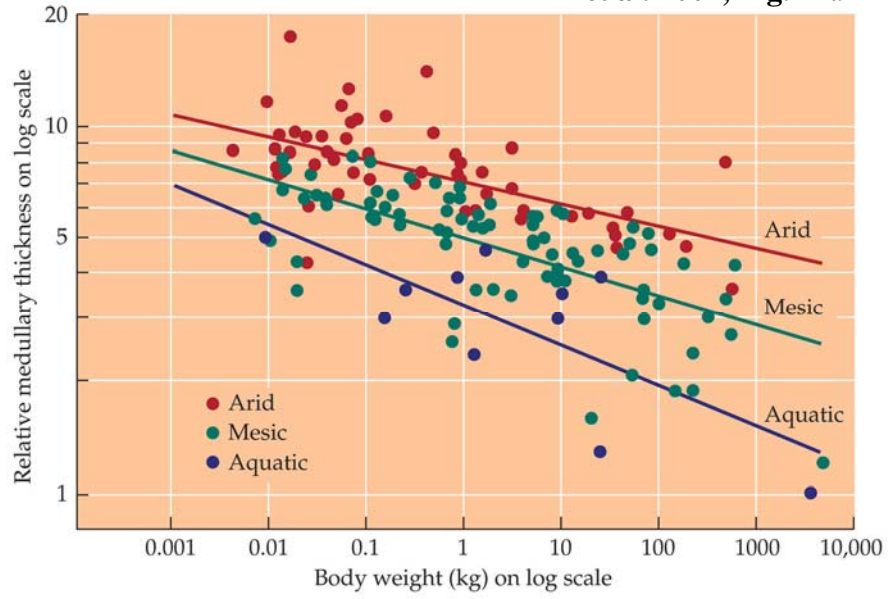
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Hill et al. 2004, Fig. 27.8, 13



Hill et al. 2004, Fig. 27.9



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