CAMPBELL
BIOLOGY
TENTH EDITION
Reece • Urry • Cain • Wasserman • Minorsky • Jackson

44 Osmoregulation and Excretion

Lecture Presentation by Nicole Tunbridge and Kathleen Fitzpatrick

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A Balancing Act

- Physiological systems of animals operate in a fluid environment
- Relative concentrations of water and solutes must be maintained within fairly narrow limits
- **Osmoregulation** controls solute concentrations and balances water gain and loss

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Figure 44.1

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Figure 44.1a

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- Desert and marine animals face desiccating environments that can quickly deplete body water
- Freshwater animals survive by conserving solutes and absorbing salts from their surroundings
- **Excretion** rids the body of nitrogenous metabolites and other waste products

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Concept 44.1: Osmoregulation balances the uptake and loss of water and solutes

- Osmoregulation is based largely on balancing the uptake and loss of water and solutes
- The driving force for movement of solutes and water is a concentration gradient of one or more solutes across the plasma membrane

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Osmosis and Osmolarity

- Water enters and leaves cells by osmosis
- **Osmolarity**, the solute concentration of a solution, determines the movement of water across a selectively permeable membrane
- If two solutions are isoosmotic, water molecules will cross the membrane at equal rates in both directions

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- If two solutions differ in osmolarity, the net flow of water is from the hypoosmotic (less concentrated) to the hyperosmotic (more concentrated) solution

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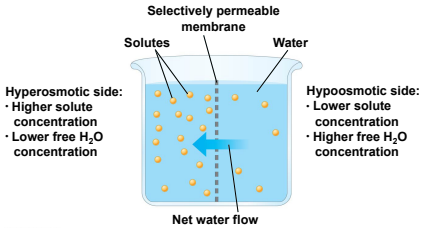
Figure 44.2



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Osmoregulatory Challenges and Mechanisms

- **Osmoconformers**, consisting only of some marine animals, are isoosmotic with their surroundings and do not regulate their osmolarity
- **Osmoregulators** expend energy to control water uptake and loss in a hyperosmotic or hypoosmotic environment

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Figure 44.3

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- Most animals are stenohaline; they cannot tolerate substantial changes in external osmolarity
- Euryhaline animals can survive large fluctuations in external osmolarity

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Marine Animals

- Most marine invertebrates are osmoconformers
- Many marine vertebrates and some marine invertebrates are osmoregulators
- Marine bony fishes are hypoosmotic to seawater
- They balance water loss by drinking large amounts of seawater and eliminating the ingested salts through their gills and kidneys

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Freshwater Animals

- Freshwater animals constantly take in water by osmosis from their hypoosmotic environment
- They lose salts by diffusion and maintain water balance by drinking almost no water and excreting large amounts of dilute urine
- Salts lost by diffusion are replaced in foods and by uptake across the gills

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Figure 44.4

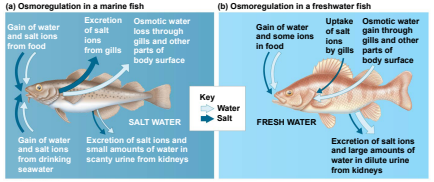

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Figure 44.4a

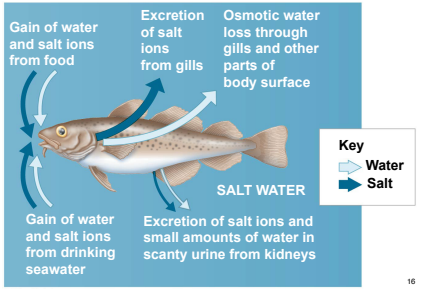

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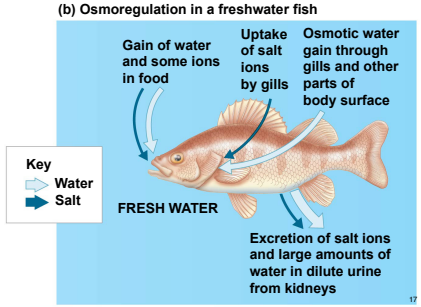
Figure 44.4b

(b) Osmoregulation in a freshwater fish



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Animals That Live in Temporary Waters

- Some aquatic invertebrates in temporary ponds lose almost all their body water and survive in a dormant state
- This adaptation is called **anhydrobiosis**

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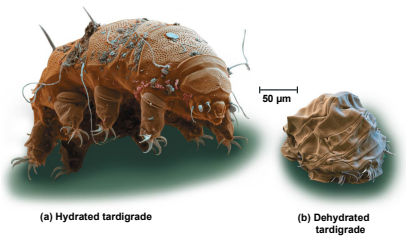
Figure 44.5



(a) Hydrated tardigrade

(b) Dehydrated tardigrade

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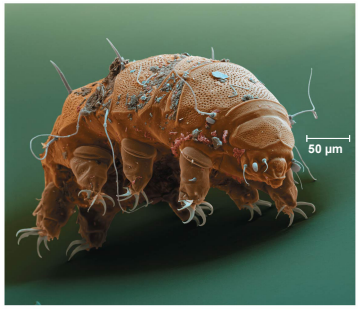
Figure 44.5a



(a) Hydrated tardigrade

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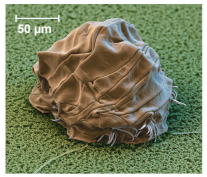
Figure 44.5b



(b) Dehydrated tardigrade

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Land Animals

- Adaptations to reduce water loss are key to survival on land
- Body coverings of most terrestrial animals help prevent dehydration
- Desert animals get major water savings from simple anatomical features and behaviors such as a nocturnal lifestyle
- Land animals maintain water balance by eating moist food and producing water metabolically through cellular respiration

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Energetics of Osmoregulation

- Osmoregulators must expend energy to maintain osmotic gradients
- The amount of energy differs based on
  - How different the animal's osmolarity is from its surroundings
  - How easily water and solutes move across the animal's surface
  - The work required to pump solutes across the membrane

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Transport Epithelia in Osmoregulation

- Animals regulate the solute content of body fluid that bathes their cells
- **Transport epithelia** are epithelial cells specialized for moving solutes in specific directions
- They are typically arranged into complex tubular networks
- An example is in nasal glands of marine birds, which remove excess sodium chloride from the blood

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Figure 44.6

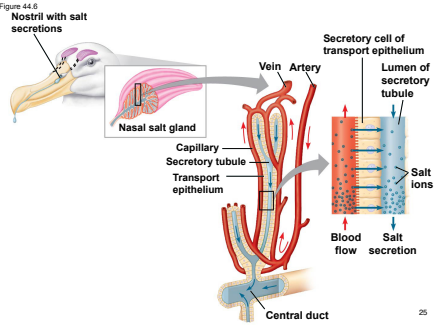

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Figure 44.6a

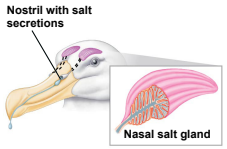

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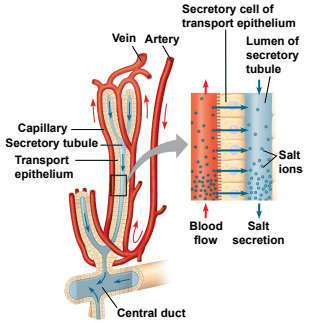
Figure 44.6b



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Concept 44.2: An animal's nitrogenous wastes reflect its phylogeny and habitat

- The type and quantity of an animal's waste products may greatly affect its water balance
- Among the most significant wastes are nitrogenous breakdown products of proteins and nucleic acids
- Some animals convert toxic **ammonia** (NH_3) to less toxic compounds prior to excretion

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Forms of Nitrogenous Waste

- Animals excrete nitrogenous wastes in different forms: ammonia, urea, or uric acid
- These differ in toxicity and the energy costs of producing them

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Ammonia

- Animals that excrete nitrogenous wastes as ammonia need access to lots of water
- They release ammonia across the whole body surface

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Urea

- Most terrestrial mammals and many marine species excrete **urea**, which is less toxic than ammonia
- In vertebrates urea is produced in the liver
- The circulatory system carries urea to the kidneys, where it is excreted
- Conversion of ammonia to urea is energetically expensive; excretion of urea requires less water than ammonia

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Uric Acid

- Insects, land snails, and many reptiles, including birds, mainly excrete **uric acid**
- Uric acid is relatively nontoxic and does not dissolve readily in water
- It can be secreted as a paste with little water loss
- Uric acid is more energetically expensive to produce than urea

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Figure 44.7

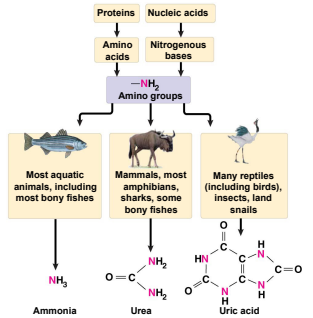

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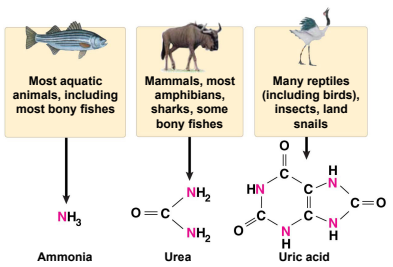
Figure 44.7a



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The Influence of Evolution and Environment on Nitrogenous Wastes

- The kinds of nitrogenous wastes excreted depend on an animal's evolutionary history and habitat, especially water availability
- Another factor is the immediate environment of the animal egg
- The amount of nitrogenous waste is coupled to the animal's energy budget

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Concept 44.3: Diverse excretory systems are variations on a tubular theme

- Excretory systems regulate solute movement between internal fluids and the external environment
- These systems are central to homeostasis

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Excretory Processes

- Most excretory systems produce urine by refining a **filtrate** derived from body fluids
- Key functions of most excretory systems
  - **Filtration**: Filtering of body fluids
  - **Reabsorption**: Reclaiming valuable solutes
  - **Secretion**: Adding nonessential solutes and wastes to the filtrate
  - **Excretion**: Processed filtrate containing nitrogenous wastes is released from the body

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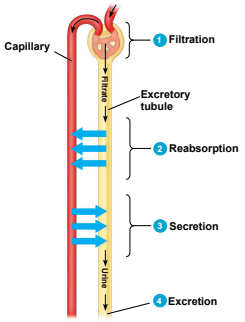
Figure 44.8



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Survey of Excretory Systems

- Systems that perform basic excretory functions vary widely among animal groups
- They usually involve a complex network of tubules

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Protonephridia

- A **protonephridium** is a network of dead-end tubules connected to external openings
- The smallest branches of the network are capped by a cellular unit called a flame bulb
- These tubules excrete a dilute fluid and function in osmoregulation

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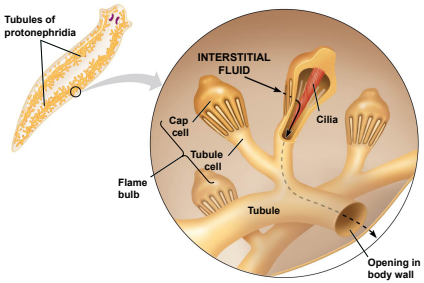
Figure 44.9



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Metanephridia

- Each segment of an earthworm has a pair of open-ended metanephridia
- Metanephridia consist of tubules that collect coelomic fluid and produce dilute urine for excretion
- Metanephridia of earthworms function in excretion and osmoregulation

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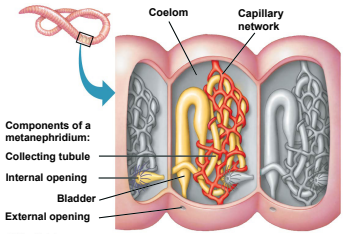
Figure 44.10



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Malpighian Tubules

- In insects and other terrestrial arthropods, **Malpighian tubules** remove nitrogenous wastes from hemolymph and function in osmoregulation
- Insects produce a relatively dry waste matter, mainly uric acid, an important adaptation to terrestrial life
- Some terrestrial insects can also take up water from the air

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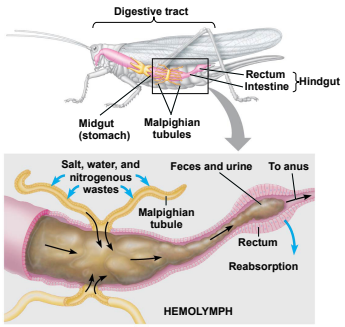
Figure 44.11



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Kidneys

- Kidneys, the excretory organs of vertebrates, function in both excretion and osmoregulation
- The numerous tubules of kidneys are highly organized
- The vertebrate excretory system also includes ducts and other structures that carry urine from the tubules out of the kidney and out of the body

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Figure 44.12a

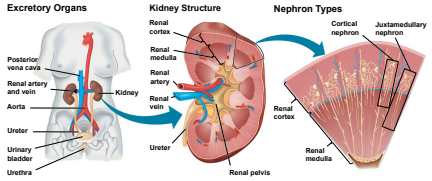

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Figure 44.12aa

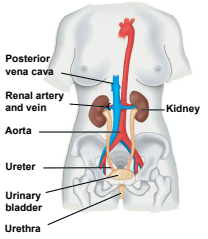

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Figure 44.12ab

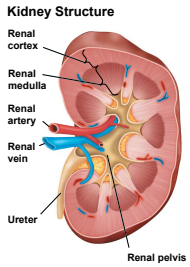

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Figure 44.12ac

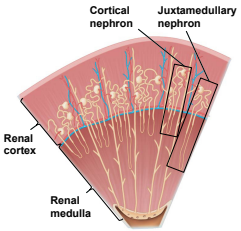

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Figure 44.12b

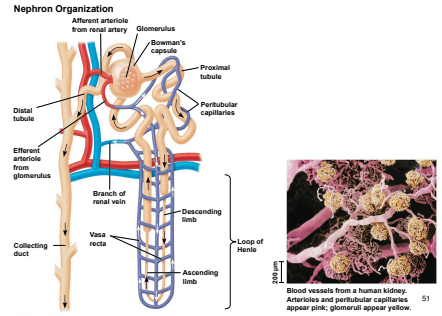

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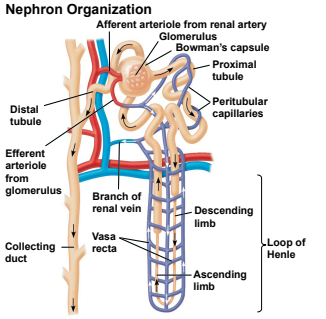
Figure 44.12ba



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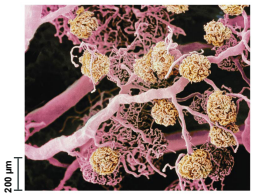

Blood vessels from a human kidney. Arterioles and peritubular capillaries appear pink; glomeruli appear yellow.

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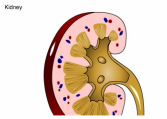
Animation: Nephron Introduction



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Concept 44.4: The nephron is organized for stepwise processing of blood filtrate

- The filtrate produced in Bowman's capsule contains salts, glucose, amino acids, vitamins, nitrogenous wastes, and other small molecules

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From Blood Filtrate to Urine: *A Closer Look*

Proximal Tubule

- Reabsorption of ions, water, and nutrients takes place in the proximal tubule
- Molecules are transported actively and passively from the filtrate into the interstitial fluid and then capillaries
- As the filtrate passes through the proximal tubule, materials to be excreted become concentrated
- Some toxic materials are actively secreted into the filtrate

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Descending Limb of the Loop of Henle

- Reabsorption of water continues through channels formed by **aquaporin** proteins
- Movement is driven by the high osmolarity of the interstitial fluid, which is hyperosmotic to the filtrate
- The filtrate becomes increasingly concentrated

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Ascending Limb of the Loop of Henle

- In the ascending limb of the loop of Henle, salt but not water is able to diffuse from the tubule into the interstitial fluid
- The filtrate becomes increasingly dilute

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Distal Tubule

- The distal tubule regulates the K^+ and NaCl concentrations of body fluids
- The controlled movement of ions (H^+ and HCO_3^-) contributes to pH regulation

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Collecting Duct

- The collecting duct carries filtrate through the medulla to the renal pelvis
- One of the most important tasks is reabsorption of solutes and water
- Urine is hyperosmotic to body fluids

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Figure 44.13

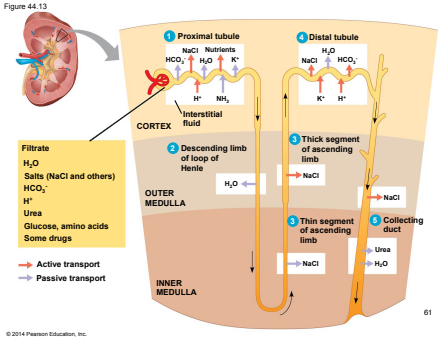

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Figure 44.13a

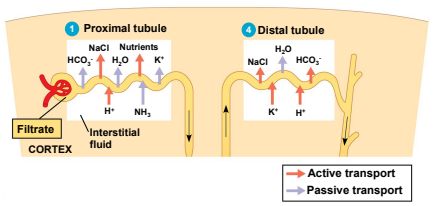

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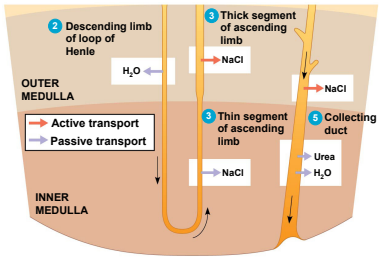
Figure 44.13b



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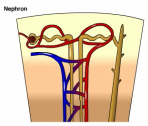
Animation: Bowman's Capsule and Proximal Tubule



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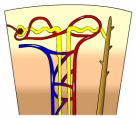
Animation: Collecting Duct



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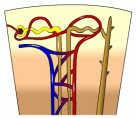
Animation: Loop of Henle and Distal Tubule



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Solute Gradients and Water Conservation

- The mammalian kidney's ability to conserve water is a key terrestrial adaptation
- Hyperosmotic urine can be produced only because considerable energy is expended to transport solutes against concentration gradients
- The two primary solutes affecting osmolarity are NaCl and urea

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Concentrating Urine in the Mammalian Kidney

- In the proximal tubule, filtrate volume decreases as water and salt are reabsorbed, but osmolarity remains the same
- As the filtrate flows to the descending limb of the loop of Henle, solutes become more concentrated due to water leaving the tubule by osmosis
- NaCl diffusing from the ascending limb maintains a high osmolarity in the interstitial fluid of the renal medulla

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- Energy is expended to actively transport NaCl from the filtrate in the upper part of the ascending limb
- The **countercurrent multiplier system** involving the loop of Henle maintains a high salt concentration in the kidney
- This system allows the vasa recta to supply the kidney with nutrients, without interfering with the osmolarity gradient

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- In the collecting duct, osmosis extracts water from the filtrate as it passes from cortex to medulla and encounters interstitial fluid of increasing osmolarity
- Urine produced is isoosmotic to the interstitial fluid of the inner medulla, but hyperosmotic to blood and interstitial fluids elsewhere in the body

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Figure 44.14-1

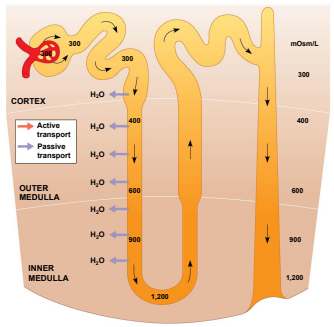

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Figure 44.14-2

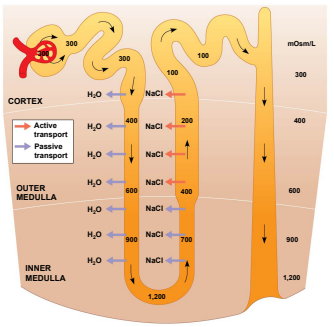

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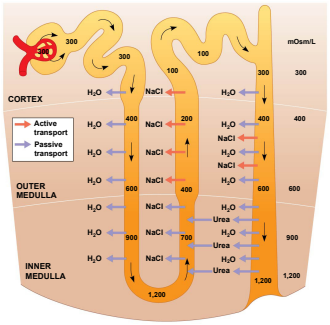
Figure 44.14-3



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Adaptations of the Vertebrate Kidney to Diverse Environments

- Variations in nephron structure and function equip the kidneys of different vertebrates for osmoregulation in various habitats

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Mammals

- The juxtamedullary nephron is key to water conservation in terrestrial animals
- Mammals that inhabit dry environments have long loops of Henle, while those in fresh water have relatively short loops

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Case Study: *Kidney Function in the Vampire Bat*

- The South American vampire bat, which feeds at night on the blood of large birds and mammals, illustrates the versatility of the mammalian kidney
- The vampire bat can alternate rapidly between producing large amounts of dilute urine and small amounts of very hyperosmotic urine

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Figure 44.15

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Birds and Other Reptiles

- Birds have shorter loops of Henle than mammals do, but conserve water by excreting uric acid instead of urea
- Other reptiles have only cortical nephrons but reabsorb water from wastes in the cloaca
- Reptiles also excrete nitrogenous waste as uric acid

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Figure 44.16

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Freshwater Fishes and Amphibians

- Freshwater fishes conserve salt in their distal tubules and excrete large volumes of very dilute urine
- Kidney function in amphibians is similar to freshwater fishes
- Amphibians conserve water on land by reabsorbing water from the urinary bladder

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Marine Bony Fishes

- Marine bony fishes are hypoosmotic compared with their environment
- Their kidneys have small glomeruli and some lack glomeruli entirely
- Filtration rates are low, and very little urine is excreted

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Figure 44.17

MAKE CONNECTIONS: Ion Movement and Gradients

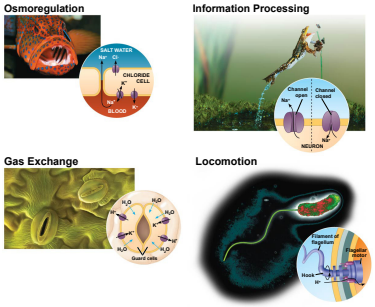

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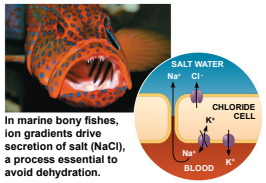
Figure 44.17a

Osmoregulation



In marine bony fishes, ion gradients drive secretion of salt (NaCl), a process essential to avoid dehydration.

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Figure 44.17aa

Osmoregulation

A marine bony fish

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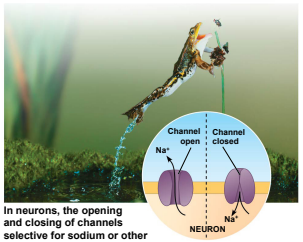
Figure 44.17b

Information Processing



In neurons, the opening and closing of channels selective for sodium or other ions underlies the transmission of information as nerve impulses

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Figure 44.17ba

Information Processing

Leap of a frog capturing prey

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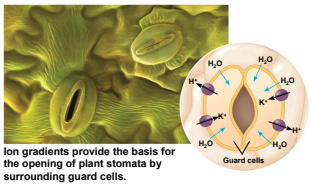
Figure 44.17c

Gas Exchange



Ion gradients provide the basis for the opening of plant stomata by surrounding guard cells.

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Figure 44.17ca

Gas Exchange

Opening of plant stomata by surrounding guard cells

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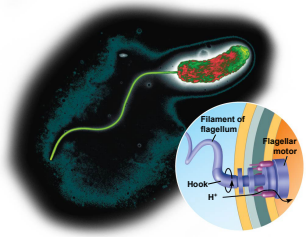
Figure 44.17d

Locomotion



A gradient of H^+ ions powers the bacterial flagellum.

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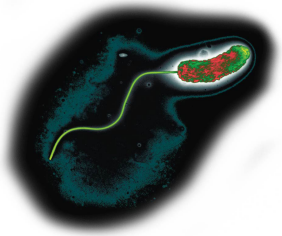
Figure 44.17da

Locomotion



A bacterial flagellum

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Concept 44.5: Hormonal circuits link kidney function, water balance, and blood pressure

- Mammals can control the volume and osmolarity of urine in response to changes in salt intake and water availability

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Homeostatic Regulation of the Kidney

- A combination of nervous and hormonal controls manages the osmoregulatory functions of the mammalian kidney
- These controls contribute to homeostasis for blood pressure and blood volume

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Antidiuretic Hormone

- Antidiuretic hormone, ADH, is also called vasopressin
- Osmoreceptor cells in the hypothalamus monitor blood osmolarity and regulate release of ADH from the posterior pituitary
- When osmolarity rises above its set point, ADH release into the blood stream increases

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Figure 44.18-1

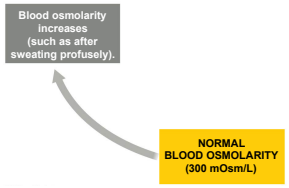

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Figure 44.18-2

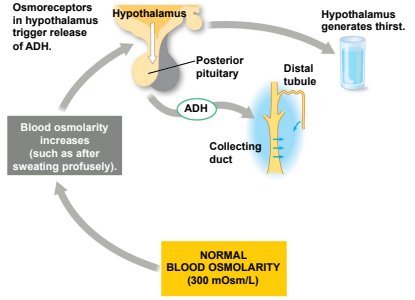

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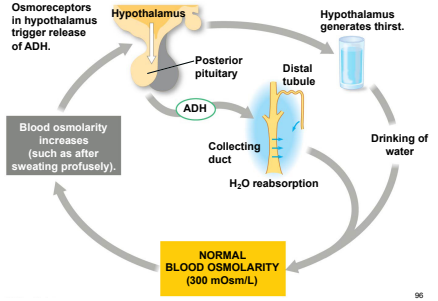
Figure 44.18-3



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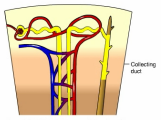
Animation: Effect of ADH



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- Binding of ADH to receptor molecules leads to a temporary increase in the number of aquaporin proteins in the membrane of collecting duct cells
- This reduces urine volume and lowers blood osmolarity

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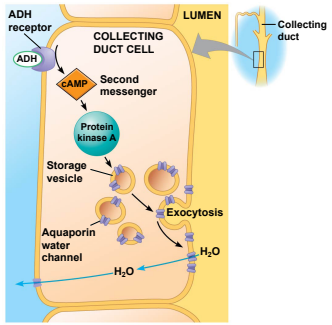
Figure 44.19



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- Alcohol is a diuretic as it inhibits the release of ADH
- Mutation in ADH production causes severe dehydration and results in *diabetes insipidus*

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Figure 44.20

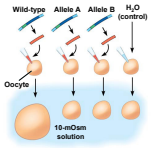
Experiment

Source of Aquaporin-2 Gene Sequence	Amino Acids 183–191* in Encoded Protein	Amino Acids 212–220* in Encoded Protein
Frog (*Xenopus laevis*)	MNPARSFAP	GIFASLIYN
Lizard (*Anolis carolinensis*)	MNPARSFGP	AVVASLLYN
Chicken (*Gallus gallus*)	MNPARSFAP	AAAASIIYN
Human (*Homo sapiens*)	MNPARSLAP	AILGSLLYN
Conserved residues	MNPARSxxP	xxxxSxxYN
Patient's gene: allele A	MNPACSLAP	AILGSLLYN
Patient's gene: allele B	MNPARSLAP	AILGPLLYN

*The numbering is based on the human aquaporin-2 protein sequence.

1 Inject wild-type and mutant aquaporin mRNA into frog oocytes.

2 Transfer to 10-mOsm solution and measure rate of oocyte swelling.



Results

Source of Injected mRNA	Rate of Swelling (μm/sec)
Human wild type	196
Patient's allele A	17
Patient's allele B	18
None	20

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Figure 44.20a

Experiment

Source of Aquaporin-2 Gene Sequence	Amino Acids 183–191* in Encoded Protein	Amino Acids 212–220* in Encoded Protein
Frog (*Xenopus laevis*)	MNPARSFAP	GIFASLIYN
Lizard (*Anolis carolinensis*)	MNPARSFGP	AVVASLLYN
Chicken (*Gallus gallus*)	MNPARSFAP	AAAASIIYN
Human (*Homo sapiens*)	MNPARSLAP	AILGSLLYN
Conserved residues	MNPARSxxP	xxxxSxxYN
Patient's gene: allele A	MNPACSLAP	AILGSLLYN
Patient's gene: allele B	MNPARSLAP	AILGPLLYN

*The numbering is based on the human aquaporin-2 protein sequence.

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Figure 44.20b

Experiment

1 Inject wild-type and mutant aquaporin mRNA into frog oocytes.

2 Transfer to 10-mOsm solution and measure rate of oocyte swelling.

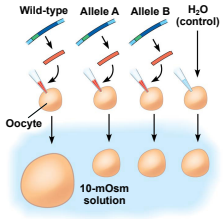

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Figure 44.20c

Results

Source of Injected mRNA	Rate of Swelling (μm/sec)
Human wild type	196
Patient's allele A	17
Patient's allele B	18
None	20

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The Renin-Angiotensin-Aldosterone System

- The **renin-angiotensin-aldosterone system** (**RAAS**) is part of a complex feedback circuit that functions in homeostasis
- A drop in blood pressure near the glomerulus causes the **juxtaglomerular apparatus (JGA)** to release the enzyme renin
- Renin triggers the formation of the peptide **angiotensin II**

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Figure 44.21-1

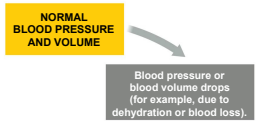

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Figure 44.21-2

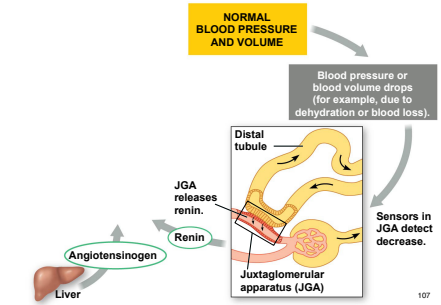

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Figure 44.21-3

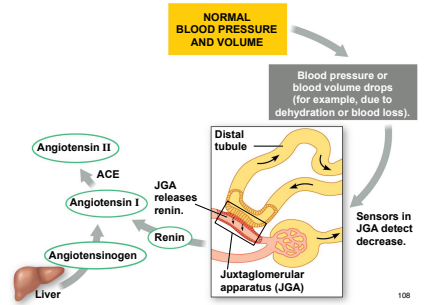

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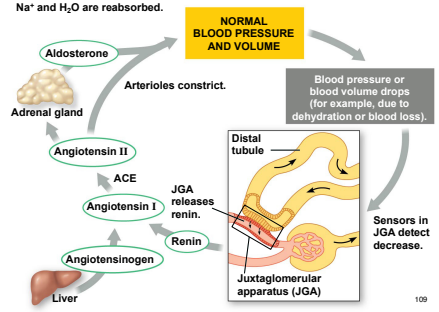
Figure 44.21-4



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- Angiotensin II
  - Raises blood pressure and decreases blood flow to the kidneys
  - Stimulates the release of the hormone **aldosterone**, which increases blood volume and pressure

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Coordination of ADH and RAAS Activity

- ADH and RAAS both increase water reabsorption, but only RAAS will respond to a decrease in blood volume
- Another hormone, **atrial natriuretic peptide** (**ANP**), opposes the RAAS
- ANP is released in response to an increase in blood volume and pressure and inhibits the release of renin

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Figure 44.UN01a

Access to Water	Mean Osmolarity (mOsm/L)		Mean Urea Concentration (m*M*)	
	Urine	Blood	Urine	Blood
Part A: Unlimited	490	350	330	7.6
Part B: None	4,700	320	2,700	11

In part A, the mice drank about 33% of their body weight each day. The change in body weight during the study was negligible for all mice.

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Figure 44.UN01b

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Figure 44.UN02

Animal	Inflow/Outflow	Urine
Freshwater fish. Lives in water less concentrated than body fluids; fish tends to gain water, lose salt	Does not drink water Salt in H_2O in (active trans-port by gills) Salt out	▶ Large volume of urine ▶ Urine is less concentrated than body fluids
Marine bony fish. Lives in water more concentrated than body fluids; fish tends to lose water, gain salt	Drinks water Salt in H_2O out Salt out (active transport by gills)	▶ Small volume of urine ▶ Urine is slightly less concentrated than body fluids
Terrestrial vertebrate. Terrestrial environment; tends to lose body water to air	Drinks water Salt in (by mouth) H_2O and salt out	▶ Moderate volume of urine ▶ Urine is more concentrated than body fluids

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Figure 44.UN02a

Animal	Inflow/Outflow	Urine
Freshwater fish. Lives in water less concentrated than body fluids; fish tends to gain water, lose salt	Does not drink water Salt in H_2O in (active trans-port by gills) Salt out	▶ Large volume of urine ▶ Urine is less concentrated than body fluids

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Figure 44.UN02b

Animal	Inflow/Outflow	Urine
Marine bony fish. Lives in water more concentrated than body fluids; fish tends to lose water, gain salt	Drinks water Salt in H_2O out Salt out (active transport by gills)	▶ Small volume of urine ▶ Urine is slightly less concentrated than body fluids

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Figure 44.UN02c

Animal	Inflow/Outflow	Urine
Terrestrial vertebrate. Terrestrial environment; tends to lose body water to air	Drinks water Salt in (by mouth) H_2O and salt out	▶ Moderate volume of urine ▶ Urine is more concentrated than body fluids

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Figure 44.UN03

	Kangaroo Rat	Human
Water Gain (mL)		
Ingested in food	0.2	750
Ingested in liquid	0	1,500
Derived from metabolism	1.8	250
Water Loss (mL)		
Urine	0.45	1,500
Feces	0.09	100
Evaporation	1.46	900

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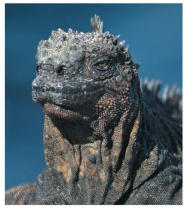
Figure 44.UN04



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