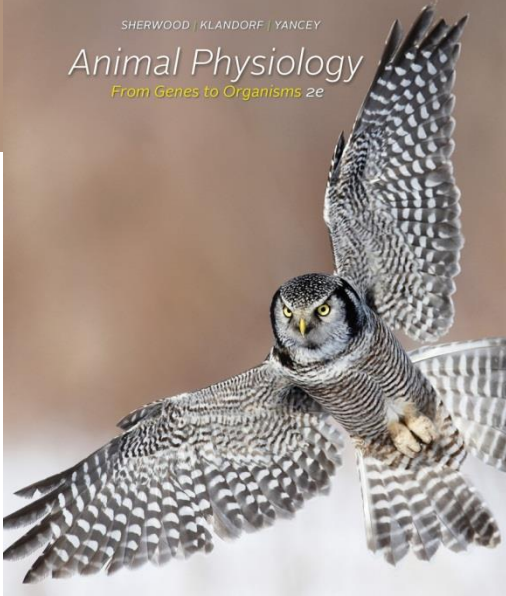


SHERWOOD | KLANDORF | YANCEY
Animal Physiology
From Genes to Organisms 2e



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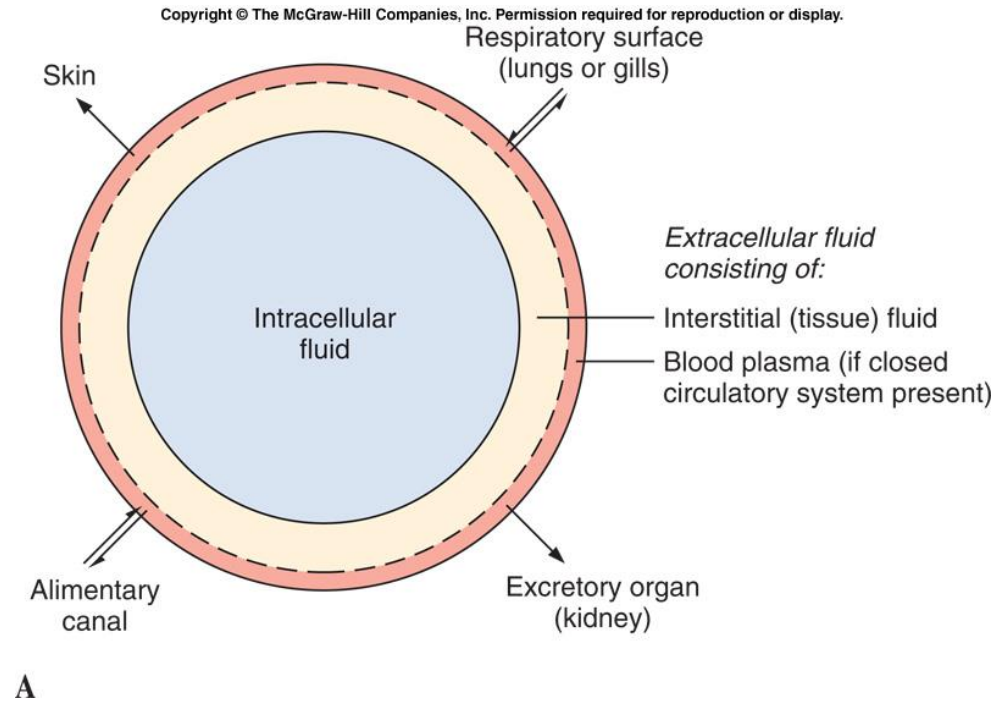
Lauralee Sherwood
Hillar Klandorf
Paul Yancey

Chapter 11 Respiratory Systems

Kip McGilliard • Eastern Illinois University

Exchanging Materials

- Every organism must exchange materials with its environment.
 - This exchange ultimately occurs at the cellular level.



Exchanging Materials



- In unicellular organisms, these exchanges occur directly with the environment.
- For most of the cells making up multicellular organisms, direct exchange with the environment is not possible.

Circulatory Systems Reflect Phylogeny



- Transport systems functionally connect the organs of exchange with the body cells.

Solubility of Gases in Distilled Water

$^{\circ}\text{C}$	<i>Oxygen</i>	<i>Carbon Dioxide</i>	<i>Nitrogen</i>	<i>Helium</i>
0	21.7	767.5	—	—
10	16.9	531.2	—	—
20	13.7	386.8	6.82	—
30	11.6	294.9	—	—
37	10.6	250.5	5.61	3.75
40	10.2	234.8	—	—

Effect of Salinity on Oxygen Solubility

$^{\circ}\text{C}$	Salinity	0‰	10‰	20‰	30‰	40‰
0		21.7	20.2	18.9	17.7	16.6
10		16.9	15.8	14.8	13.9	13.1
20		13.7	12.9	12.2	11.5	10.8
30		11.6	11.0	10.4	9.86	9.33
40		10.2	9.71	9.26	8.73	8.35

Effects of high altitude on atmospheric pressure (P_b ; kPa), ambient pO_2 (kPa), and alveolar pO_2 and pCO_2 ($p_A O_2$, and $p_A CO_2$; kPa) for a human.

Altitude	P_b	Ambient pO_2	$p_A O_2$	$p_A CO_2$
0	101	21.1	13.8	5.3
3100	70.6	14.6	8.9	4.8
4340	61.9	12.8	6.0	—
6200	46	9.7	5.3	3.2
7100	—————	normal “ceiling”	✓	—————
8848	33	6.9	4.0	1.5
9200	30	6.3	2.8	—
12300	19	3.9	1.1	—
14460	—————	“ceiling” with pure O_2	—————	—————
15400	12	2.4	0.1	—
20000	6	1.3	0	0

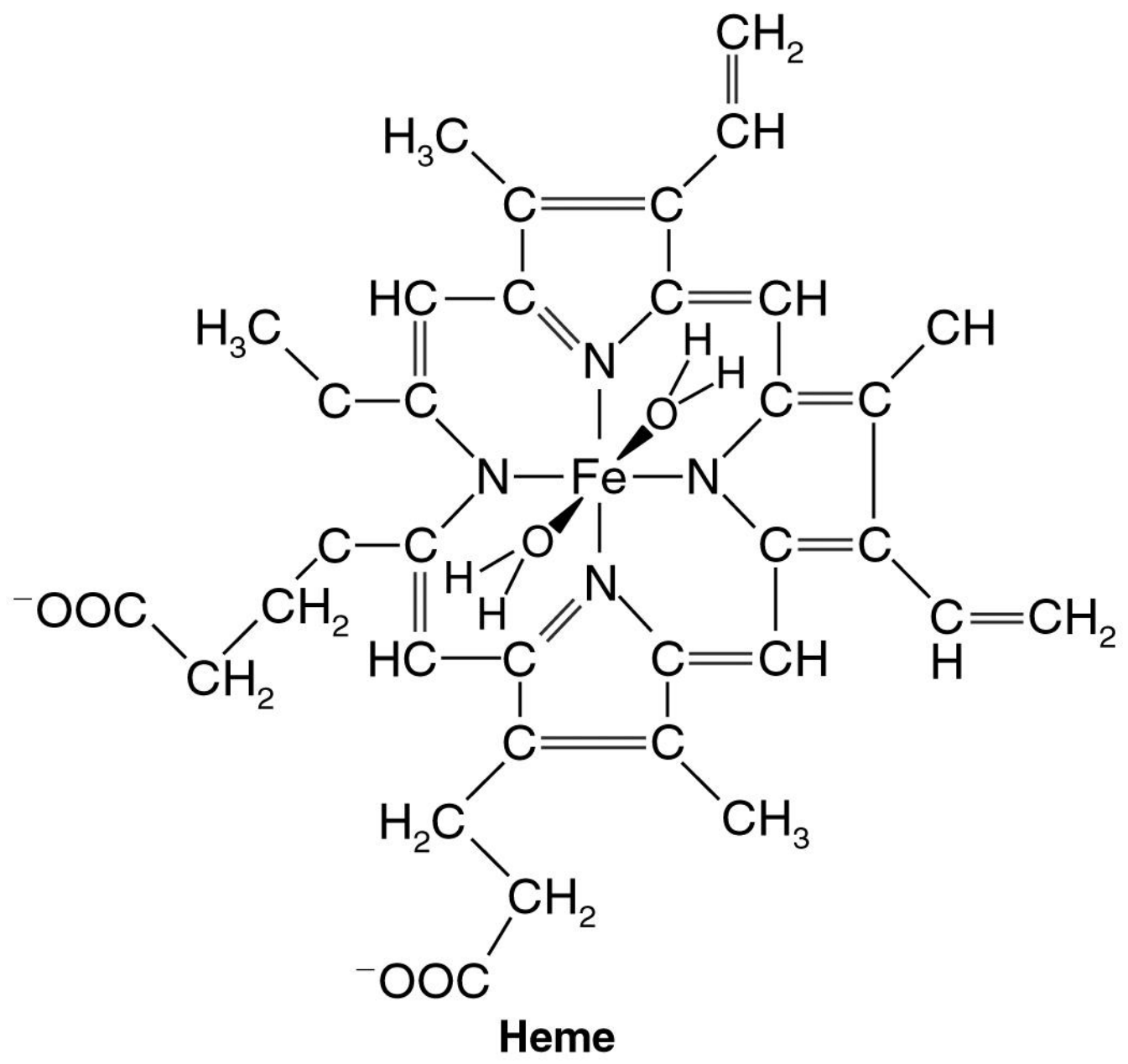
Sea level

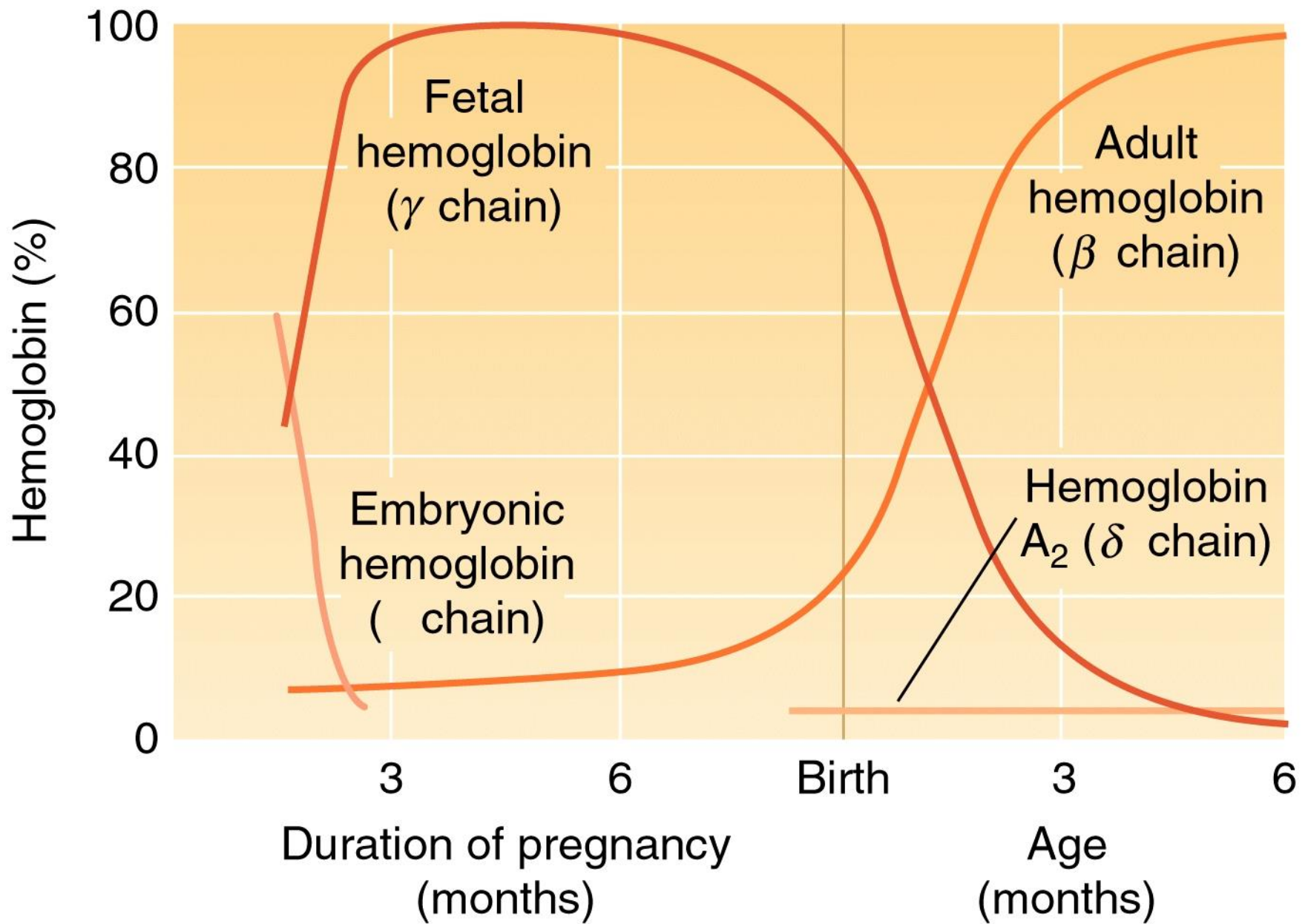
$$P_{O_2} = 760 * 0.2094 = 159 \text{ mmHg}$$

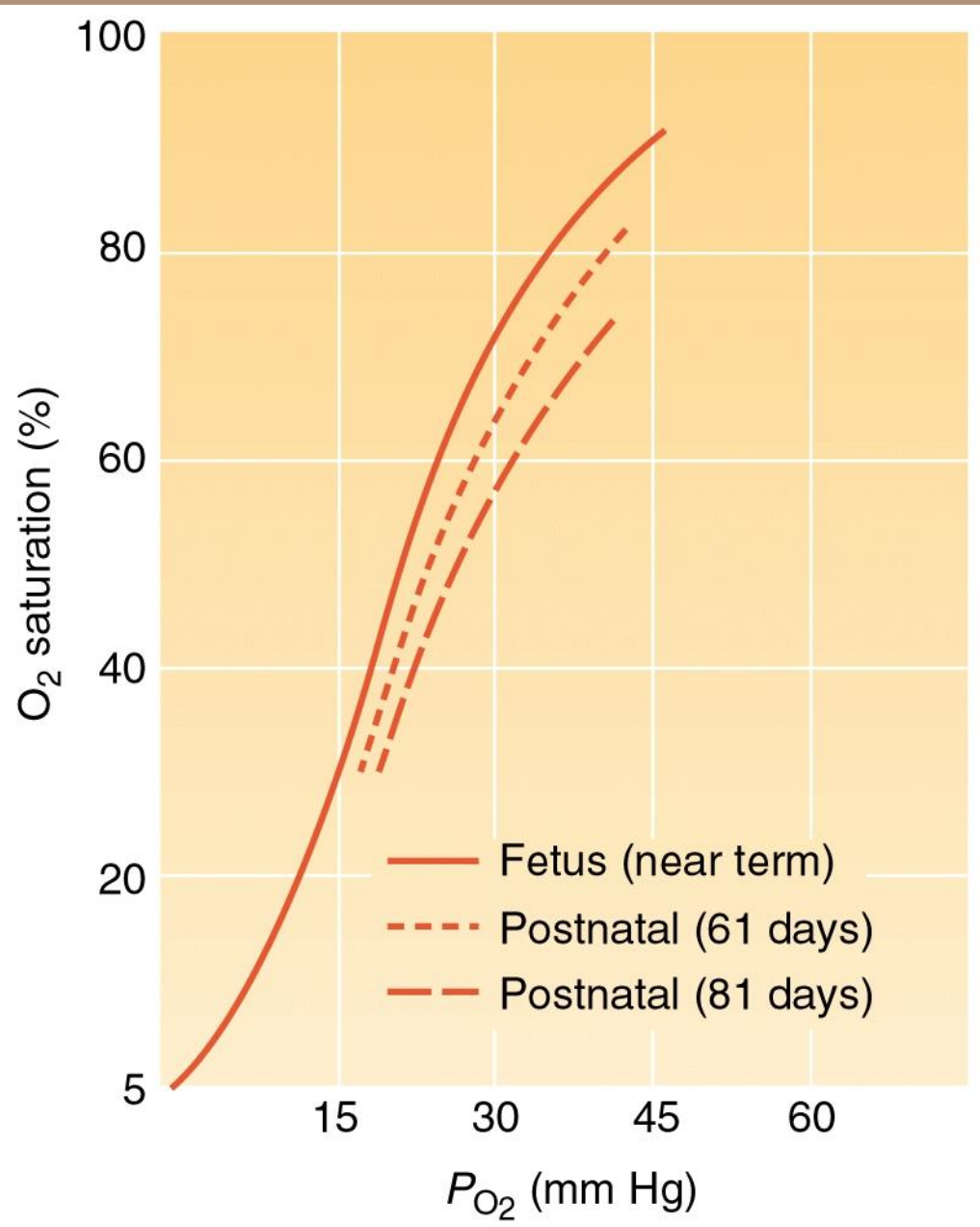
$$P_{O_2} = (760 - 18) * 0.2094 = 155 \text{ mmHg}$$

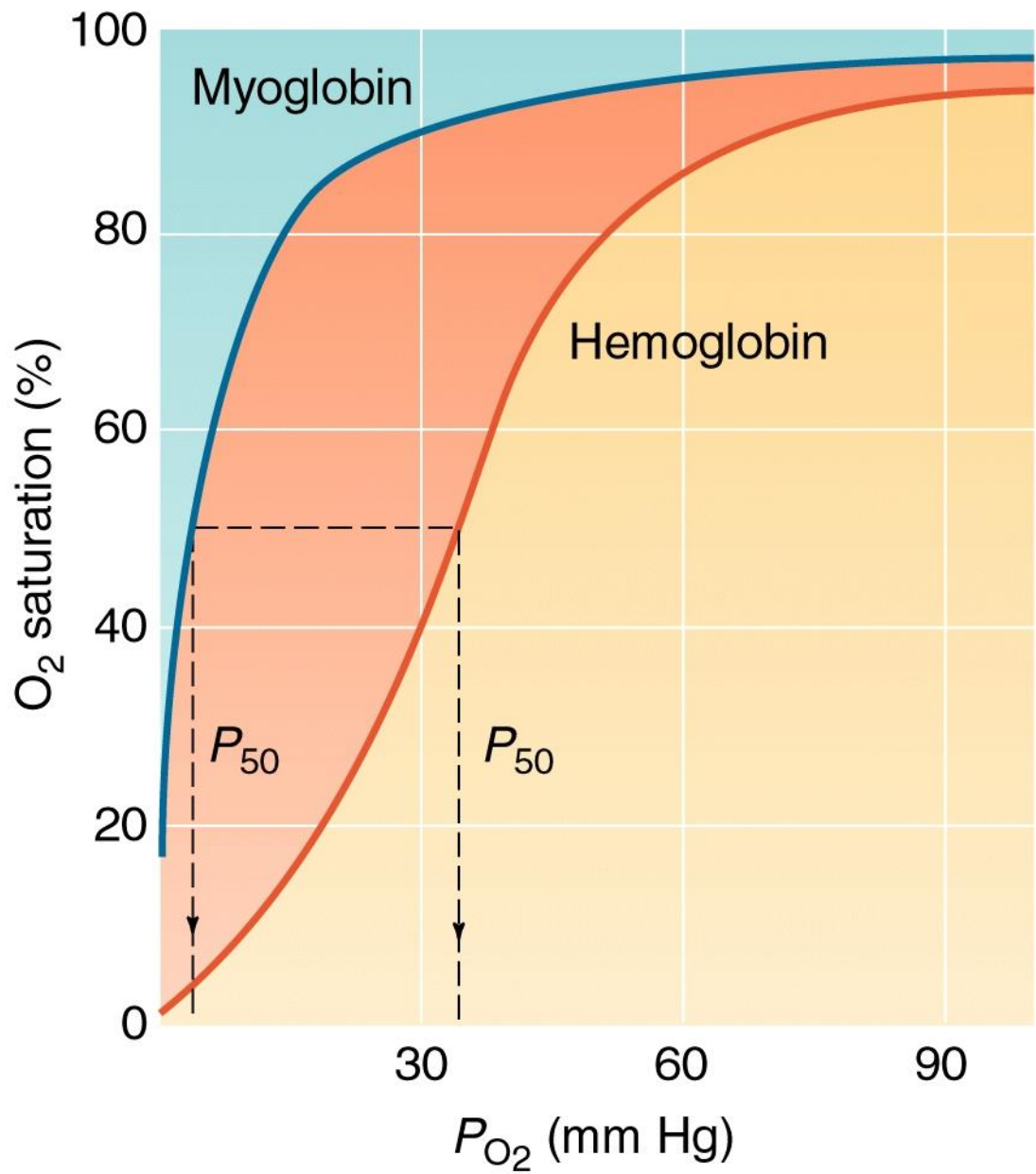
Partial pressures (kPa) for oxygen and nitrogen (dry, CO₂-free values for ambient air), alveolar carbon dioxide, and plasma-dissolved O₂ (ml O₂ per liter plasma; assuming plasma solubility of O₂ is 0.209 ml liter⁻¹ kPa⁻¹) and fat N₂ content (ml N₂ per liter body fat; assuming fat solubility of N₂ is 0.67 ml liter⁻¹ kPa⁻¹ dissolved N₂) for a human scuba diver in equilibrium with the ambient hydrostatic pressure as a function of depth of diving.

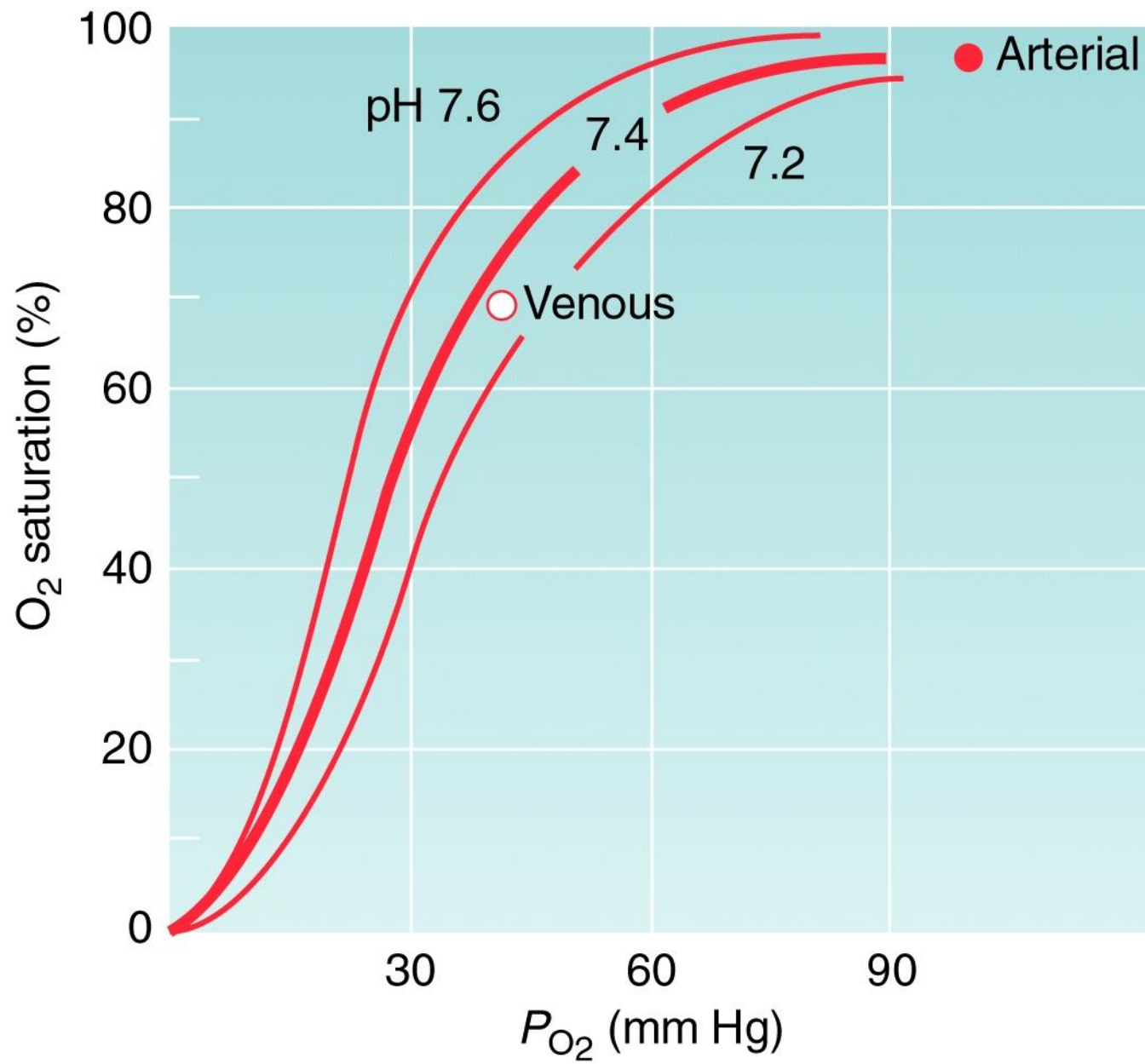
Depth (m)	0	50	100	500
Ambient Pressure	101	202	1111	5151
pO ₂	21.1	42.4	233.5	1082.6
pN ₂	79.8	159.7	878.3	4072.5
Alveolar pCO ₂	5.32	5.32	5.32	5.32
Plasma O ₂	4.4	8.8	48.3	223.9
Fat N ₂	53	106	582	2700

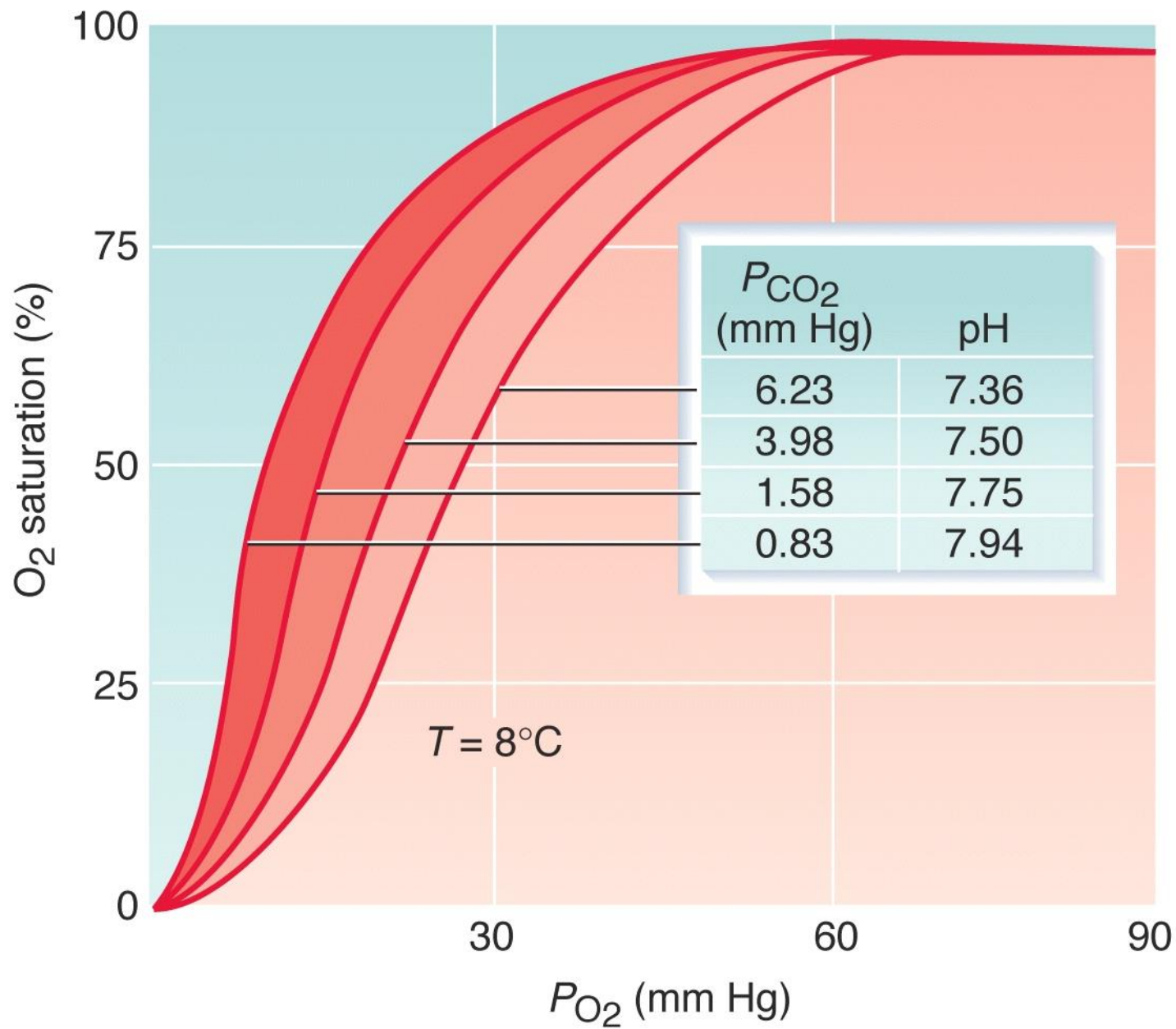












11.1 Gas Demands: General Problems and Evolutionary Solutions



- Four steps in external respiration
 - **Ventilation**
 - Bulk transport of external media across a gas exchange surface
 - **Respiratory exchange**
 - Gas diffusion between the environmental medium and internal body fluids
 - **Circulation**
 - Bulk transport of the ECF
 - **Cellular exchange**
 - Gas diffusion between the cell's immediate surroundings and its mitochondria

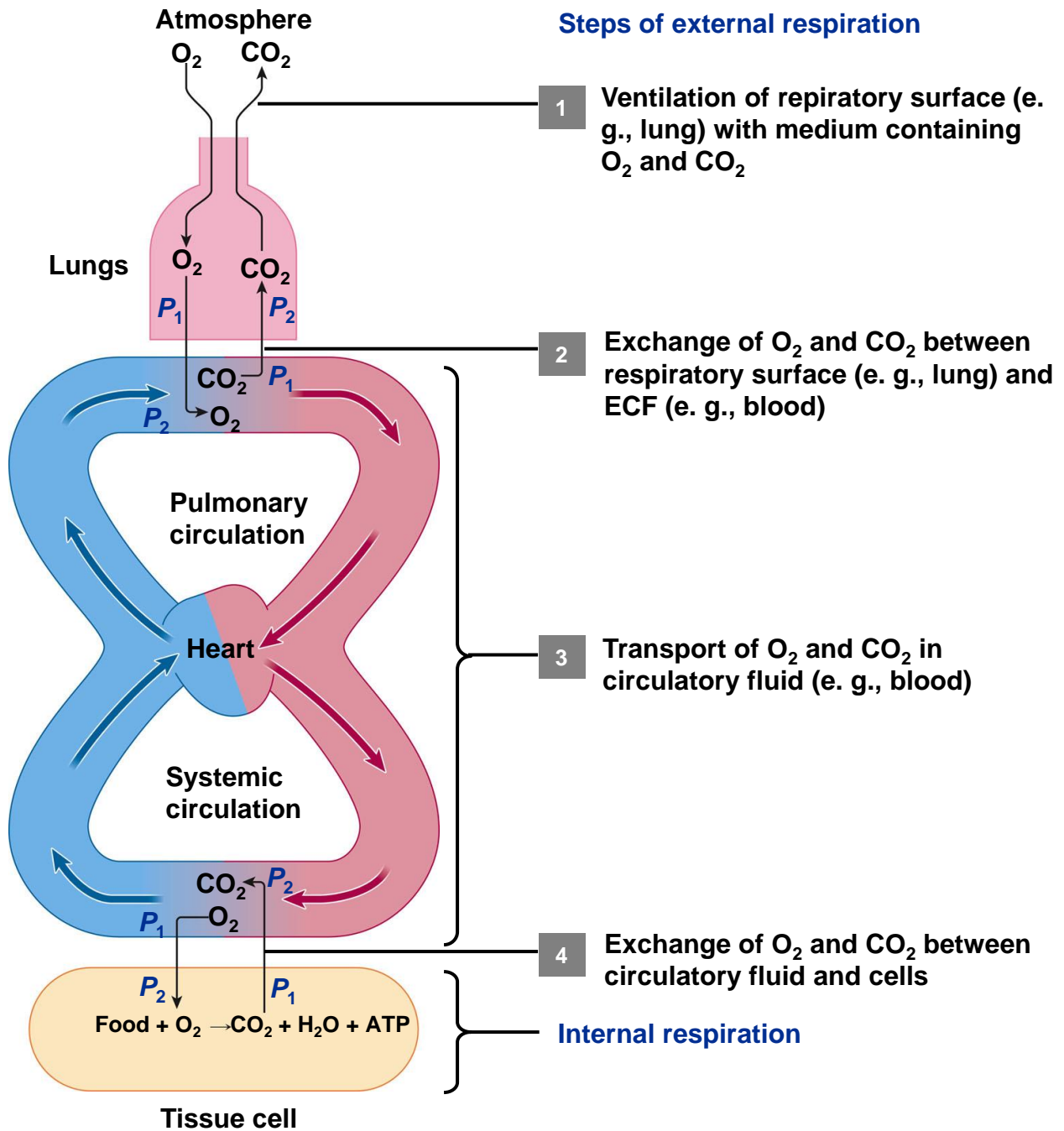


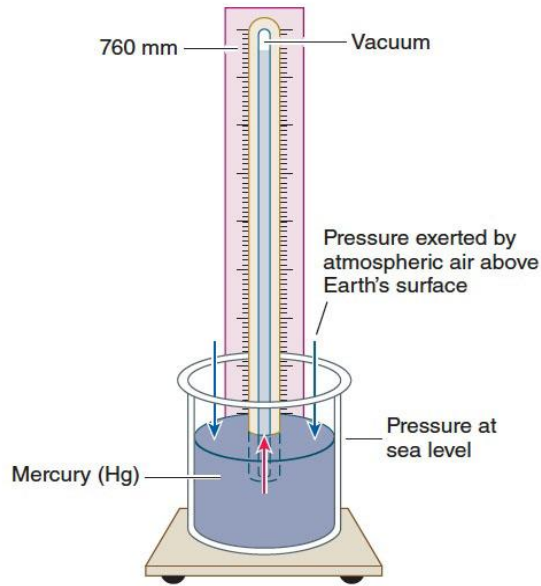
Figure 11-1 p494

11.1 Gas Demands: General Problems and Evolutionary Solutions

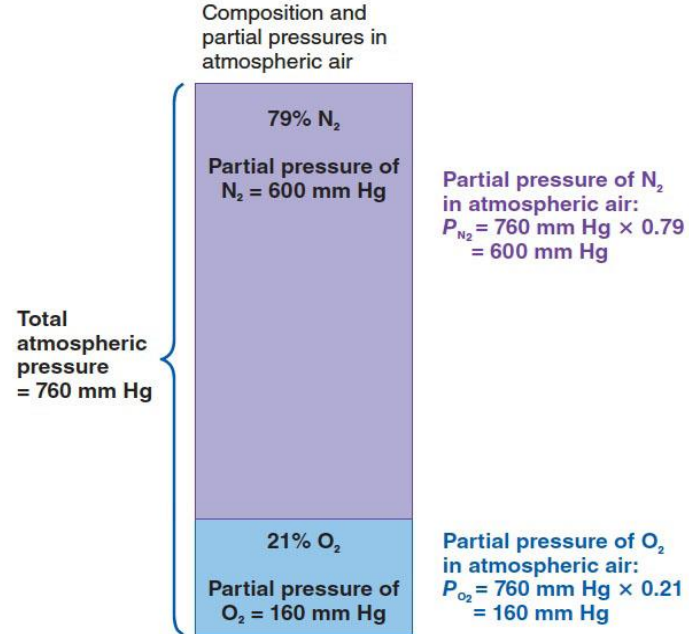


- Gas diffusion follows Fick's law
 - For gases, **concentration gradient** is replaced by **partial pressure gradient**
 - The **partial pressure** of a gas (P_{gas}) is the pressure exerted independently by the gas within a mixture of gases
 - Example: P_{O_2} in dry atmospheric air (21% O_2) is $0.21 \times 760 \text{ mmHg} = 160 \text{ mmHg}$
 - Water that is in **equilibrium** with air has the **same gas partial pressures** as the air
 - **Concentrations may be different**, depending on the solubility of the gas

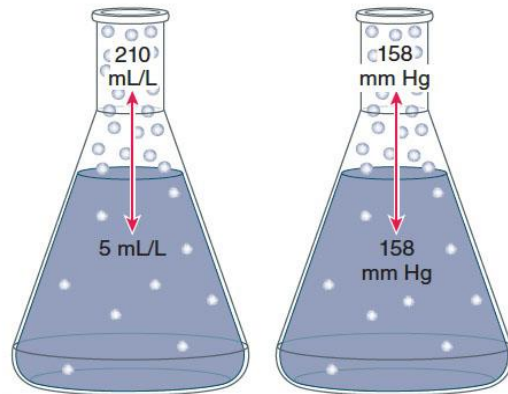
11.1 Gas Demands: General Problems and Evolutionary Solutions



(a)



(b)



(c)

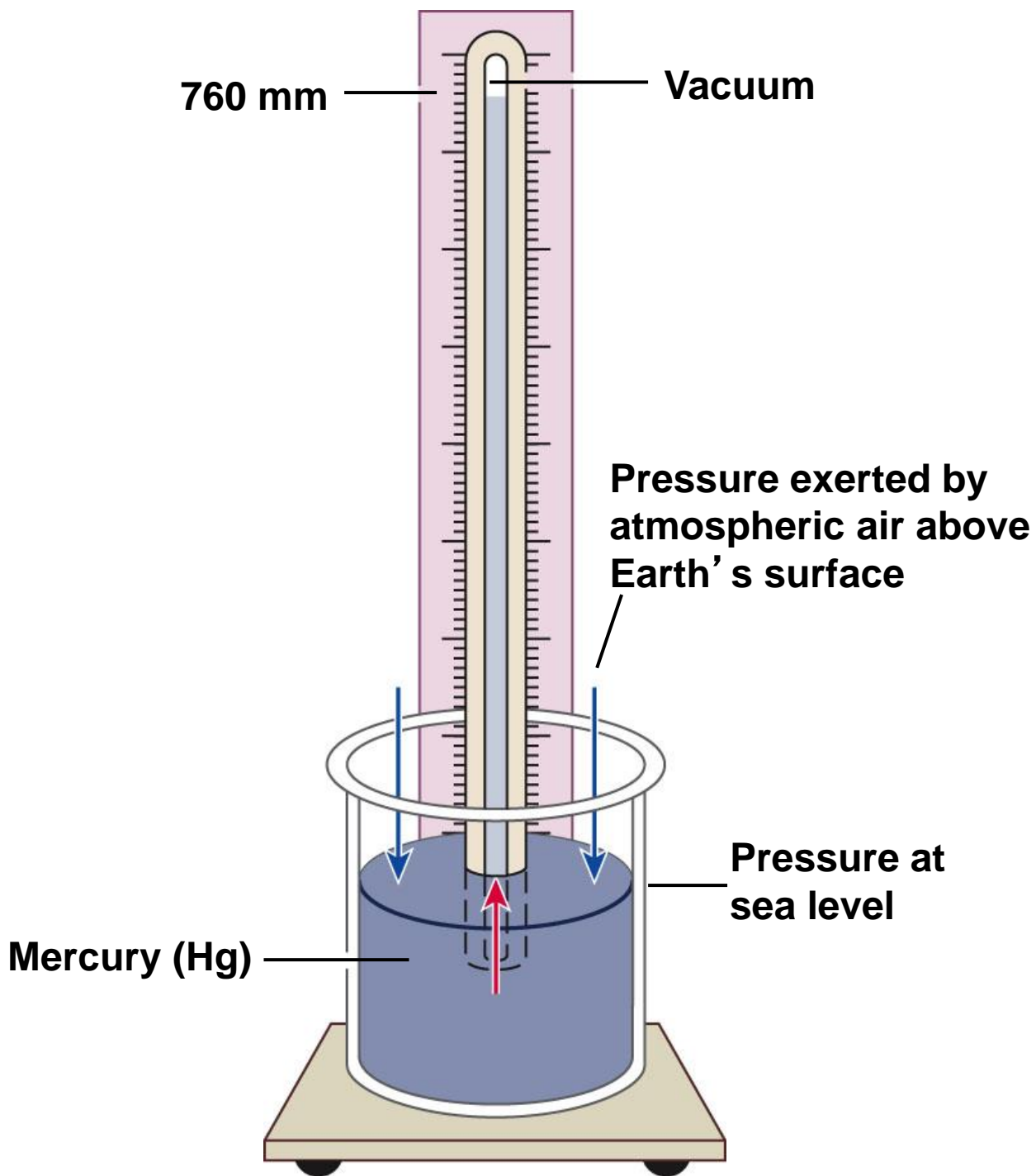
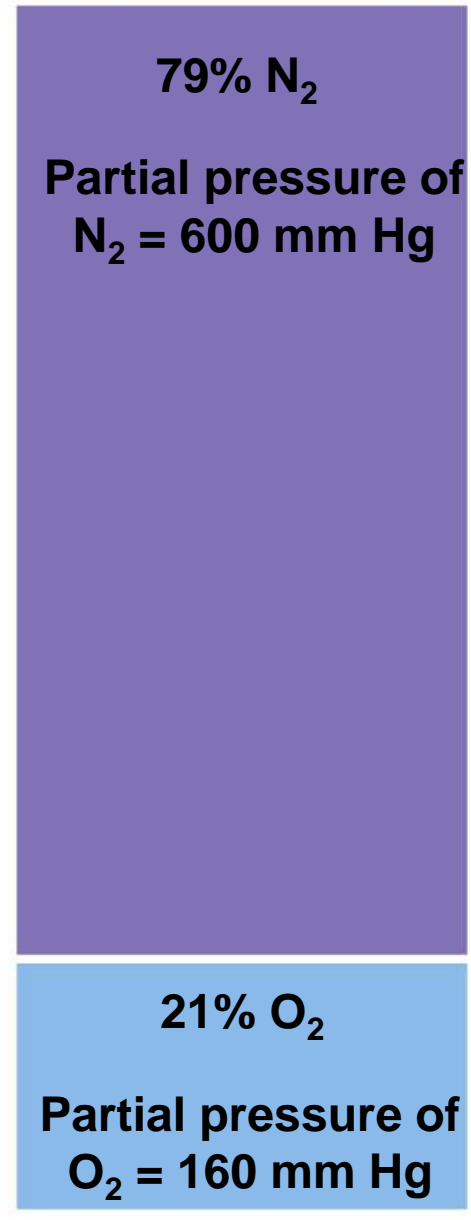


Figure 11-2a p495

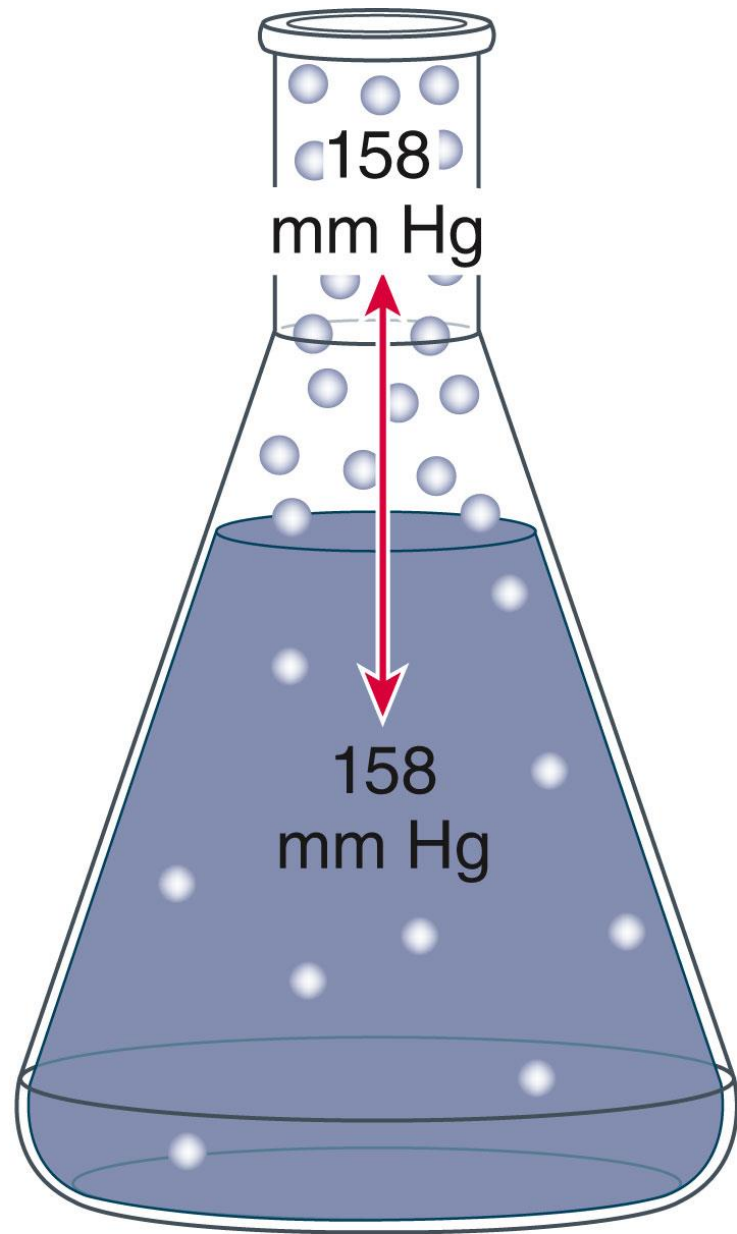
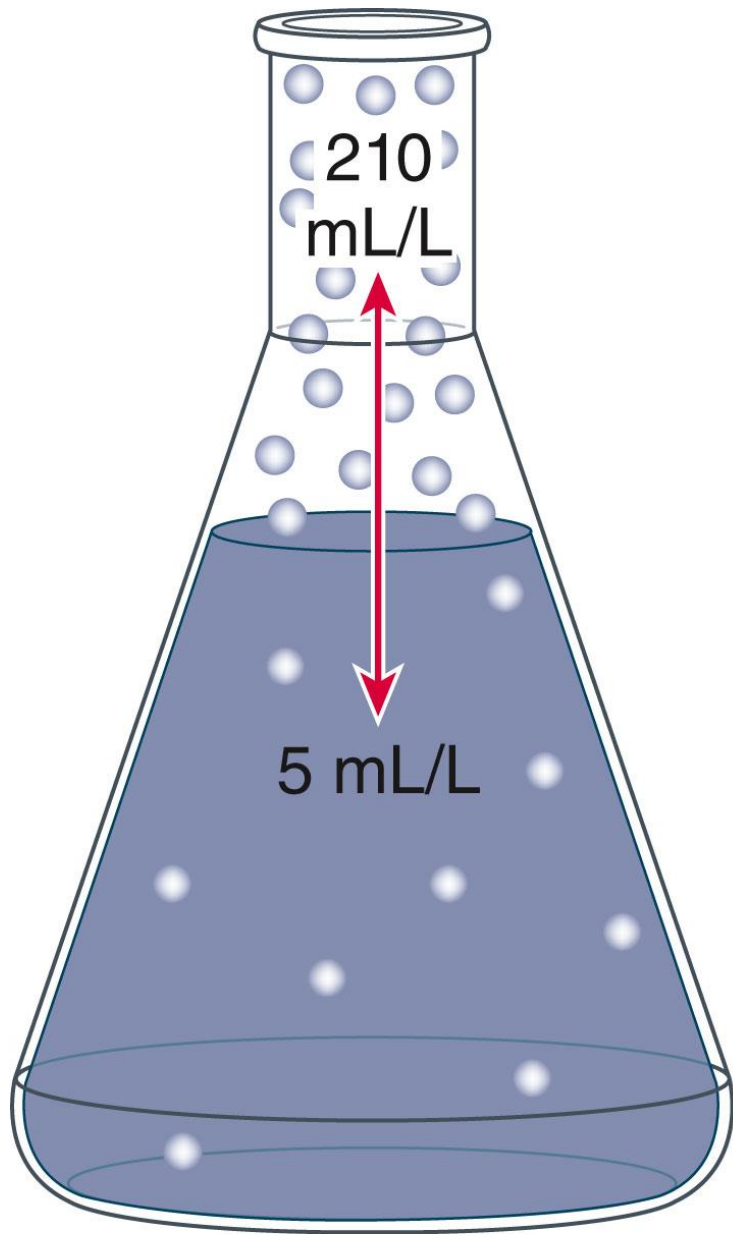
Composition and partial pressures in atmospheric air

Total atmospheric pressure = 760 mm Hg



Partial pressure of N₂ in atmospheric air:
 $P_{N_2} = 760 \text{ mm Hg} \times 0.79$
 $= 600 \text{ mm Hg}$

Partial pressure of O₂ in atmospheric air:
 $P_{O_2} = 760 \text{ mm Hg} \times 0.21$
 $= 160 \text{ mm Hg}$



(c)

11.1 Gas Demands: General Problems and Evolutionary Solutions

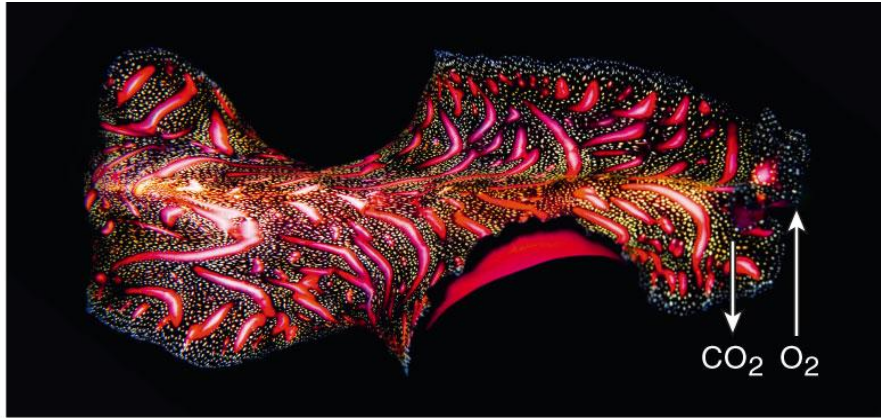


- Diversity of gas exchange structures
 - **Plasma membrane** of unicellular organisms
 - **Skin** of small multicellular organisms
 - Some have **cilia** to create feeding and breathing currents
 - **Evaginated surfaces (gills)** of large aquatic animals
 - **Invaginated surfaces (tracheae or lungs)** of terrestrial animals

11.1 Gas Demands: General Problems and Evolutionary Solutions



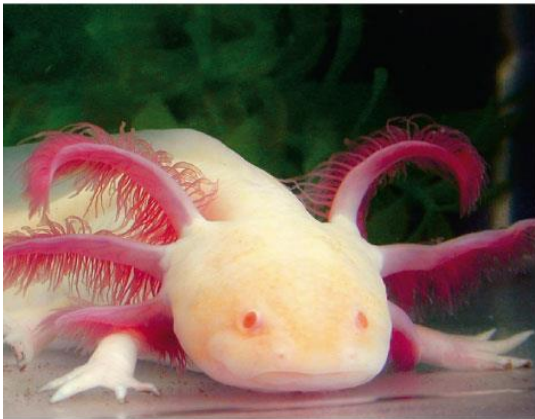
(a)



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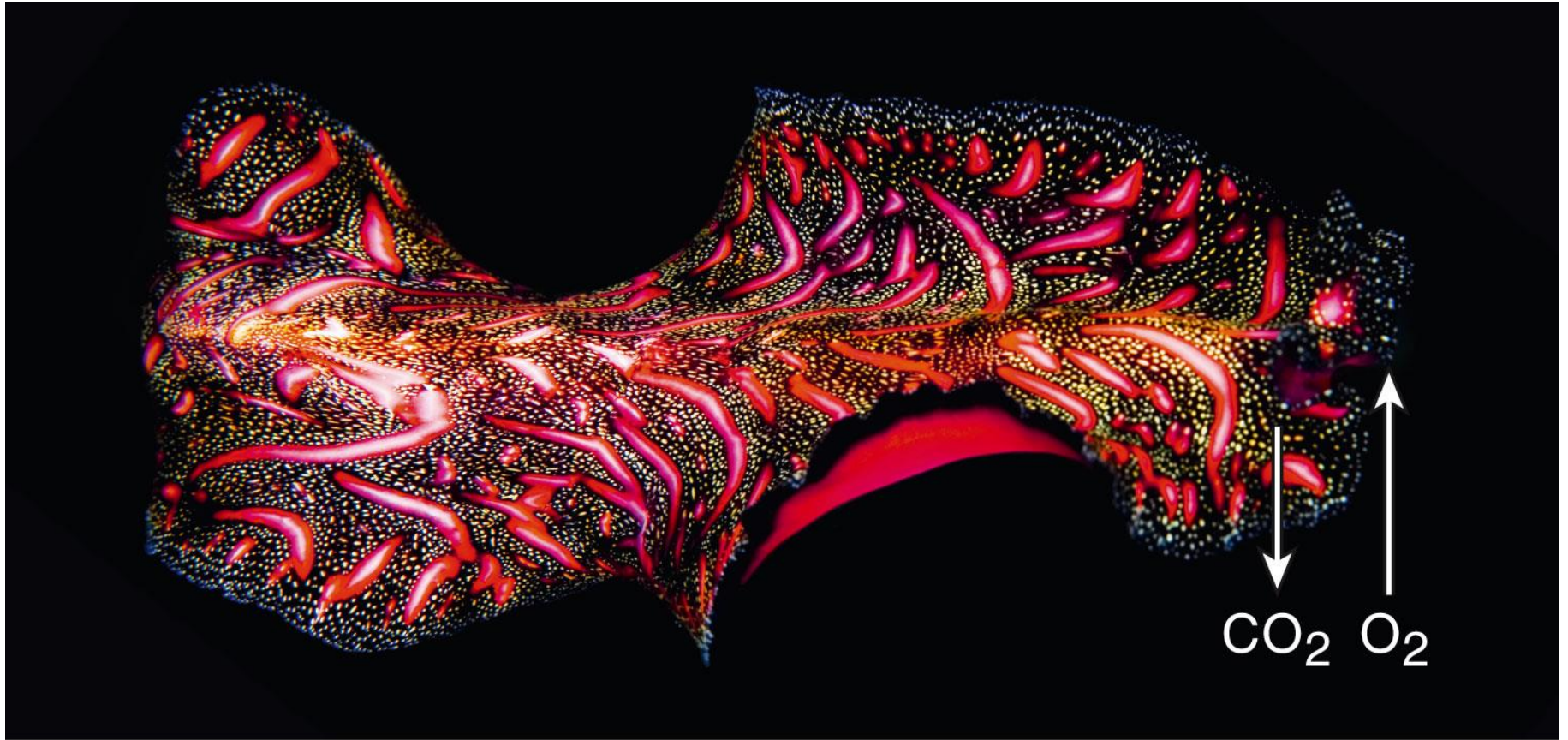
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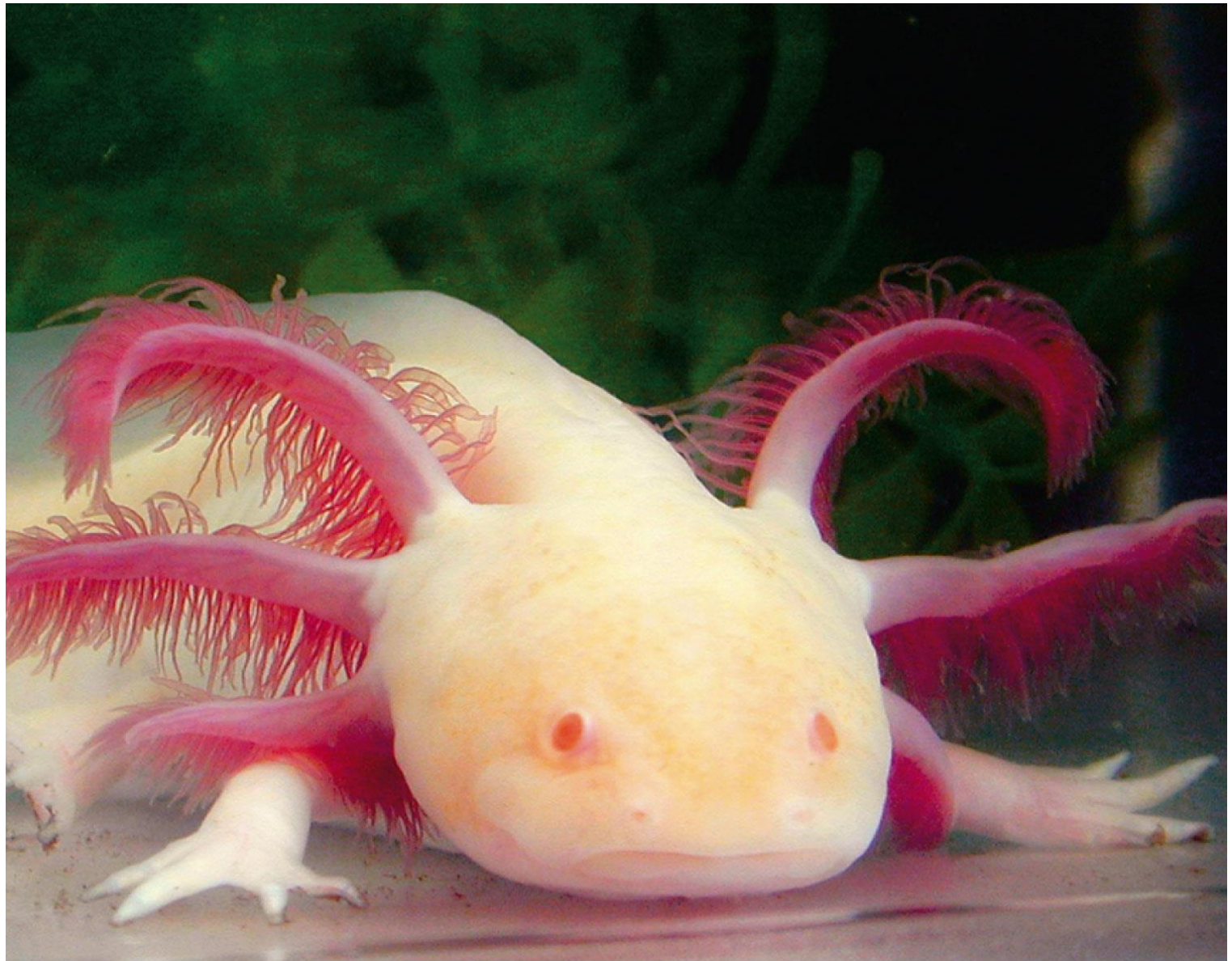
(f)



(a)



(b)



(d)



(e)



(f)

11.1 Gas Demands: General Problems and Evolutionary Solutions



- Breathing can be **tidal** or **flow-through**
 - **Tidal breathing**
 - External medium is moved in and out of the same opening through **inhalation** and **exhalation**
 - Fresh medium is only brought in half the time and is mixed with depleted medium
 - **Flow-through breathing**
 - External medium enters one opening and leaves through a separate opening
 - Flow of fresh medium can be continuous and very little mixing occurs
 - **More efficient gas exchange** than tidal breathing

11.2 Water Respirers



- Water is a more difficult medium than air for gas exchange
 - **Higher viscosity** than air
 - O₂ is **less soluble** in water
 - Rate of **diffusion** of gases is slower
 - Solubility of O₂ decreases with increasing **salinity**
 - Solubility of O₂ decreases with increasing **temperature**
 - O₂ content in water is more variable due to **habitat variation**
 - Environmental water contains many **more components** than air

11.2 Water Respirers



- Integumentary respiration
 - Flatworms and Cnidaria
 - Enhanced by **internal circulation** (e.g. earthworm)
 - Important in **amphibians, aquatic reptiles and most fishes**
 - During hibernation, frogs and turtles exchange all of their respiratory gases across the skin
 - Eels exchange 60% of gases through highly vascular skin

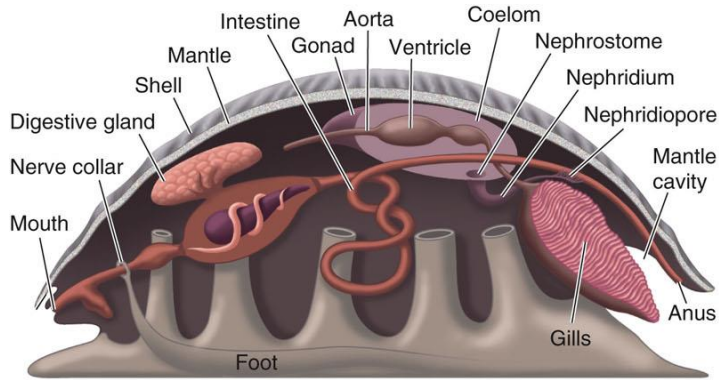
11.2 Water Respirers



■ Gills

- **Evaginations of tissue** protruding into the external medium
- **Delicate** structures composed of thin cell layers
 - Protected by shells, toxins, withdrawal, exoskeletons, bony plates
- **Highly perfused** by a circulatory system
- May have **flow-through** breathing mechanisms

11.2 Water Respirers



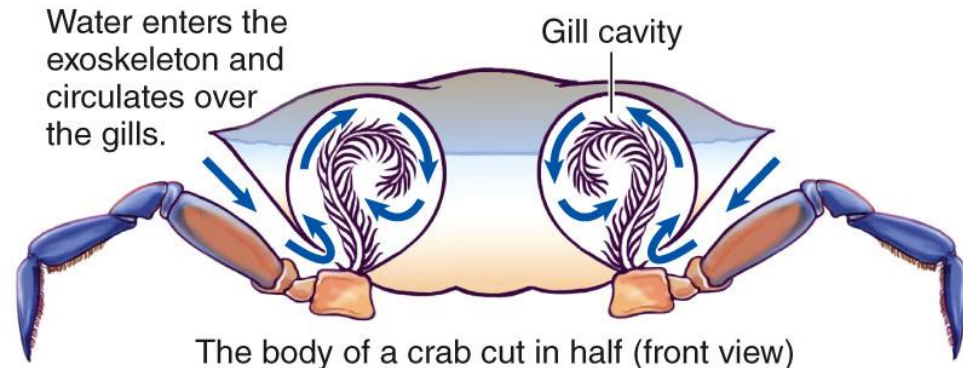
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(a)



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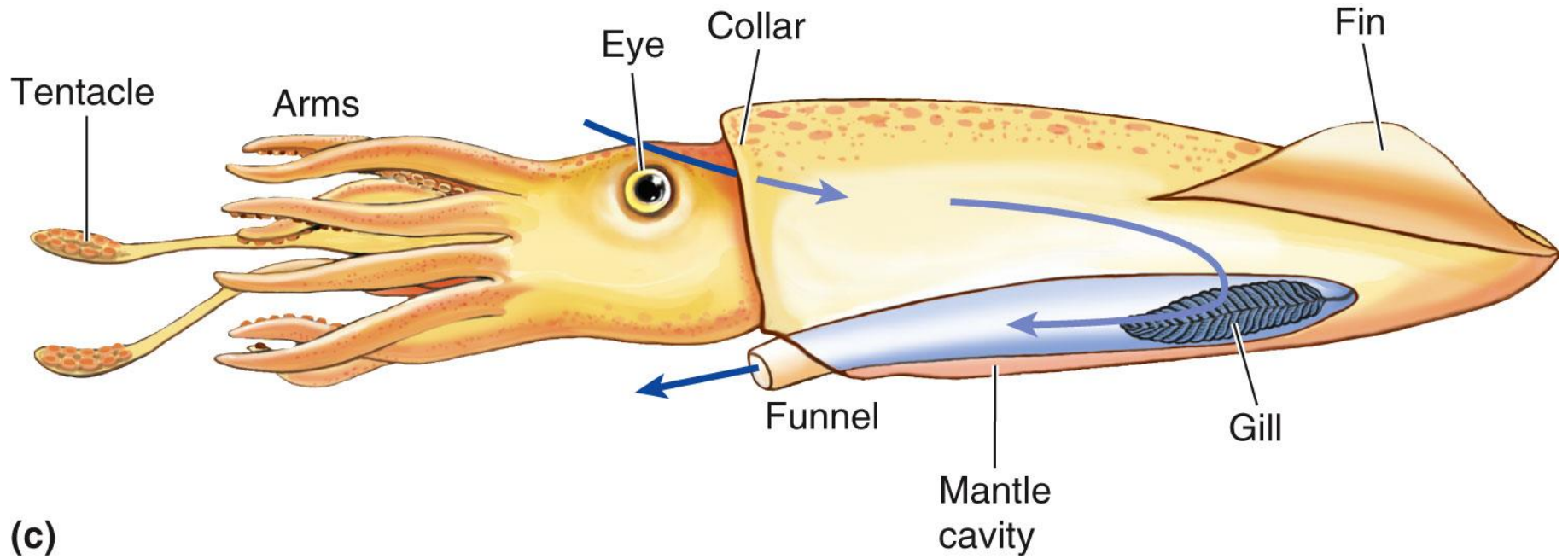
(b)

11.2 Water Respirers



- Muscle-driven breathing
 - **Cephalopods**
 - During **inhalation**, the funnel closes and **mantle cavity expands**, drawing water in
 - During exhalation, the mantle opening seals up, the **mantle contracts**, and the funnel opens, expelling water out the siphon
 - Also used for **jet propulsion**

11.2 Water Respirers

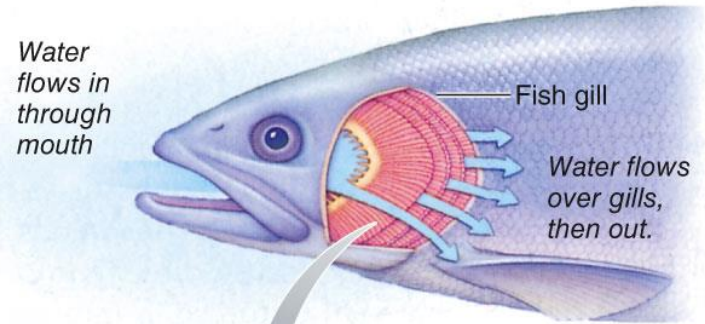


11.2 Water Respirers

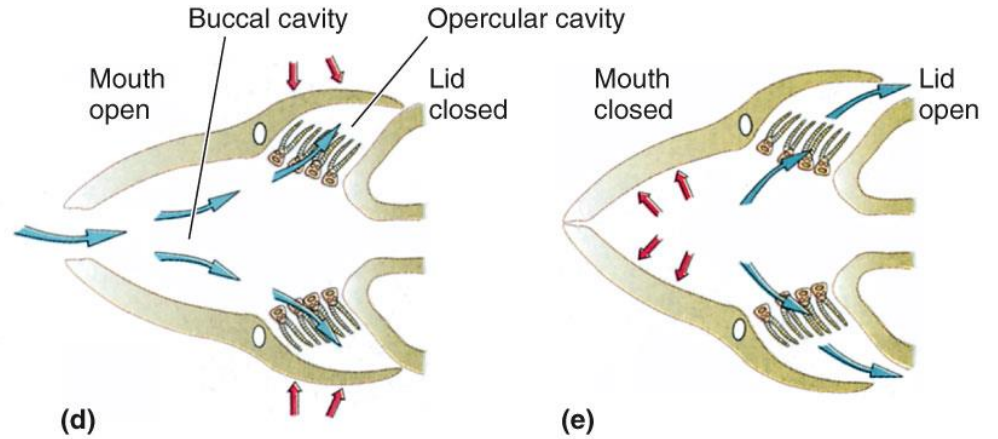


- Muscle-driven breathing in fishes
 - **Skeletal muscle pumps** in buccal and opercular cavities
 - Mouth opens and O₂-rich water is drawn into the mouth by **negative pressure**
 - Then the mouth closes, the **opercular cavity constricts** and opercula open, forcing water through the gills and out the opercular exit
 - **Lamprey** uses **tidal flow** in and out of the opercular opening, because its mouth remains attached to the host while feeding

11.2 Water Respirers

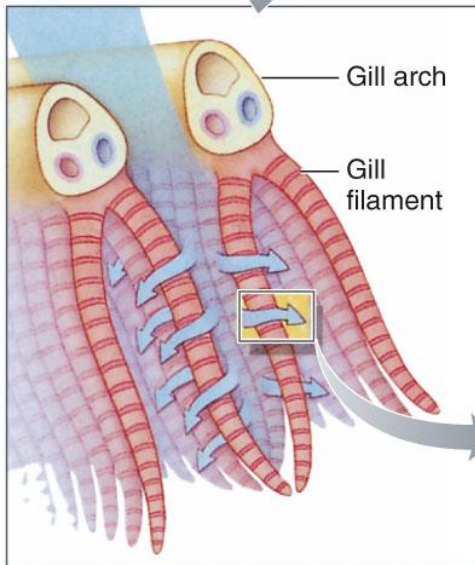


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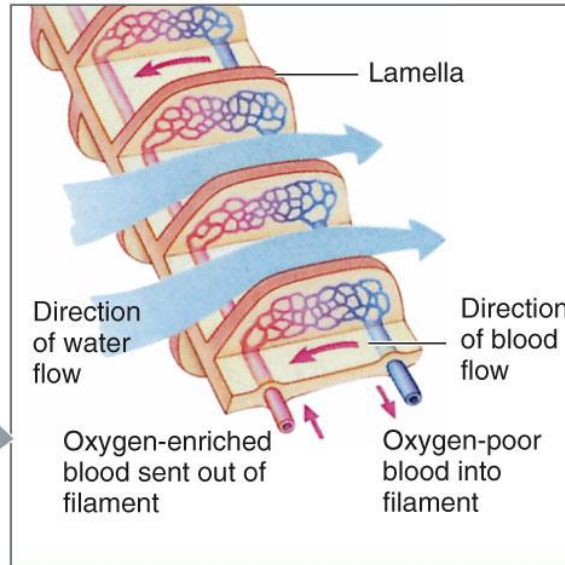


(d)

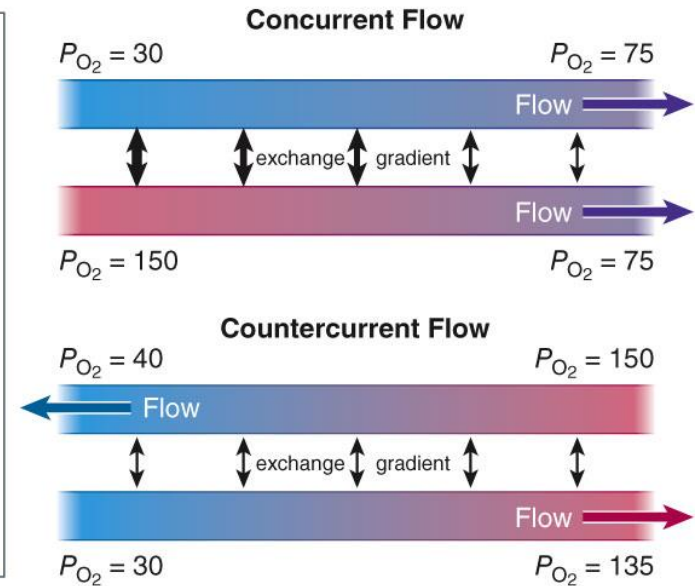
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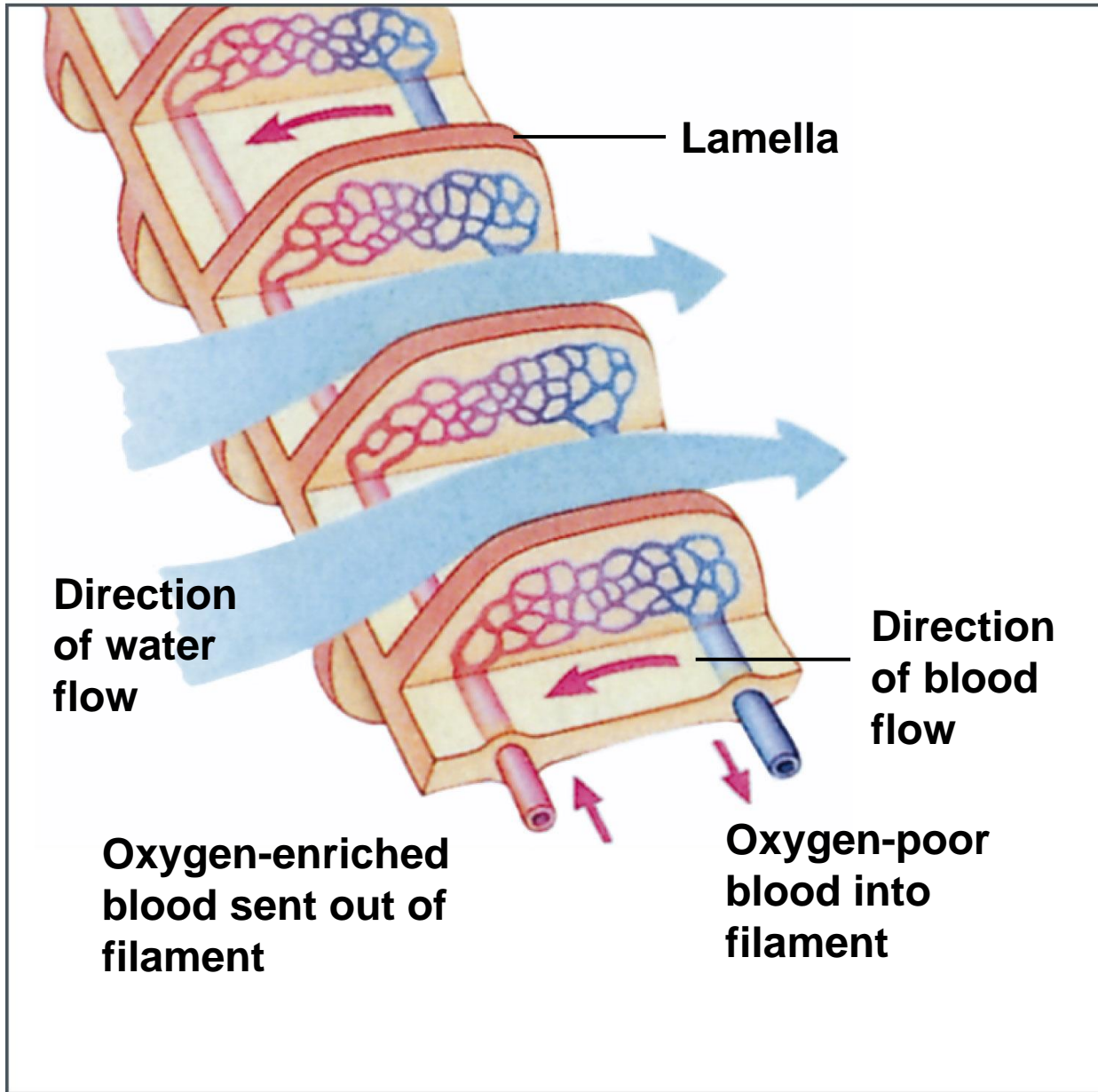
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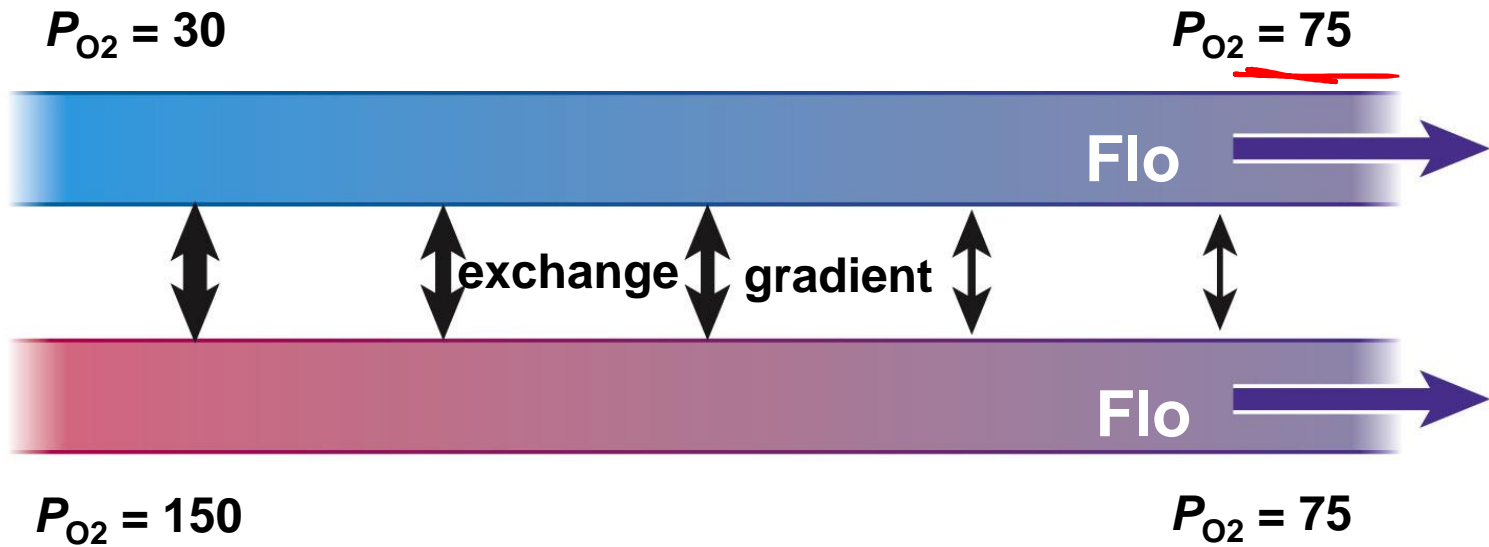
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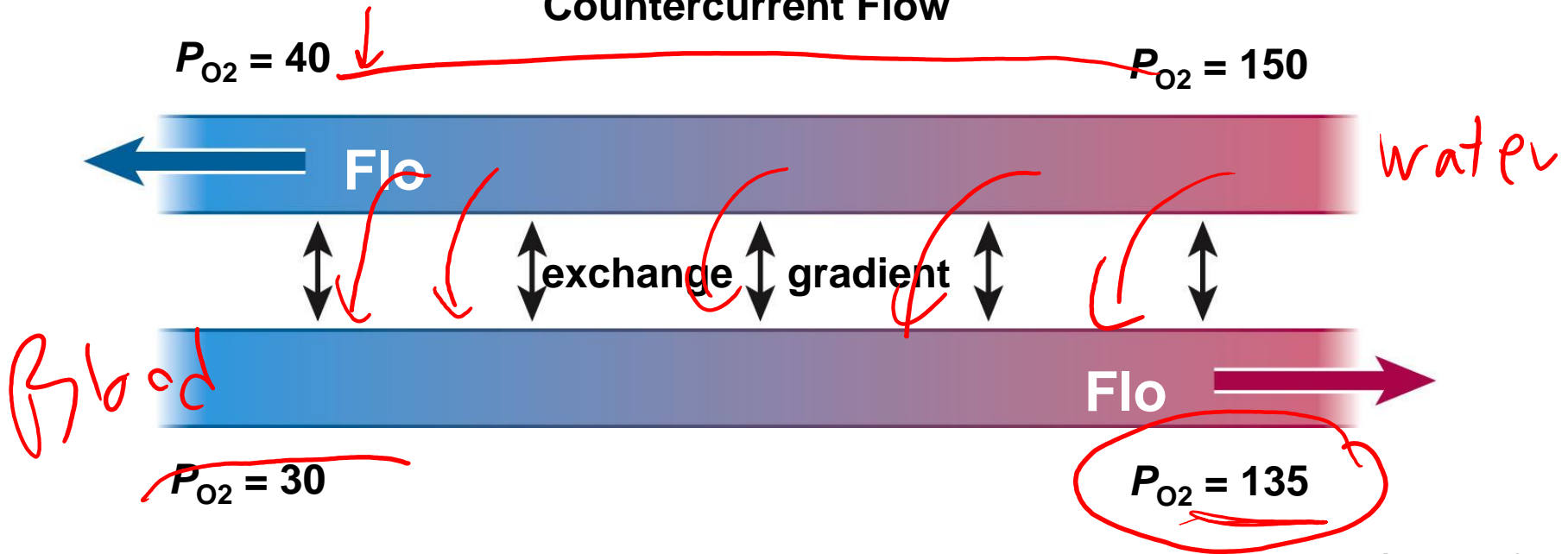
(f)



Concurrent Flow



Countercurrent Flow



11.2 Water Respirers



- Muscle-driven breathing in fishes
 - In **ram ventilation**, bulk transport is created by the animal's swimming motion
 - **Obligate ram breathers** (e.g. tuna and sharks) must swim in order to breathe
 - **Facultative ram breathers** (e.g. rainbow trout) switch from buccal-opercular breathing to ram ventilation when swimming above certain velocities

11.2 Water Respirers



- Muscle-driven breathing in fishes
 - **Countercurrent blood flow** enhances gas pressure gradients
 - Blood flows in a direction **opposite** to that of water flow
 - Blood continually encounters water whose O_2 content is higher
 - Provides much **greater efficiency** of gas exchange

11.3 Air Respirers: Overview and Nonvertebrates



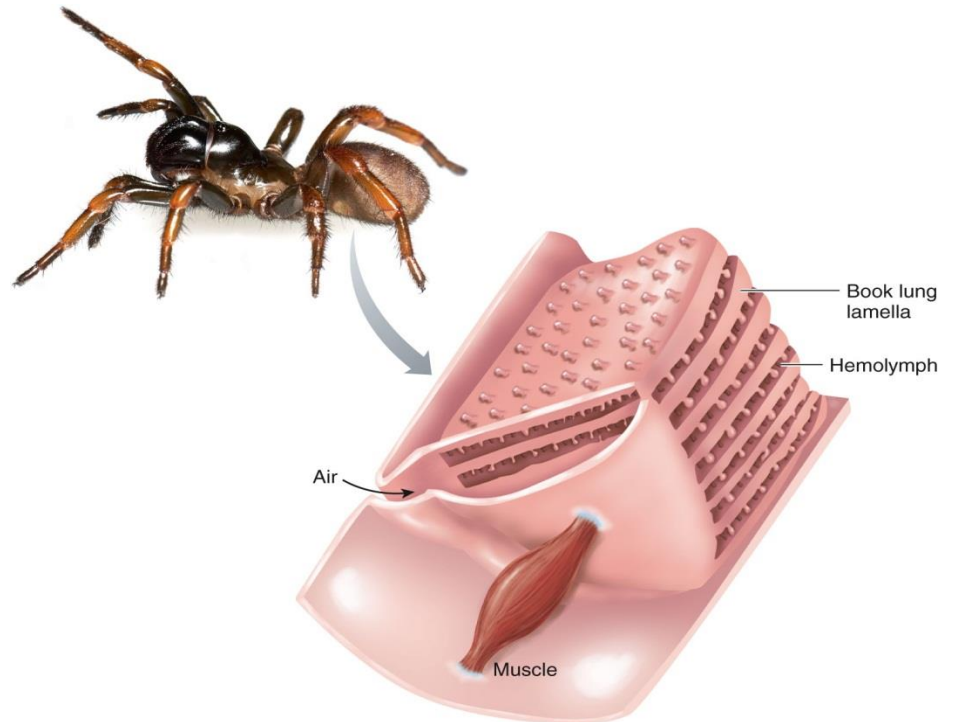
- Air respirers vs. water respirers
 - Air is much **less viscous** than water, allowing **easier bulk transport**
 - Air **contains more O₂** than water
 - Reduced need for surface area
 - Permits less efficient tidal breathing
 - Thin **respiratory surfaces** exposed to air must be kept **moist**
 - Remain in a moist environment or
 - Have covered or **fully internal** gas exchange structures

11.3 Air Respirers: Overview and Nonvertebrates



■ Arthropods

- Scorpions and some spiders have **book lungs**
 - **Stacks of lamellae** invaginating from the cuticle into the abdomen



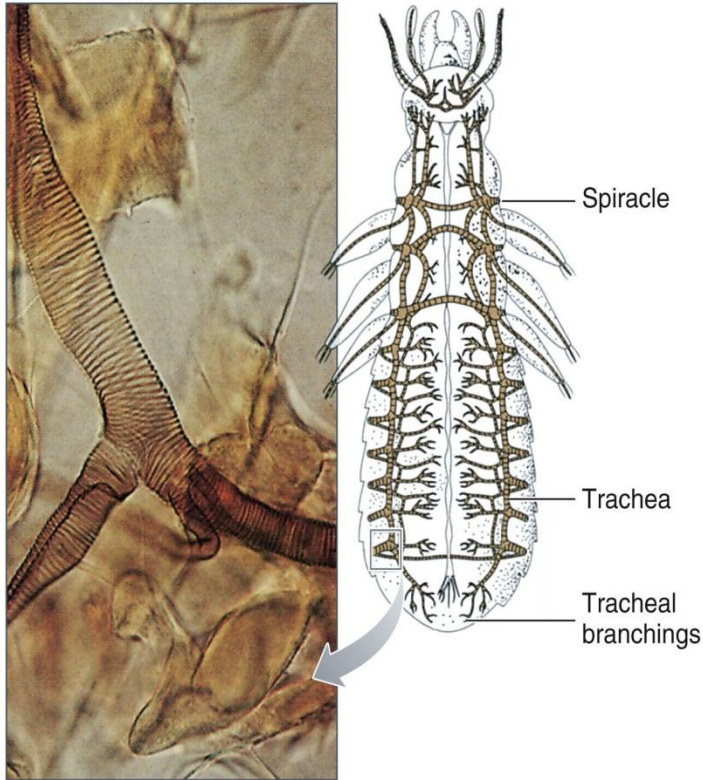
11.3 Air Respirers: Overview and Nonvertebrates



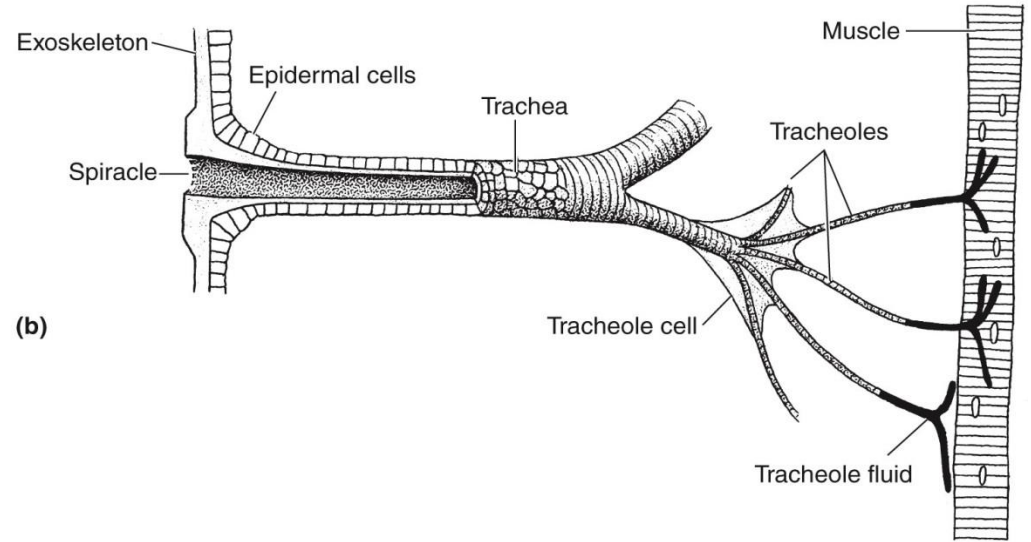
■ Arthropods

- Insects and many spiders have **tracheae**.
 - Tubular extensions into the tissues reinforced with rings of chitin
 - Break up into finer branches (**tracheoles**)
 - Tracheae connect to outside through openings in the exoskeleton (**spiracles**)
 - **Distribution of tracheae** reflects the O₂ demands of tissues
 - Larger and flying insects have active tidal pumping of air

11.3 Air Respirers: Overview and Nonvertebrates



(a)



11.4 Air Respirers: Vertebrates



- Bimodal breathers
 - The first **air breathers** evolved in tropical lowlands where stagnant ponds were subject to **hypoxia** or **desiccation**.
 - **Bimodal breathers** have gills and other respiratory exchange structures (e.g. skin)
 - **Lungs in fishes** were simple ventral evaginations of the pharynx

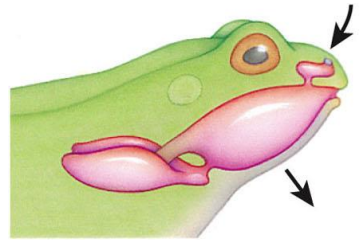
11.4 Air Respirers: Vertebrates



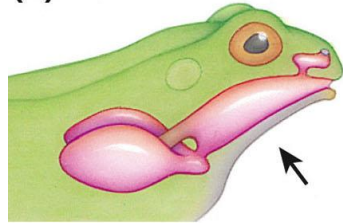
■ Amphibians

- **Bimodal** or **trimodal breathers** (gills, lungs, integument) to support aquatic and terrestrial lifestyles
- In frogs, **larval stages** have **gills**; **adults** have simple, noncompartmentalized **lungs**
- Air is forced into lungs by **positive pressure** from a **buccal pump**
- Several inspiratory oscillations fill lungs; empty in one long exhalation
- Adaptation to air-breathing included a decrease in affinity of **hemoglobin** to O_2

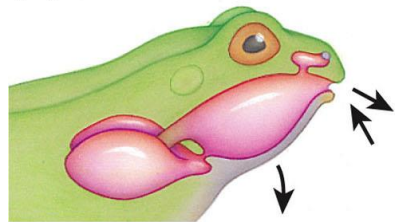
11.4 Air Respirers: Vertebrates



(a)



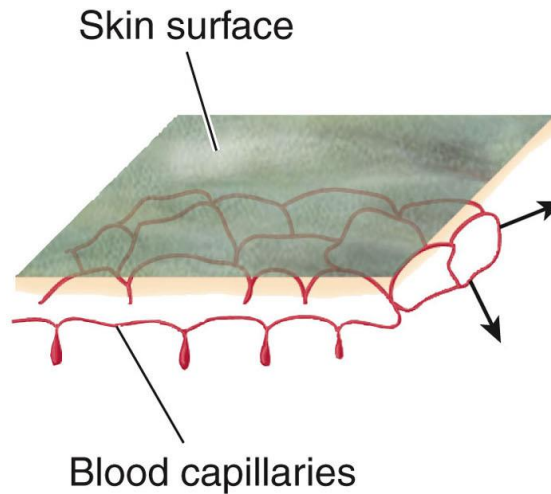
(b)



(c)



(d)



(e)

11.4 Air Respirers: Vertebrates



■ Reptiles

- Lungs in reptiles, birds and mammals are **compartmentalized** and fill by **negative pressure**
- Reptile lungs are expandable, tidally ventilated sacs
- Vascularized ingrowths or dividing walls (**septa**) subdivide pulmonary lumen
 - Air sacs are called **ediculae** (spherical) or **faveoli** (oblong)

11.4 Air Respirers: Vertebrates



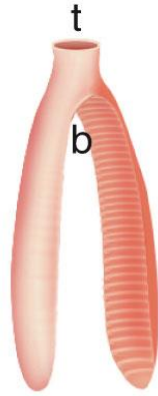
■ Reptiles

- **Lizards** and **snakes** rely on costal (rib) muscles for expansion of lungs
- **Turtles** (with fixed ribs) use limb extension
- **Crocodylians** have a connective tissue **diaphragm** adhering tightly to the anterior surface of the liver
 - **Diaphragmaticus muscle** contracts during inhalation
 - **Flow-through** system in secondary and tertiary bronchi

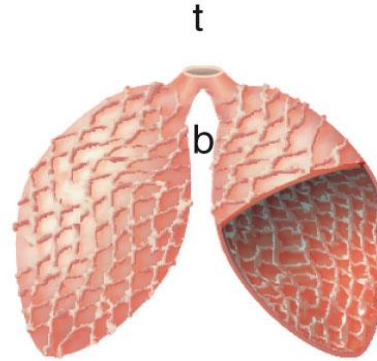
11.4 Air Respirers: Vertebrates



Amphibian
(salamander;
still rather like
fishes, early
amphibians)

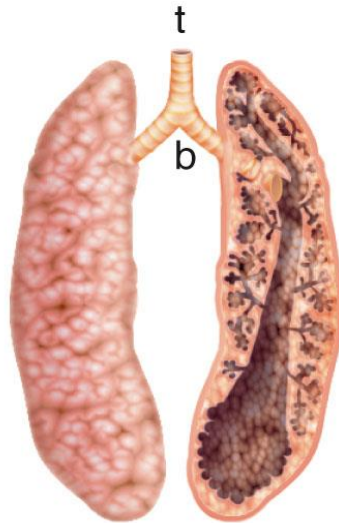


Amphibian
(frog; only
adults are
adapted to
dry habitats)

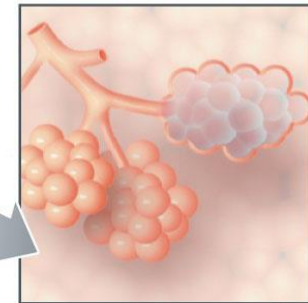
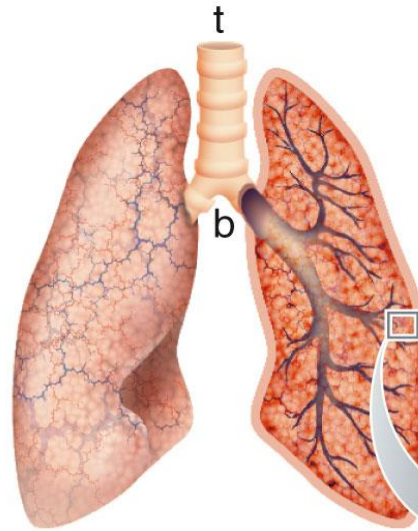


(a)

Reptile
(lizard;
adapted
to dry
habitats)

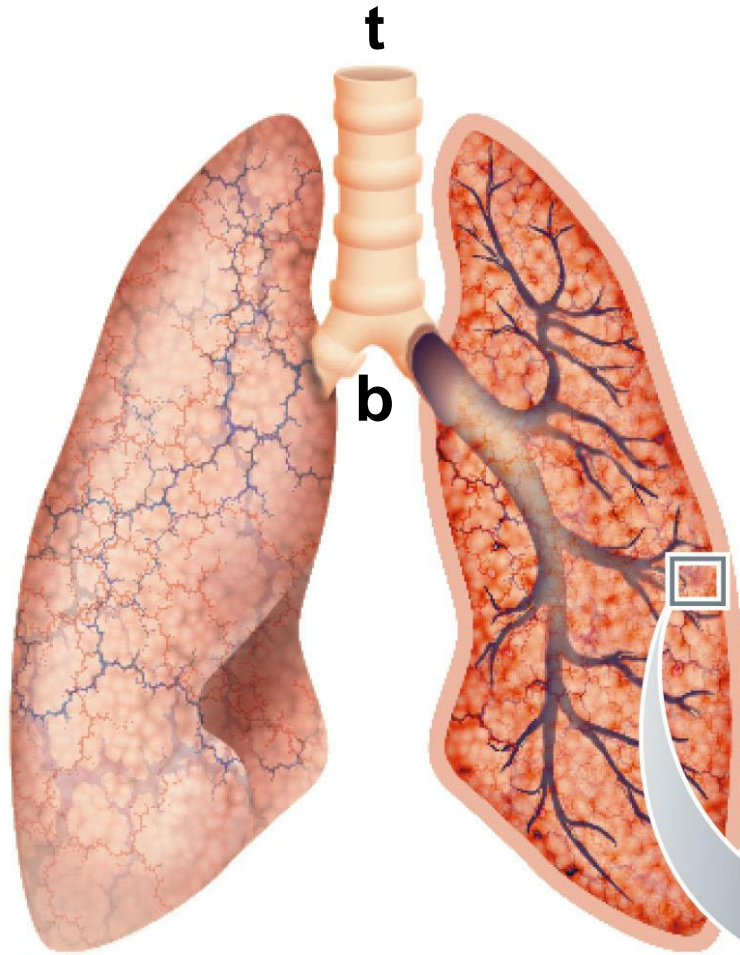


Mammal
(human;
adapted to
dry habitats)

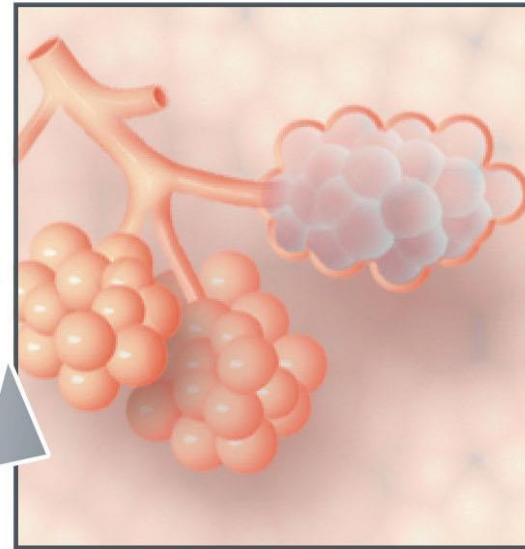


(b)

(c)



**Mammal
(human;
adapted to
dry habitats)**



11.4 Air Respirers: Vertebrates



- Birds and mammals
 - **Surface area** of lungs for gas exchange is expanded to support increased metabolic rates
 - Very small **alveoli** in mammals
 - **Parabronchi** with **air capillaries** in birds
 - Oxygenated blood from lung is completely **separated** from systemic venous blood by **four-chambered heart**
 - Small percentage of skin breathing in most mammals

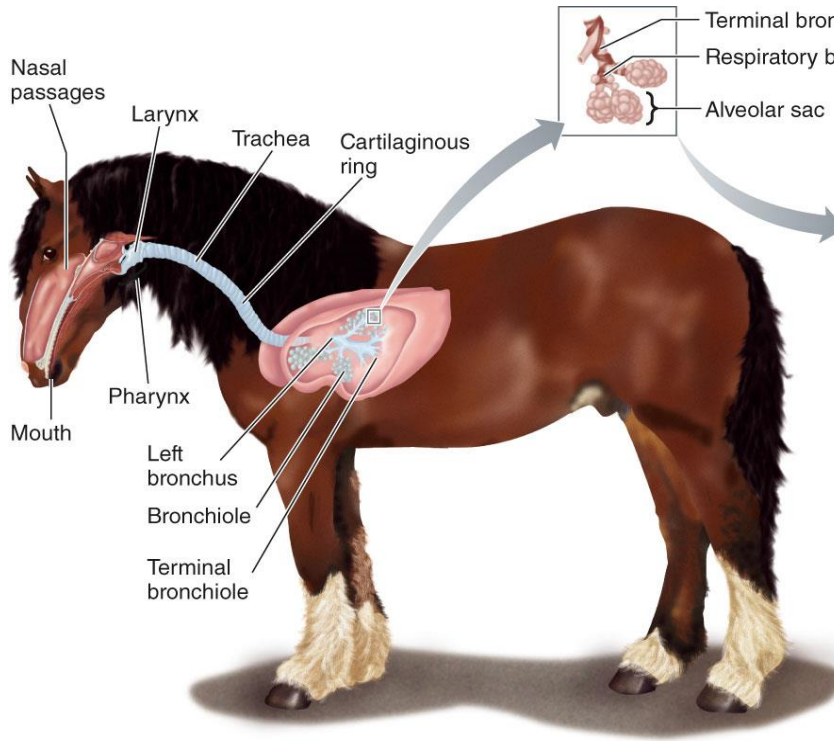
11.4 Air Respirers: Vertebrates



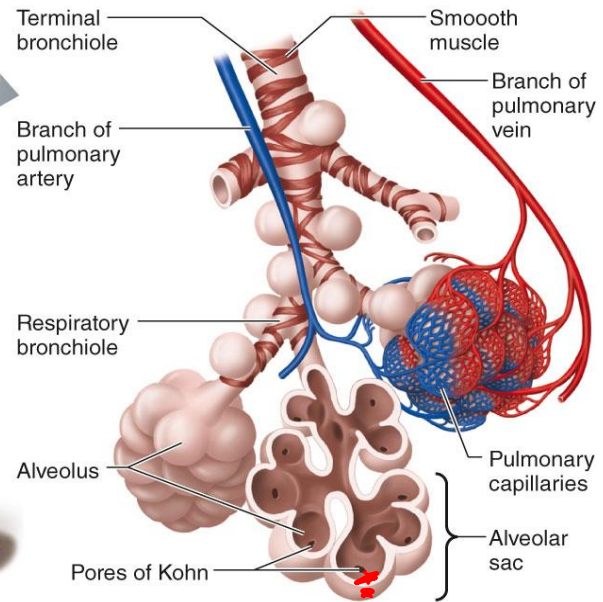
■ Mammalian airways

- **Nasal passages**
 - **Maxilloturbinals** retain heat and water
- **Pharynx** is a common passageway for air and food
- **Trachea** and esophagus exit pharynx
 - Reflexes close off trachea during swallowing
- **Bronchi**
 - Trachea divides into **right** and **left bronchi**, each entering a lung
 - Bronchi **branch** within lungs
 - Trachea and large bronchi are supported by **cartilaginous rings**
- **Bronchioles** -- smaller branches
 - Walls contain **smooth muscle** innervated by the **autonomic nervous system**
 - **Terminal bronchioles** open into **alveoli**

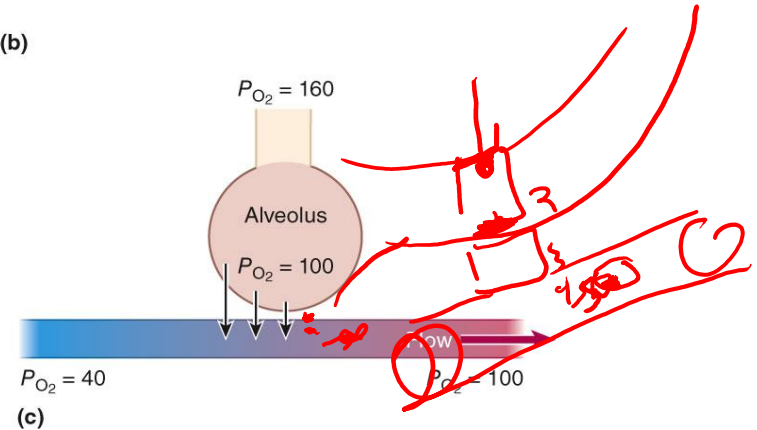
11.4 Air Respirers: Vertebrates



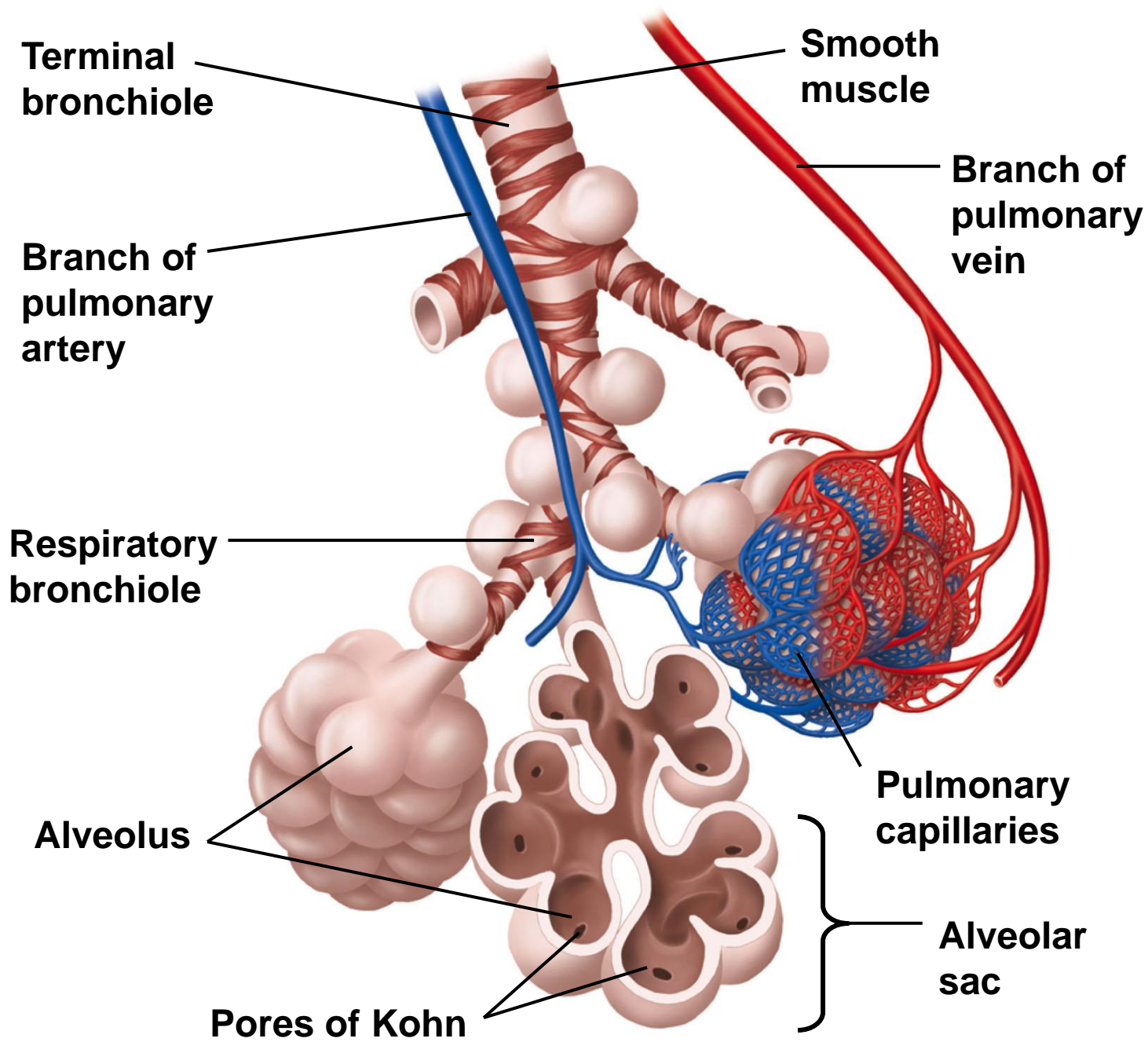
(a)



(b)



(c)



(b)

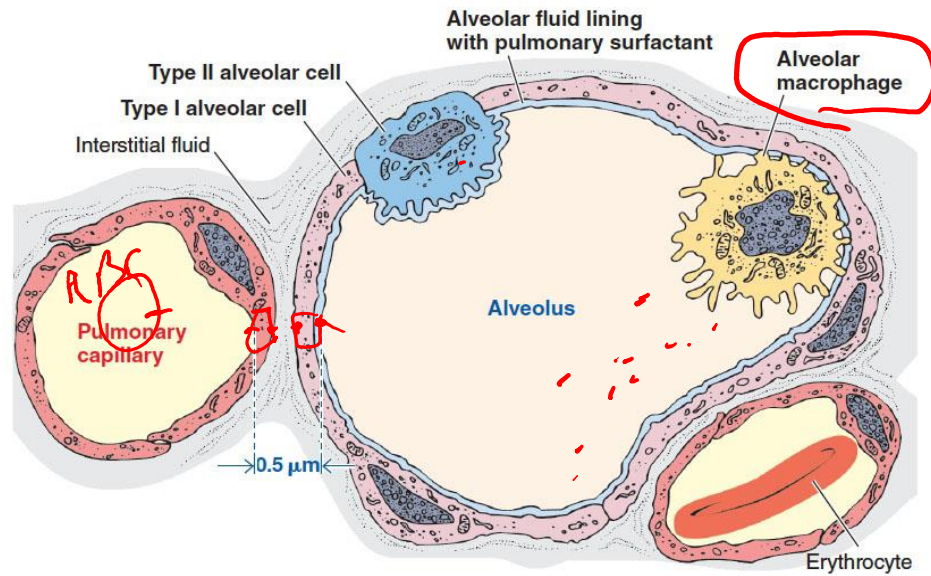
11.4 Air Respirers: Vertebrates



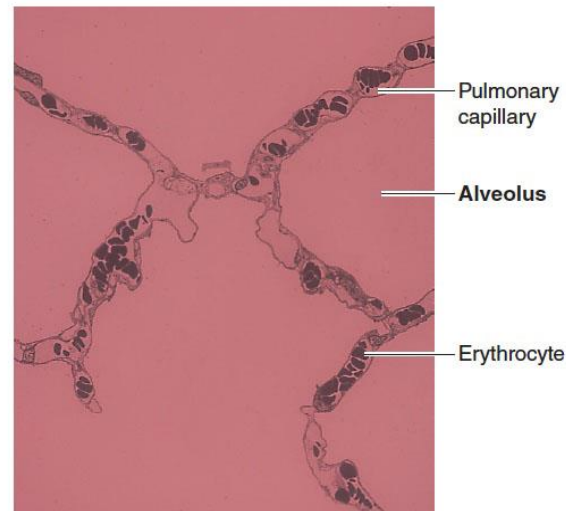
■ Alveoli

- Very small, tidally ventilated sacs
- **Gas exchange**
 - Large surface area
 - Single layer of highly flattened **Type I alveolar cells**
 - Dense **network of capillaries** surrounding alveoli
 - Thin **interstitial space**
 - Achieve **partial pressures** of gases in blood comparable to those in inspired air
- **Type II alveolar cells** secrete **pulmonary surfactant**
 - Facilitates alveolar expansion
- **Pores of Kohn** permit airflow between adjacent alveoli (**collateral ventilation**)

11.4 Air Respirers: Vertebrates



(a)



(b) Transmission electron micrograph of several alveoli and surrounding pulmonary capillaries

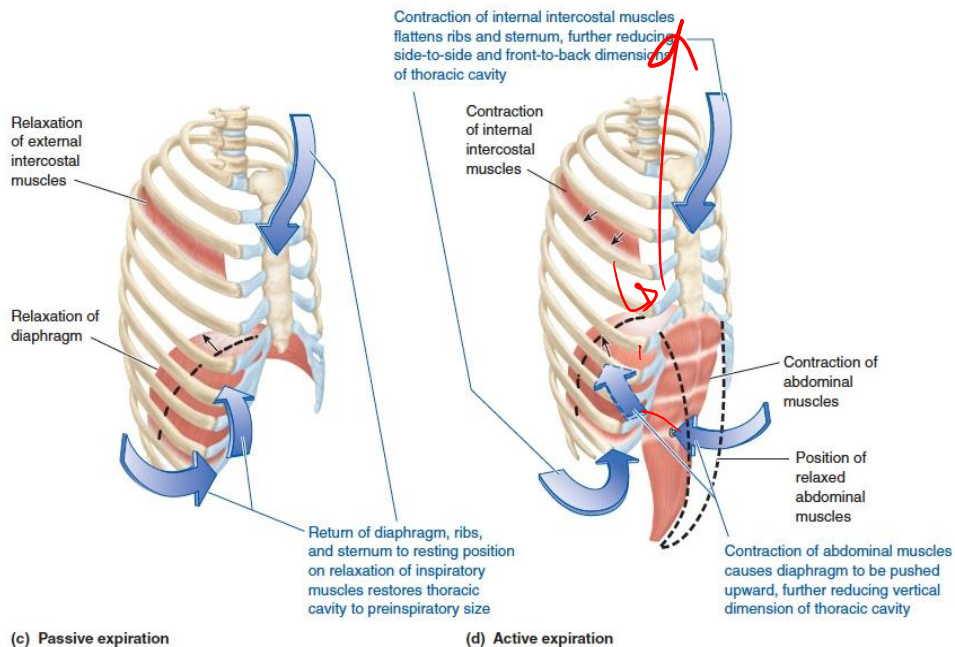
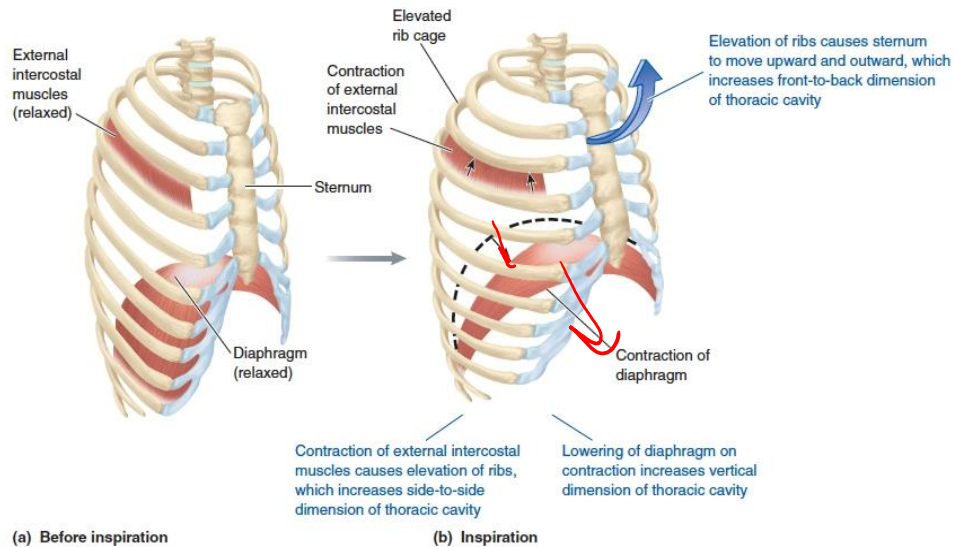
11.4 Air Respirers: Vertebrates



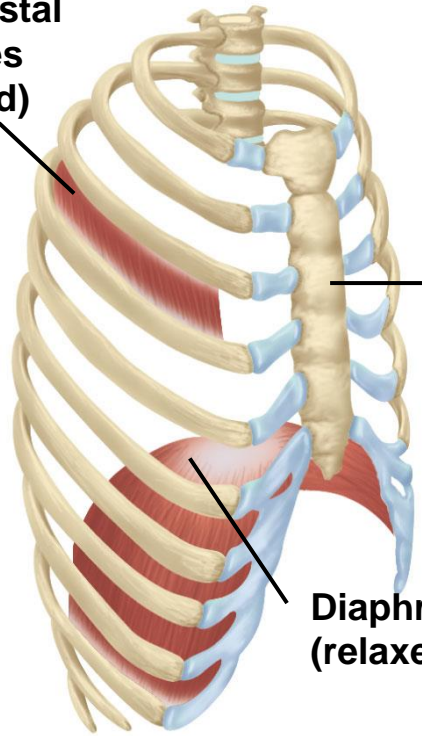
■ Respiratory cycle

- **Inspiration** involves **contraction** of inspiratory muscles
 - ✓ • **Diaphragm** contracts downward
 - ✓ • **External intercostal muscles** expand ribs outward, enlarging the thoracic cavity
- **Exhalation** normally involves **relaxation** of inspiratory muscles and **elastic recoil** of chest wall and lungs
- **Active exhalation** involves contraction of **abdominal wall muscles** and **internal intercostal muscles**

11.4 Air Respirers: Vertebrates



External intercostal muscles (relaxed)



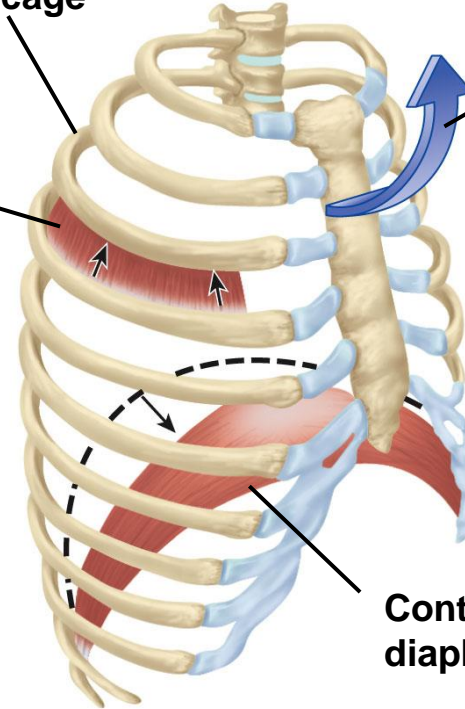
Diaphragm (relaxed)

Contraction of external intercostal muscles causes elevation of ribs, which increases side-to-side dimension of thoracic cavity

Elevated rib cage

Contraction of external intercostal muscles

Sternum



Contraction of diaphragm

Lowering of diaphragm on contraction increases vertical dimension of thoracic cavity

Elevation of ribs causes sternum to move upward and outward, which increases front-to-back dimension of thoracic cavity

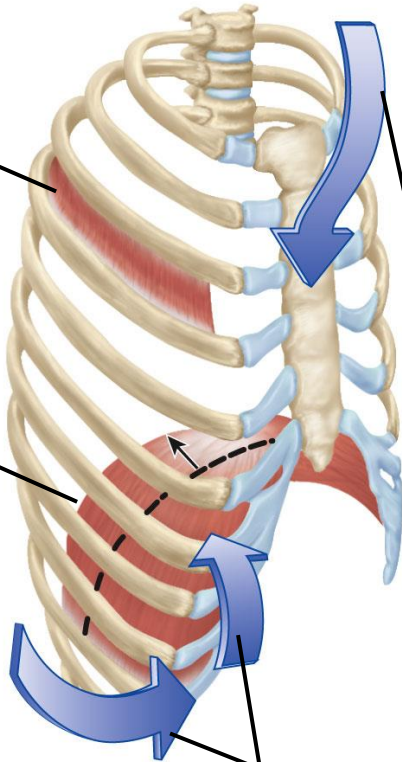
(a) Before inspiration

(b) Inspiration

Contraction of internal intercostal muscles flattens ribs and sternum, further reducing side-to-side and front-to-back dimensions of thoracic cavity

Relaxation of external intercostal muscles

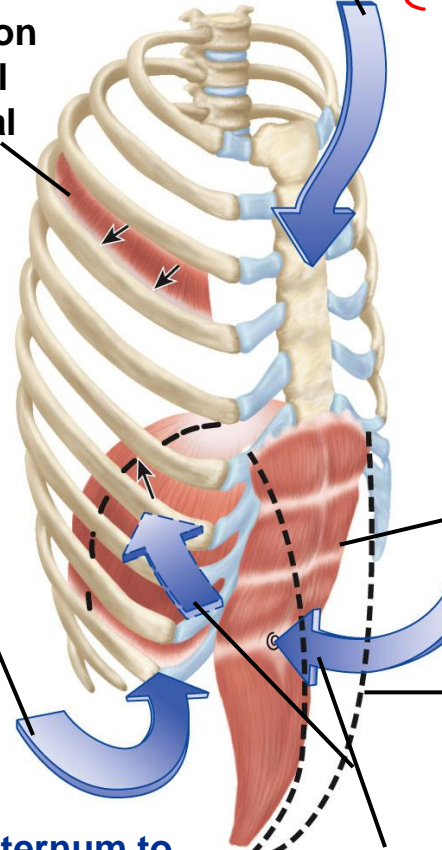
Relaxation of diaphragm



Return of diaphragm, ribs, and sternum to resting position on relaxation of inspiratory muscles restores thoracic cavity to preinspiratory size

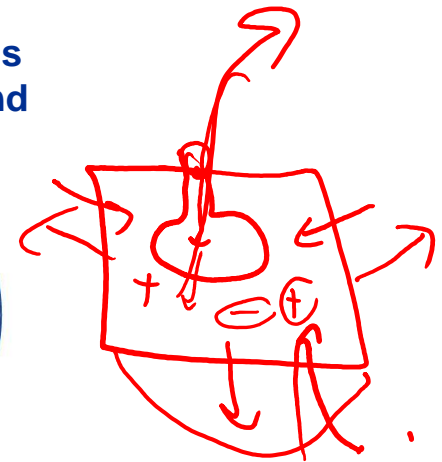
(c) Passive expiration

Contraction of internal intercostal muscles



Contraction of abdominal muscles causes diaphragm to be pushed upward, further reducing vertical dimension of thoracic cavity

(d) Active expiration



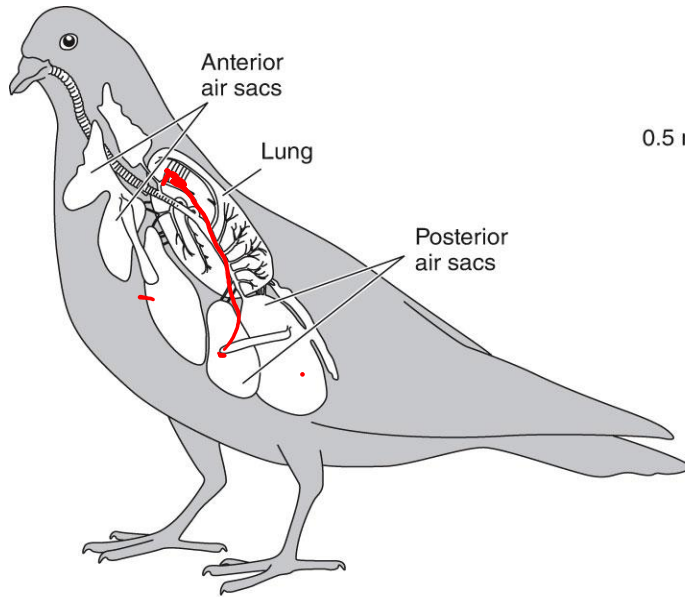
11.4 Air Respirers: Vertebrates



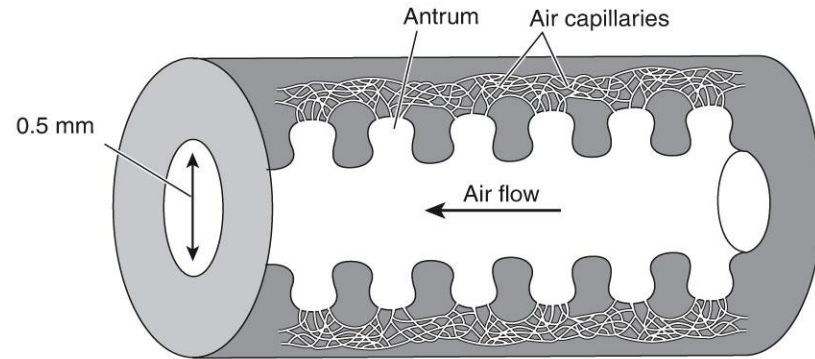
■ Birds

- Complete **separation** of ventilation and gas exchange
- Lungs are **smaller** than in mammals and **inelastic**
- Ventilation of expandable **air sacs** perform tidal function without gas exchange
- Air enters **nasal passages, trachea, bronchi** and **air sacs**
- Bronchi gives rise to **secondary bronchi**
 - Air flows from **dorsobronchi** to **ventrobronchi** through parallel **parabronchi**
- **Air capillaries** branch from **parabronchi**

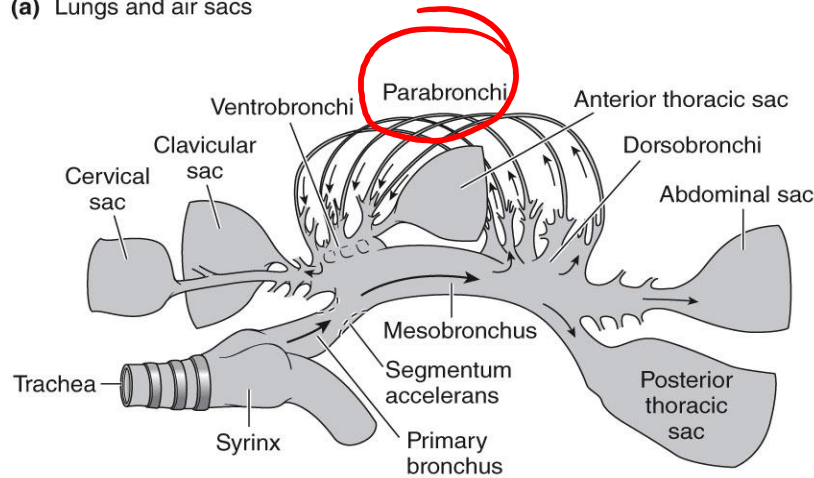
11.4 Air Respirers: Vertebrates



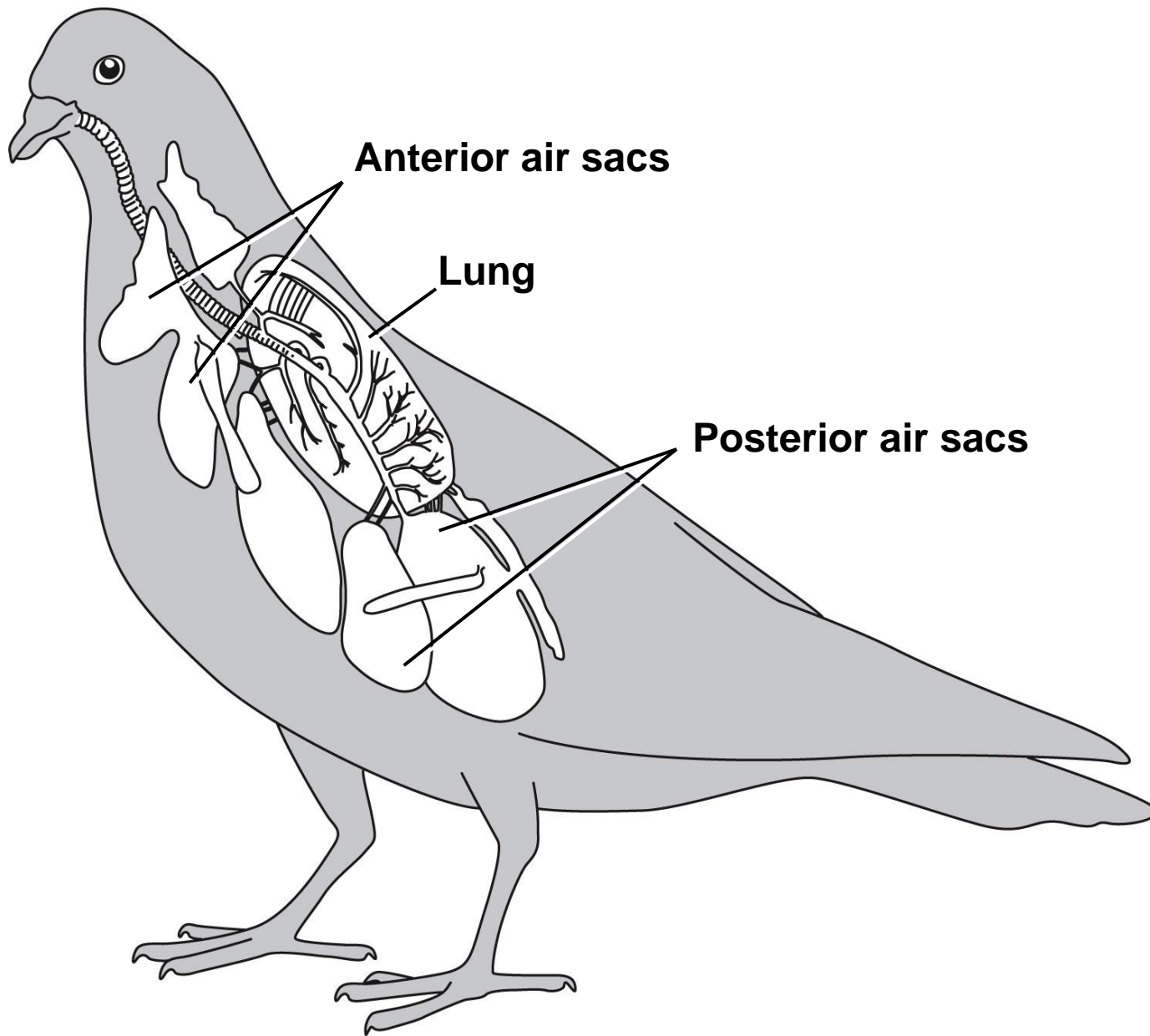
(a) Lungs and air sacs



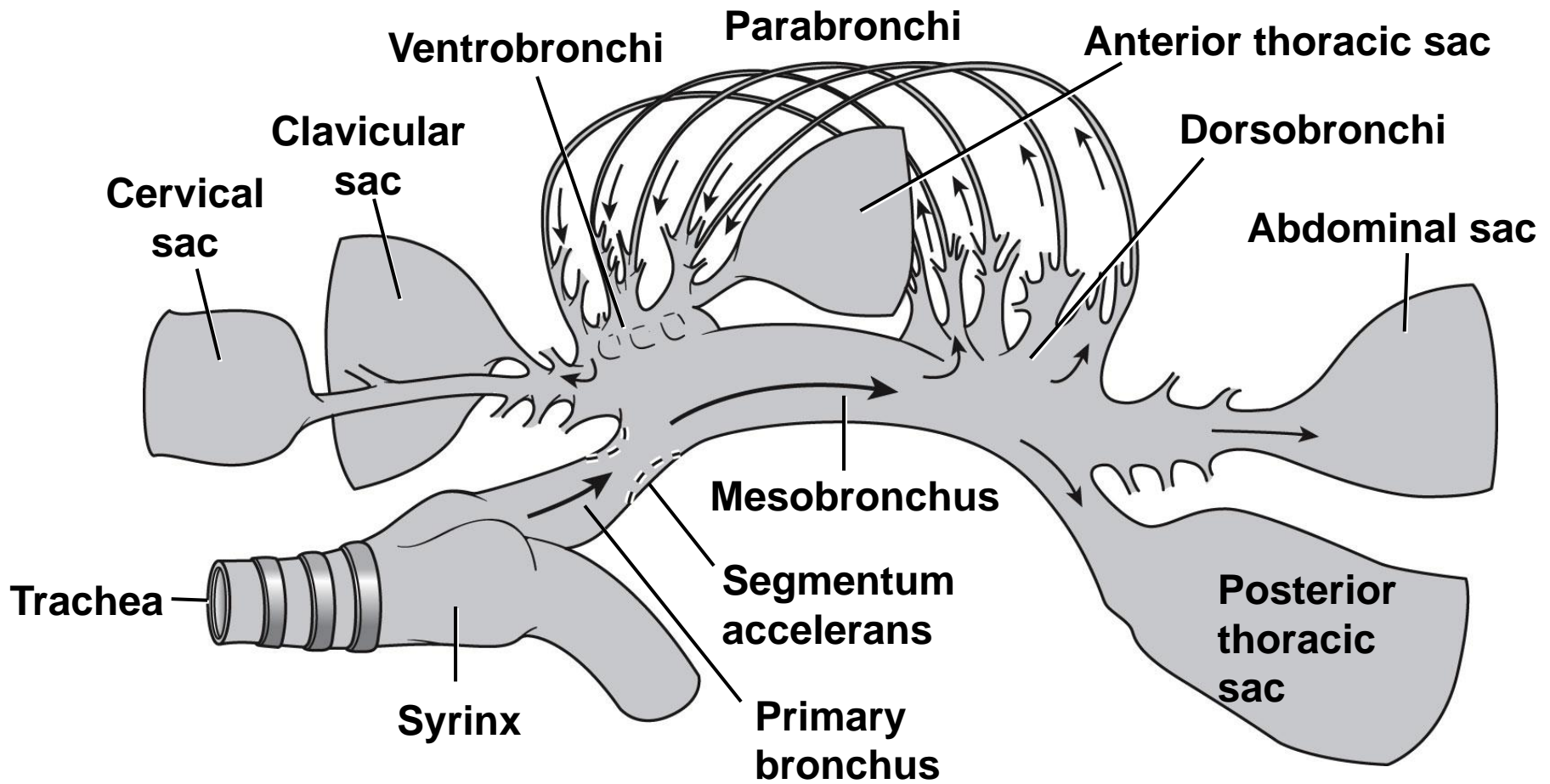
(c) Parabronchus and air capillaries



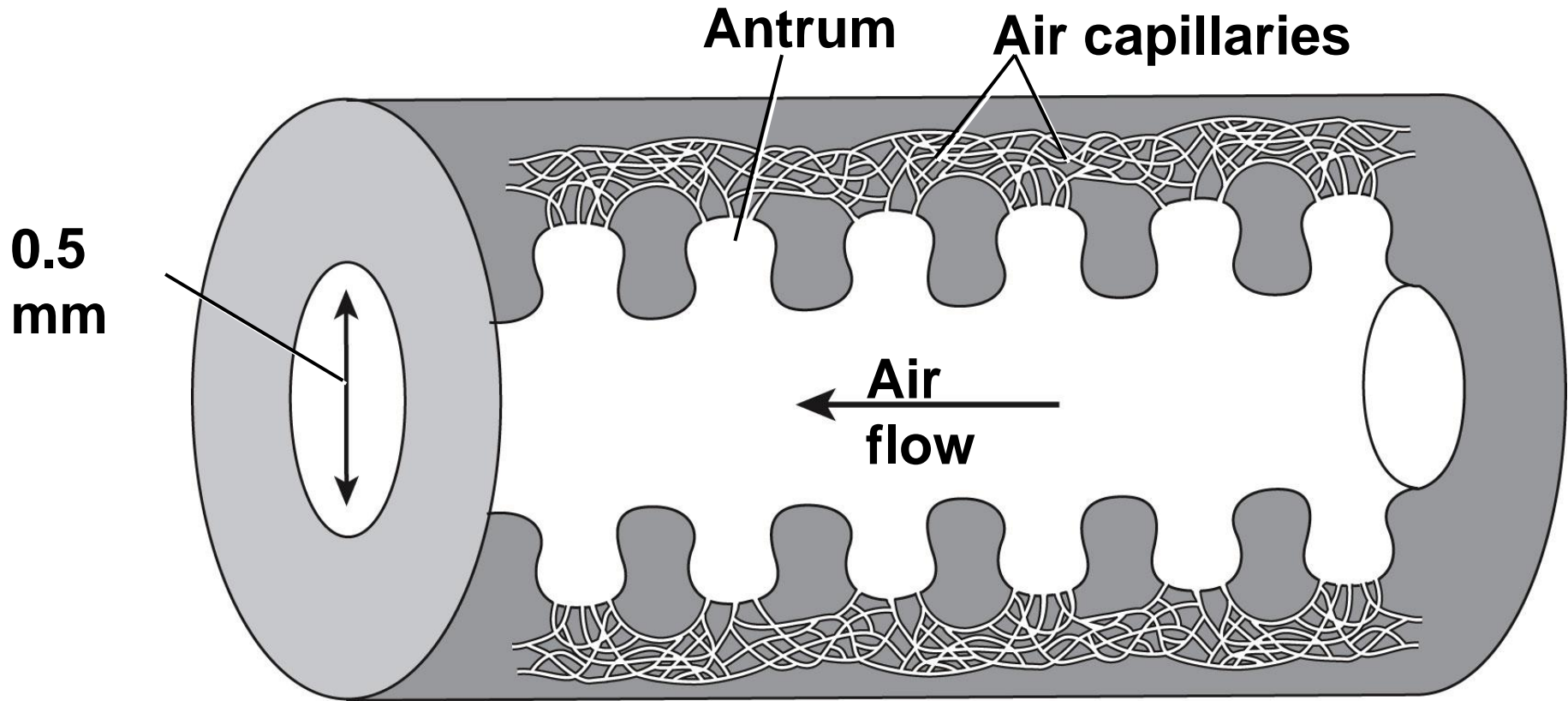
(b) Schematic of air sacs and bronchi showing aerodynamic valve (segmentum accelerans; see text p. 515)



(a) Lungs and air sacs

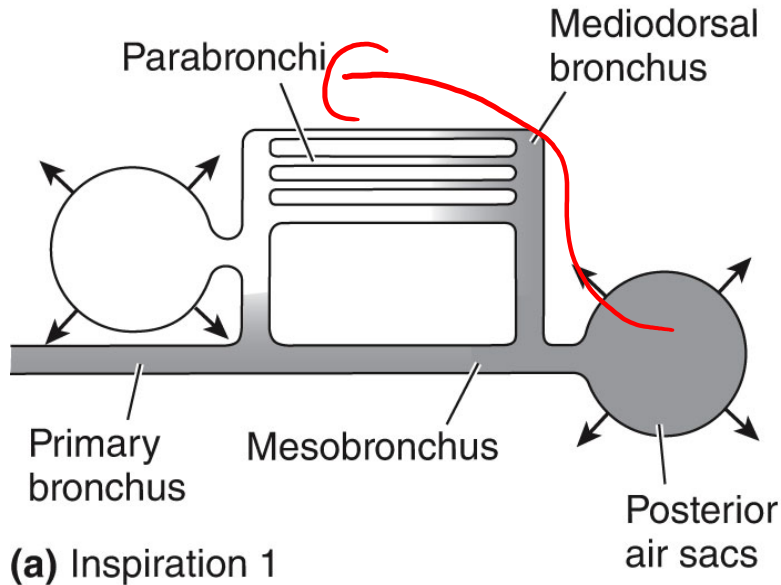


(b) Schematic of air sacs and bronchi showing aerodynamic valve (segmentum accelerans; see text p. 515)

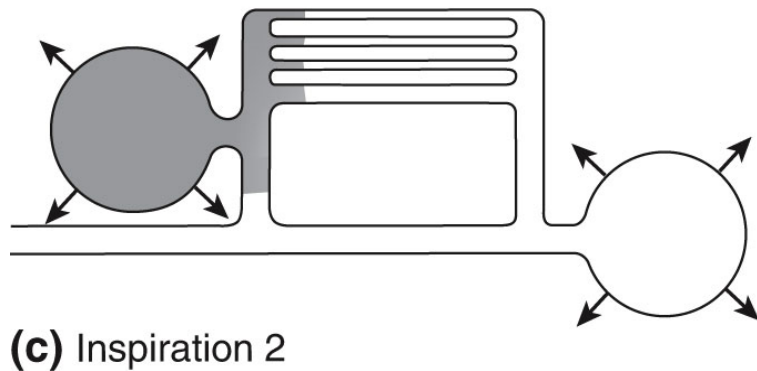
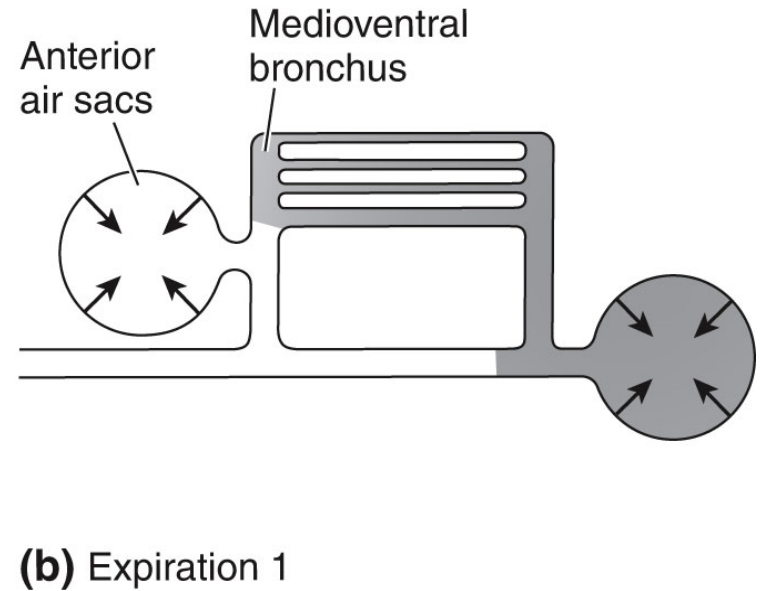


(c) Parabronchus and air capillaries

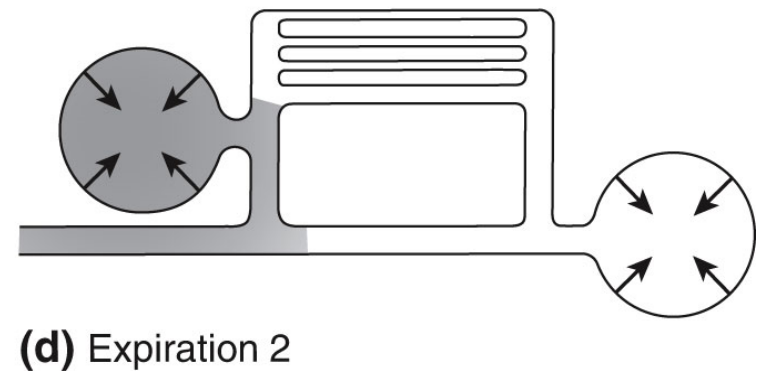
11.4 Air Respirers: Vertebrates



Cycle 1



Cycle 2



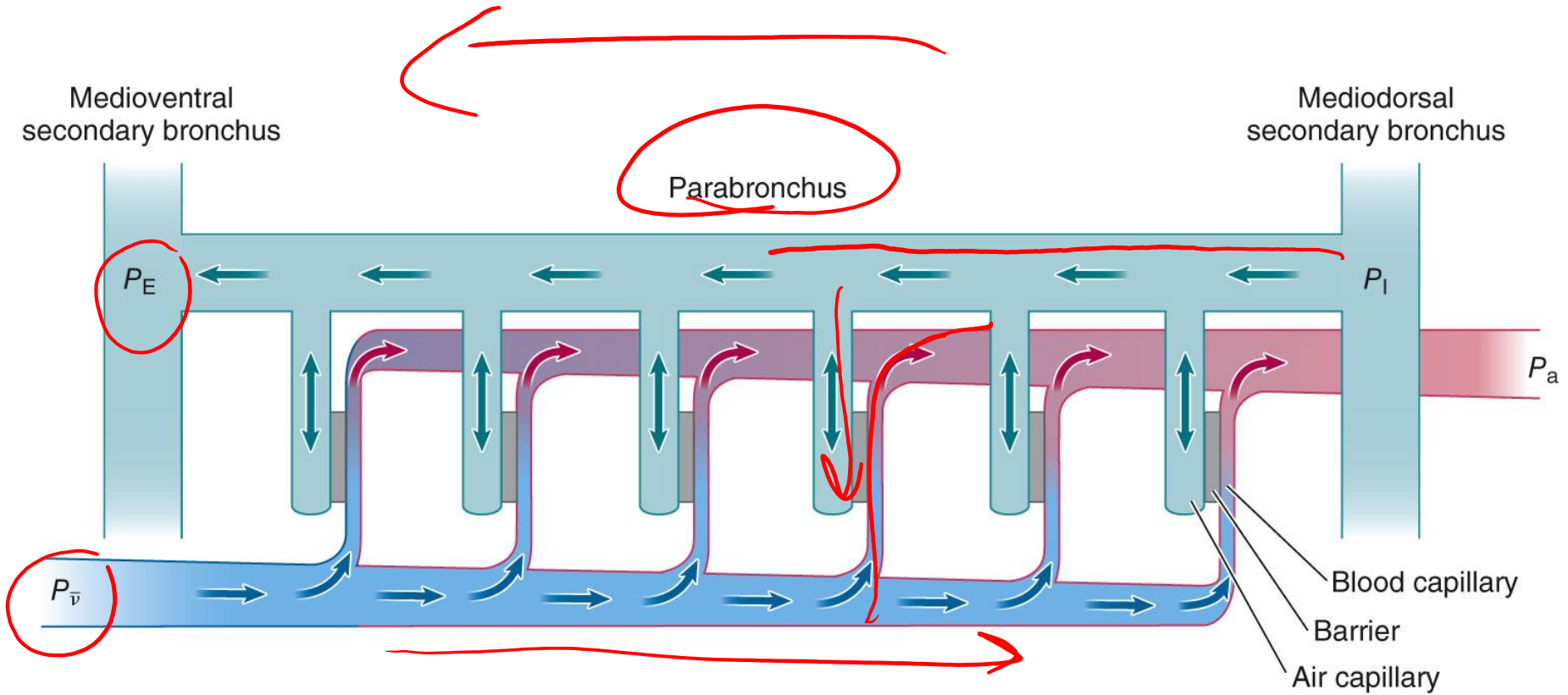
11.4 Air Respirers: Vertebrates



▪ **Air capillaries vs. alveoli**

- Air capillaries are **narrower** than alveoli
- Epithelial cells are **thinner**
- **Flow-through** design
- **Rigid** -- resist damage
- **Greater blood volume** in pulmonary capillaries
- **Crosscurrent blood flow** in parabronchi provides more efficient uptake of O_2

11.4 Air Respirers: Vertebrates



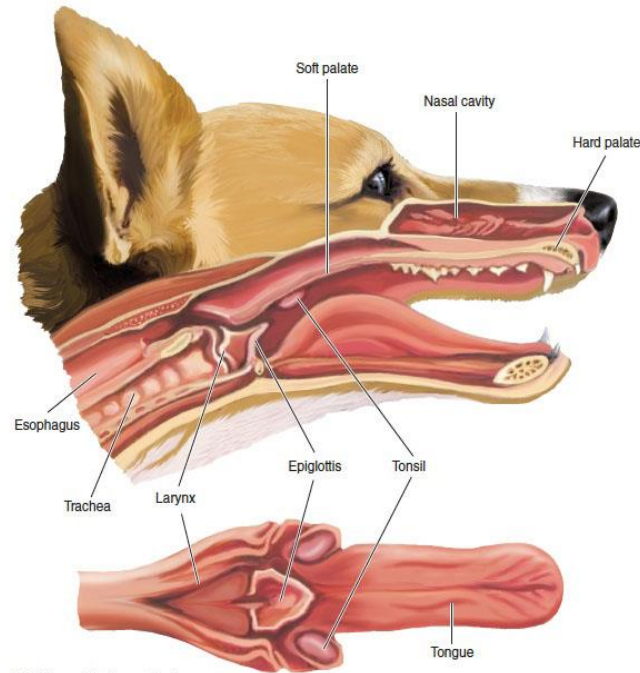
11.4 Air Respirers: Vertebrates



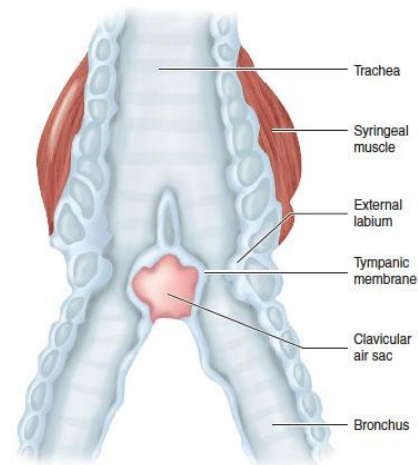
▪ **Nonrespiratory functions** of aerial respiratory systems

- Regulation of **water loss** and **heat exchange**
 - Moistening of inspired air is essential to prevent desiccation of respiratory surfaces
- **Improved venous return** -- respiratory pump
- • **Acid-base balance**
- • **Defense** against inhaled foreign matter
- **Removal, modification, activation or inactivation** of substances passing through the pulmonary circulation
- **Olfaction**
- **Vocalization**
 - **Larynx** in mammals
 - **Syrinx** in birds -- the number of syringial muscles relates to complexity of song

11.4 Air Respirers: Vertebrates



(a) Mammalian larynx (dog)



(b) Bird syrinx

11.5 Breathing: Respiratory Mechanics in Mammals



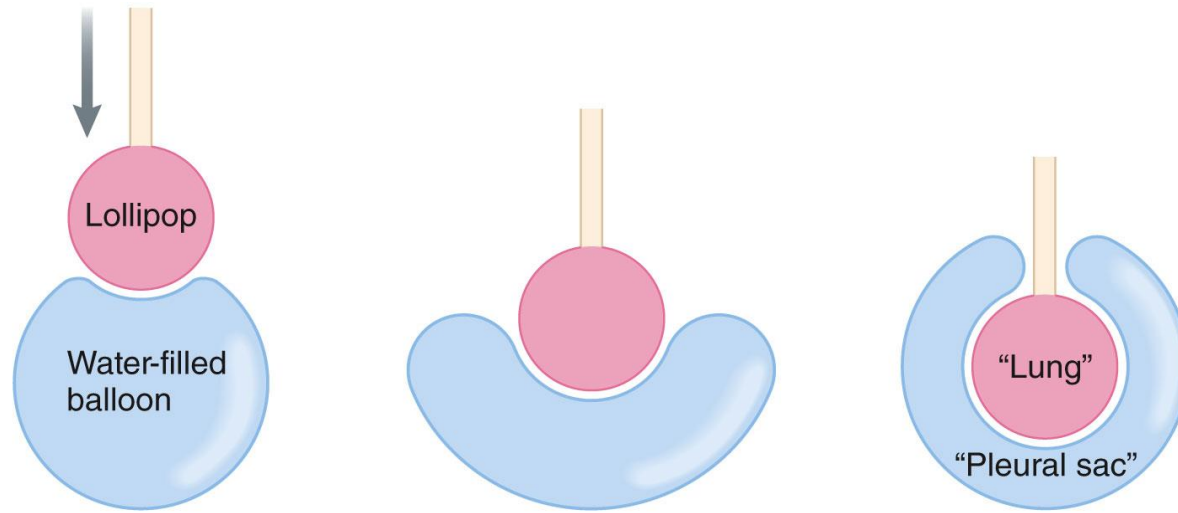
- Air flows according to **pressure gradients**
 - **Atmospheric pressure** (760 mmHg at sea level)
 - Decreases with increasing altitude
 - **Intra-alveolar pressure** -- seeks equilibrium with atmospheric pressure
 - **Intrapleural pressure**
 - Usually less than atmospheric pressure
 - (4 mmHg less on average)

11.5 Breathing: Respiratory Mechanics in Mammals

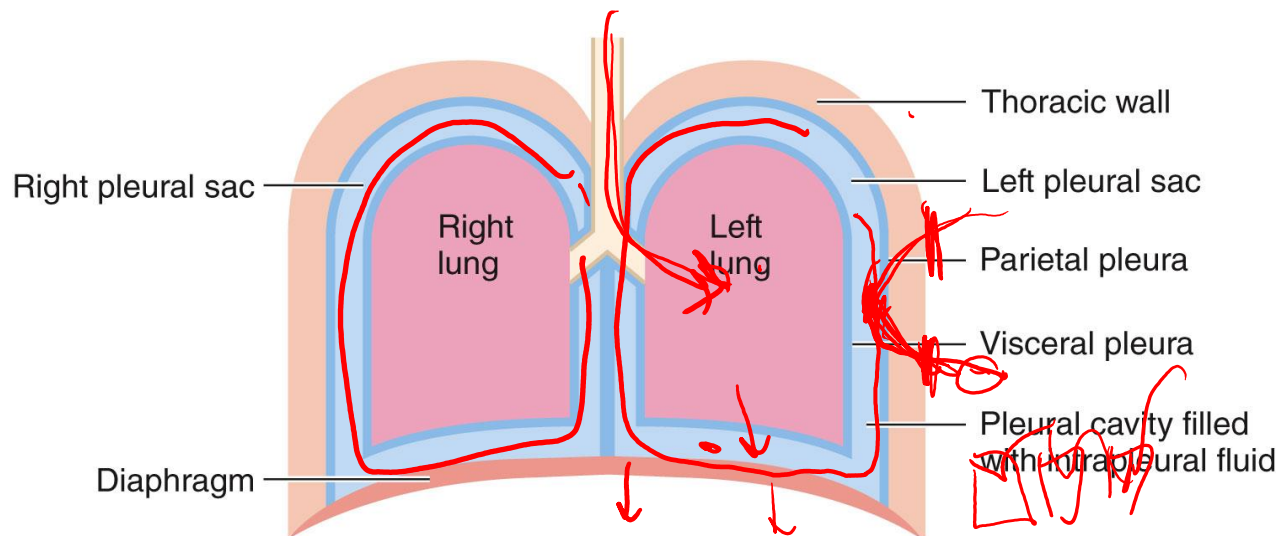


- Influence of intrapleural pressure
 - **Pleural sac** separates lungs from the thoracic wall
 - **Pleural cavity** contains **intrapleural fluid**
 - Polar water molecules in intrapleural fluid resist being pulled apart -- hold pleural surfaces together
 - Lungs are stretched and follow movements of the chest wall because of **transmural pressure gradient**
 - **Intrapleural pressure** and **intra-alveolar pressure decrease** when the chest wall expands during **inspiration** and **increase** during **expiration**
 - **Boyle's law** -- At any constant temperature, the pressure exerted by a gas varies inversely with the volume of the gas

11.5 Breathing: Respiratory Mechanics in Mammals

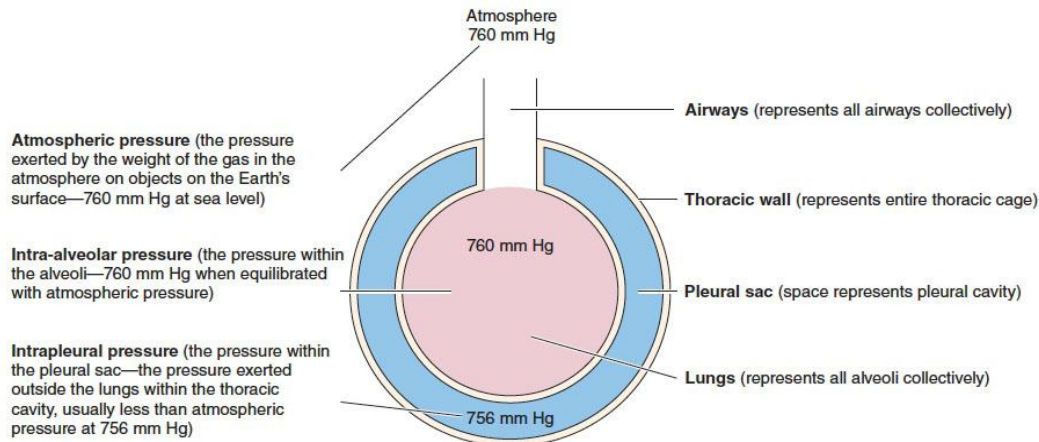


(a) Analogy of relationship between lung and pleural sac

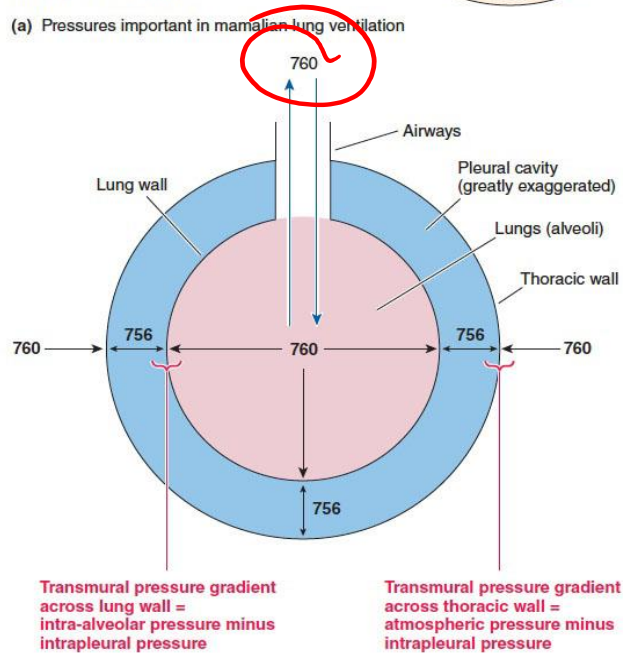


(b) Relationship of lungs to pleural sacs, thoracic wall, and diaphragm

11.5 Breathing: Respiratory Mechanics in Mammals

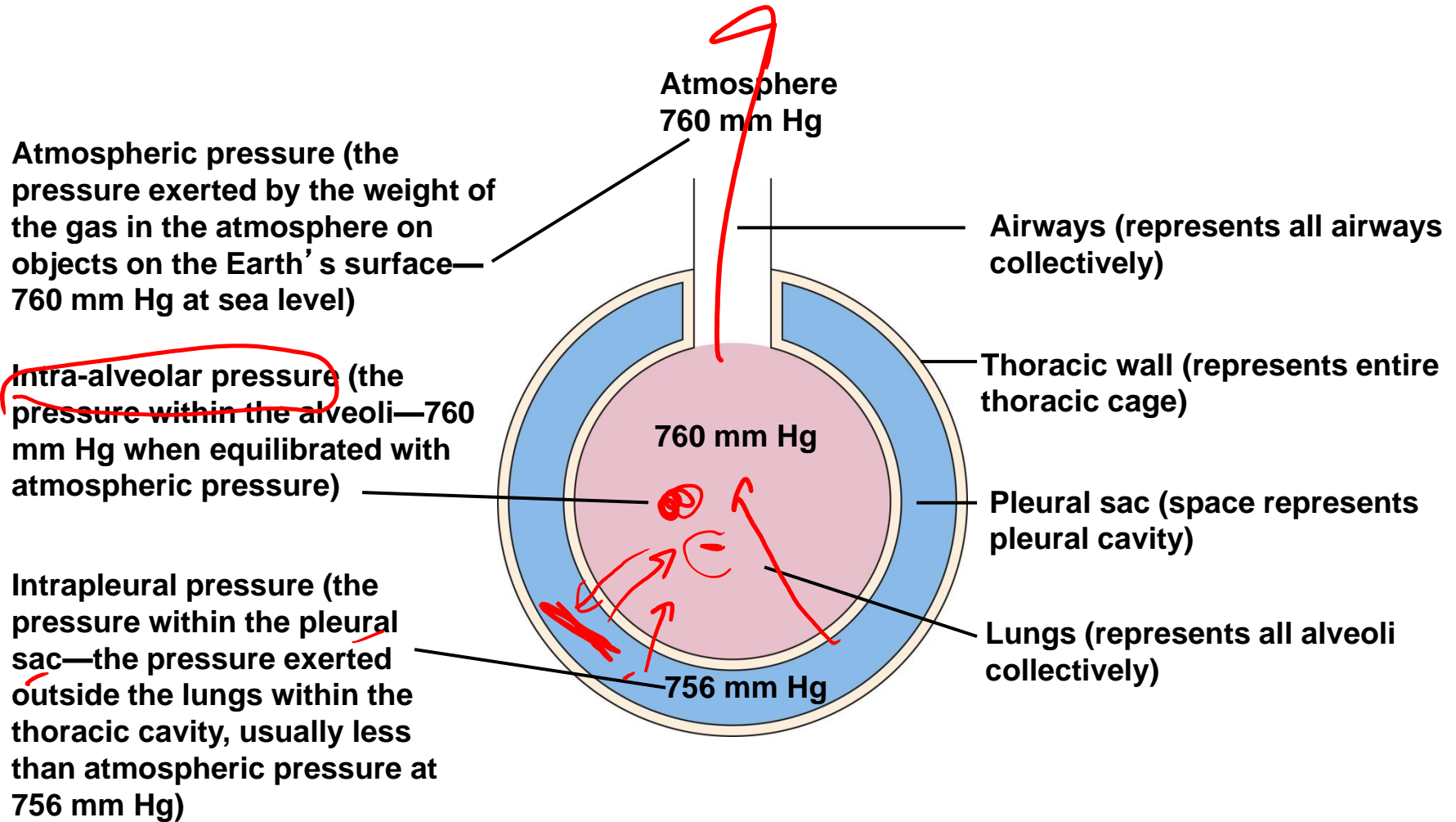


(a) Pressures important in mammalian lung ventilation

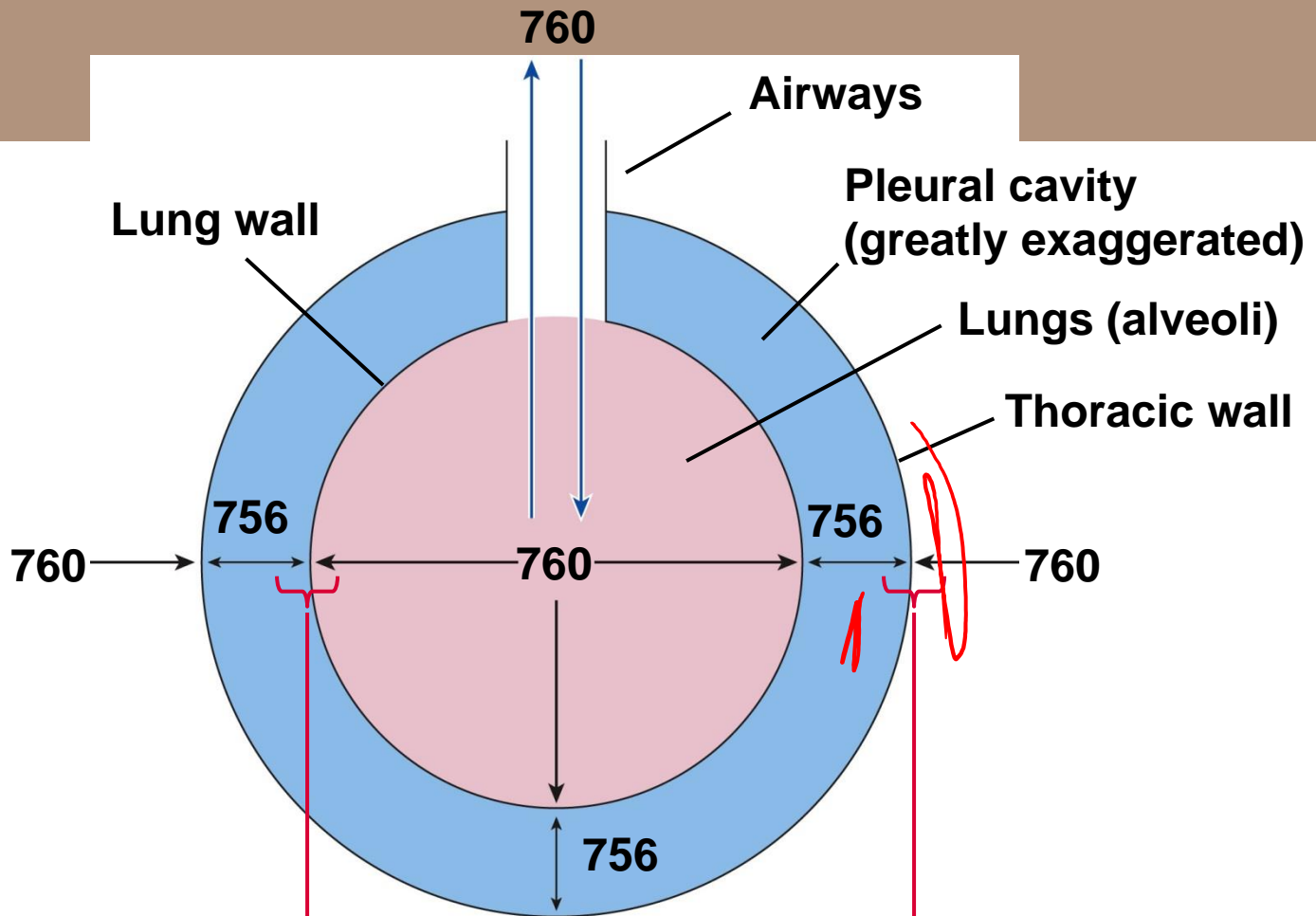


Numbers are mm Hg pressure.

(b) Transmural pressure gradient



(a) Pressures important in mammalian lung ventilation



~~Transmural pressure gradient across lung wall = intra-alveolar pressure minus intrapleural pressure~~

Transmural pressure gradient across thoracic wall = atmospheric pressure minus intrapleural pressure

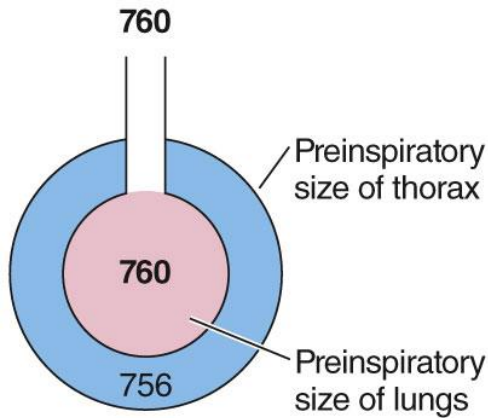
Numbers are mm Hg pressure.

(b) Transmural pressure gradient

11.5 Breathing: Respiratory Mechanics in Mammals



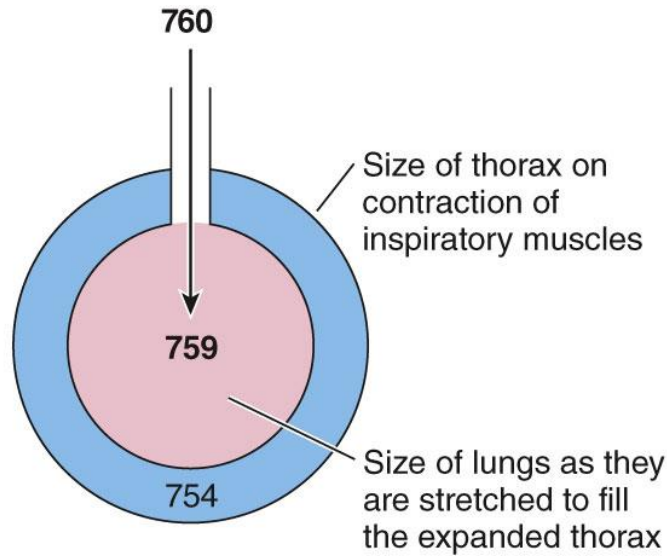
Equilibrated;
no net movement of air



Before inspiration

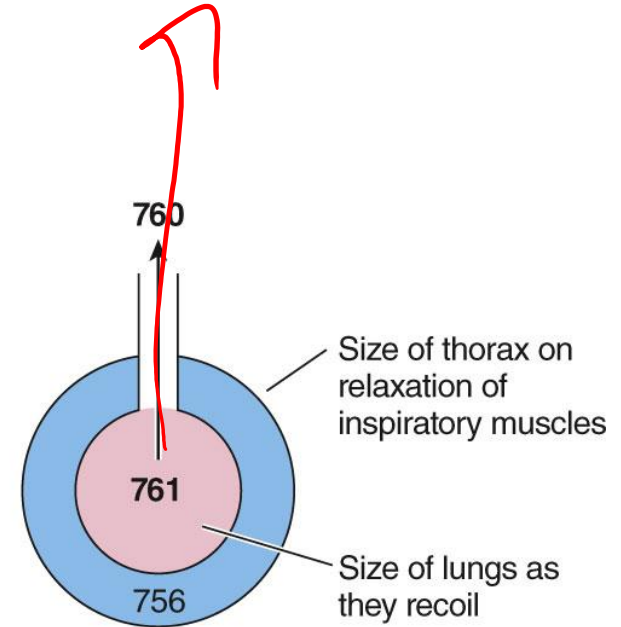
Numbers are mm Hg pressure.

(a)



During inspiration

(b)



During expiration

(c)

11.5 Breathing: Respiratory Mechanics in Mammals



- **Airway resistance** is normally low
 - Depends on **radius** of the conducting system
 - Pressure gradients of 1 - 2 mmHg produce adequate rates of air flow
 - Diseases causing narrowing of airways greatly **increase resistance** and the **work of breathing**
 - **Chronic obstructive pulmonary diseases (COPD)** -- chronic bronchitis, asthma, emphysema
 - **Equine restrictive lung diseases**



11.5 Breathing: Respiratory Mechanics in Mammals

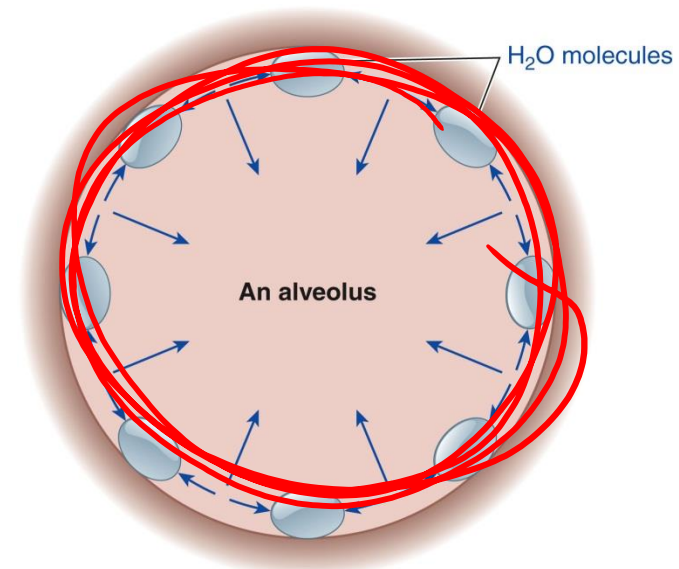


- **Elasticity** of lungs depends on **connective tissue** and **alveolar surface tension**

- Pulmonary connective tissue contains large amounts of **elastin** -- rebound after being stretched

- Alveolar surface tension is reduced by **pulmonary surfactant**

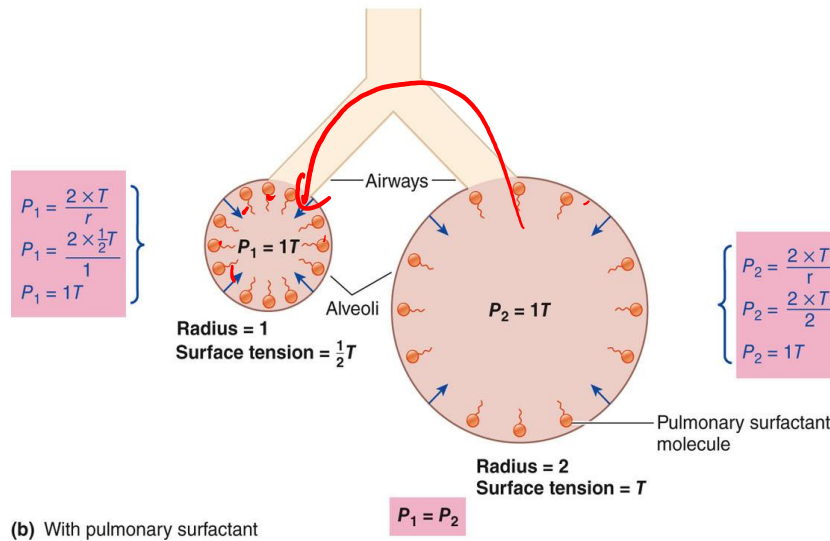
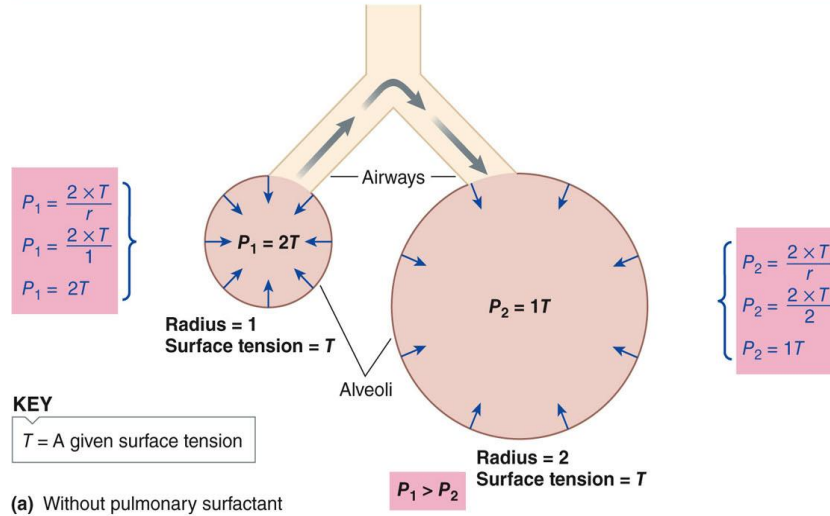
- Increases pulmonary compliance
- Reduces the lungs' tendency to recoil
- Prevents collapse of smaller alveoli (predicted by LaPlace's law: $P = 2T/r$)



11.5 Breathing: Respiratory Mechanics in Mammals



Law of LaPlace:
 Magnitude of inward-directed pressure (P) in a bubble (alveolus) = $\frac{2 \times \text{Surface tension } (T)}{\text{Radius } (r) \text{ of bubble (alveolus)}}$





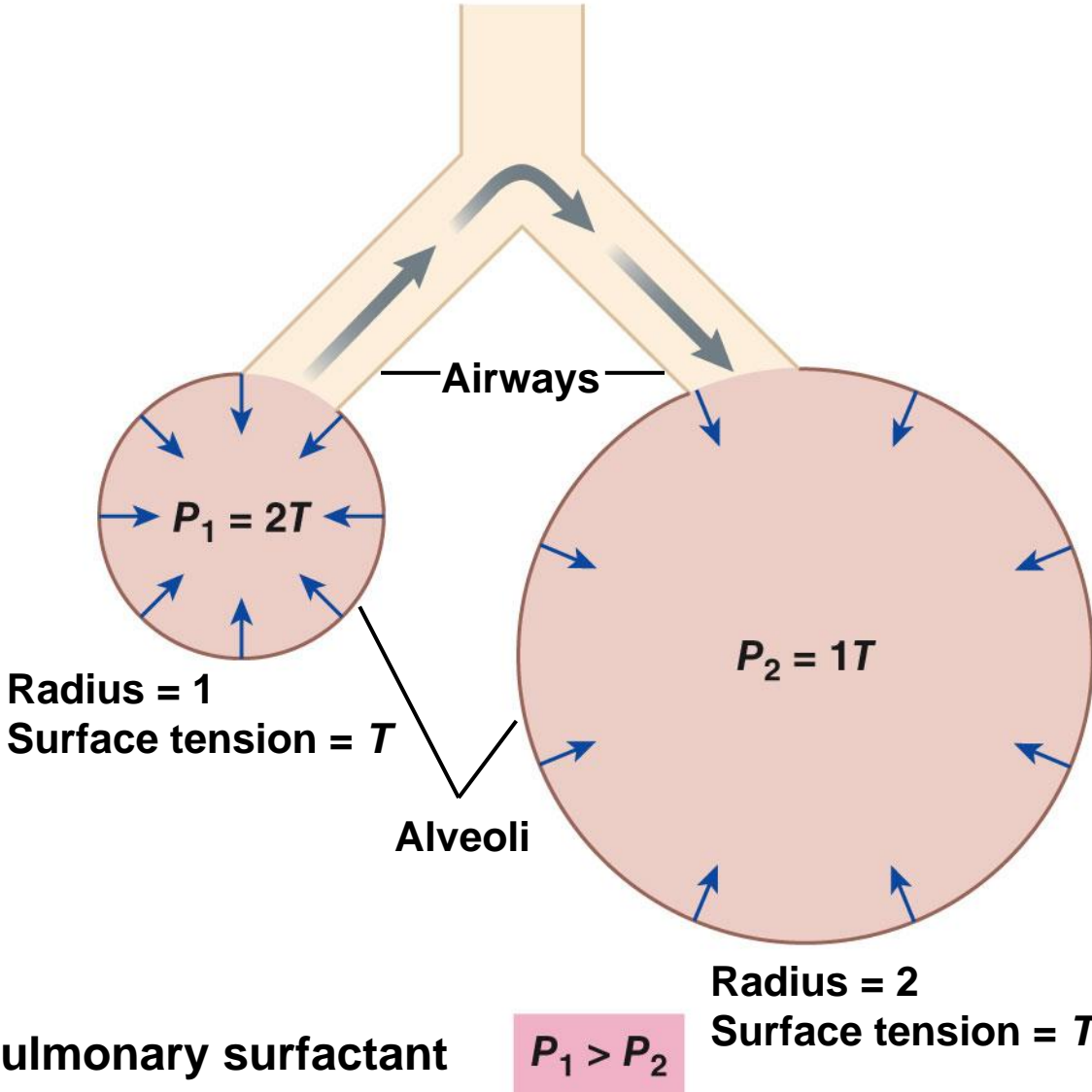
Law of LaPlace:

Magnitude of inward-directed pressure (P) in a bubble (alveolus) = $\frac{2 \times \text{Surface tension } (T)}{\text{Radius } (r) \text{ of bubble (alveolus)}}$

$$P_1 = \frac{2 \times T}{r}$$

$$P_1 = \frac{2 \times T}{1}$$

$$P_1 = 2T$$



$$P_2 = \frac{2 \times T}{r}$$

$$P_2 = \frac{2 \times T}{2}$$

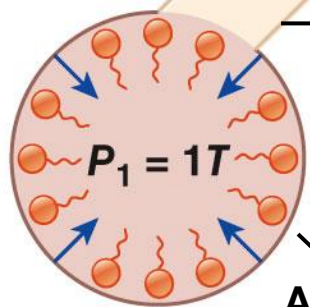
$$P_2 = 1T$$

$$P_1 = \frac{2 \times T}{r}$$

$$P_1 = \frac{2 \times \frac{1}{2}T}{1}$$

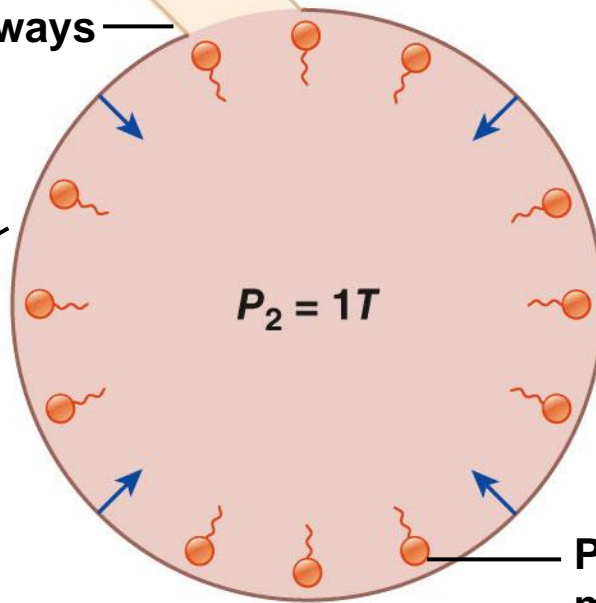
$$P_1 = 1T$$

Radius = 1
Surface tension = $\frac{1}{2} T$



Airways

Alveoli



Radius = 2
Surface tension = T

Pulmonary surfactant molecule

$$P_2 = \frac{2 \times T}{r}$$

$$P_2 = \frac{2 \times T}{2}$$

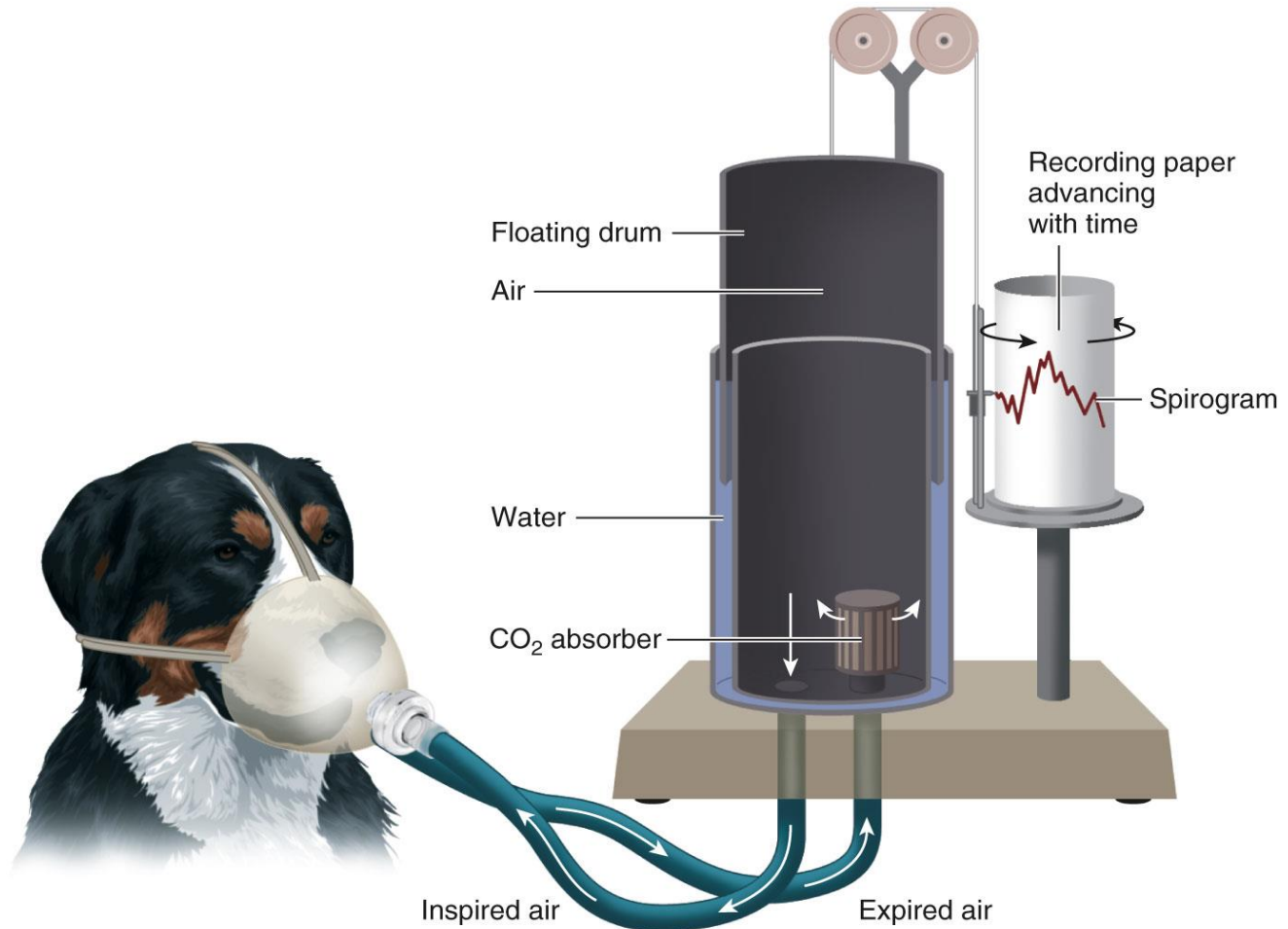
$$P_2 = 1T$$

$$P_1 = P_2$$

(b) With pulmonary surfactant

11.6 Breathing: Lung Volumes in Mammals

- Measurement of lung volumes with a **spirometer**

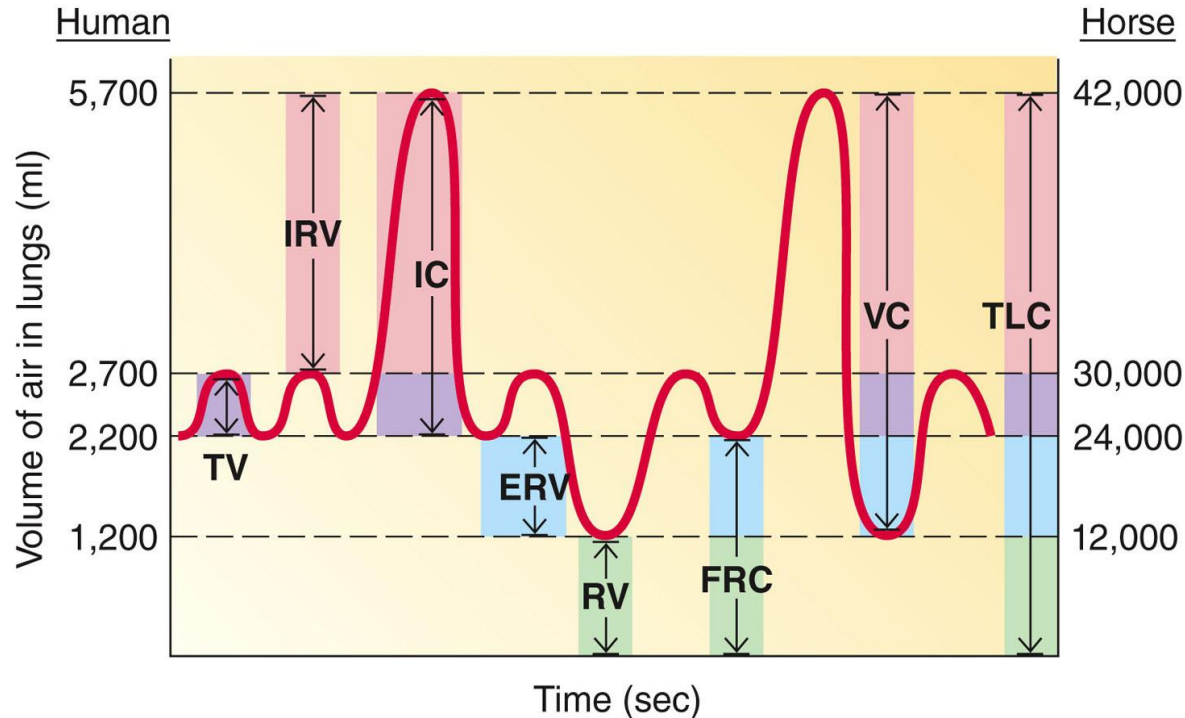


11.6 Breathing: Lung Volumes in Mammals



- Lung volumes and capacities
 - **Total lung capacity (TLC)** = Maximum amount of air that the lungs can hold (~5.7 L in humans)
 - **Tidal volume (TV)** = Volume of air entering or leaving the lungs during a single breath (resting TV ~ 0.5 ml)
 - **Functional residual capacity (FRC)** = Volume of air in the lungs at the end of a normal passive expiration (~2.2 L)
 - **Residual volume (RV)** = Minimum volume of air remaining in the lungs after a maximal expiration (~1.2 L)
 - **Vital capacity (VC)** = Maximum volume of air that can be moved out during a single breath following maximal inspiration (~4.5 L)

11.6 Breathing: Lung Volumes in Mammals



	Human	Horse
TV = Tidal volume	500 mL	6,000 mL
IRV = Inspiratory reserve volume	3,000 mL	12,000 mL
IC = Inspiratory capacity	3,500 mL	18,000 mL
ERV = Expiratory reserve volume	1,000 mL	12,000 mL
RV = Residual volume	1,200 mL	12,000 mL
FRC = Functional residual capacity	2,200 mL	24,000 mL
VC = Vital capacity	4,500 mL	30,000 mL
TLC = Total lung capacity	5,700 mL	42,000 mL

(b) Spirogram and table of values for adult male human and horse

11.6 Breathing: Lung Volumes in Mammals



- **Pulmonary ventilation** (minute ventilation)

Pulmonary ventilation = tidal volume x respiratory rate
(L/min) (L/breath) (breaths/min)

- Scales with **body size**

- **Tidal volume** increases with increasing body size (m_b), while **respiratory rate** decreases with increasing body size:

$$TV = 0.0062m_b^{1.01}$$

$$RR = 53.5m_b^{-0.26}$$

11.6 Breathing: Lung Volumes in Mammals



- Please note some significant errors on page 523

3. Functional Reserve Capacity (FRC)

Pulmonary ventilation = tidal volume x respiratory rate
(L/min) (L/breath) (breaths/min)

11.6 Breathing: Lung Volumes in Mammals



Animal at Rest	Pulmonary Ventilation (PV)	=	Resting Tidal Volume (rTV)	×	Respiratory Rate
Rat (0.22 kg)	0.12 L/min	=	0.001 L/breath	×	120 breaths/min
Human (70 kg)	6.0 L/min	=	0.4 L/breath	×	15 breaths/min
Giraffe (400 kg)	30 L/min	=	3.3 L/breath	×	9 breaths/min
Horse (450 kg)	72 L/min	=	6 L/breath	×	12 breaths/min
Elephant (7,000 kg)	235 L/min	=	47 L/breath	×	5 breaths/min
Active Animals			Active TV		
Human, fast run:	150 L/min	=	2.5 L/breath	×	60 breaths/min
Horse, fast trot:	1,500 L/min	=	25 L/breath	×	60 breaths/min

11.6 Breathing: Lung Volumes in Mammals

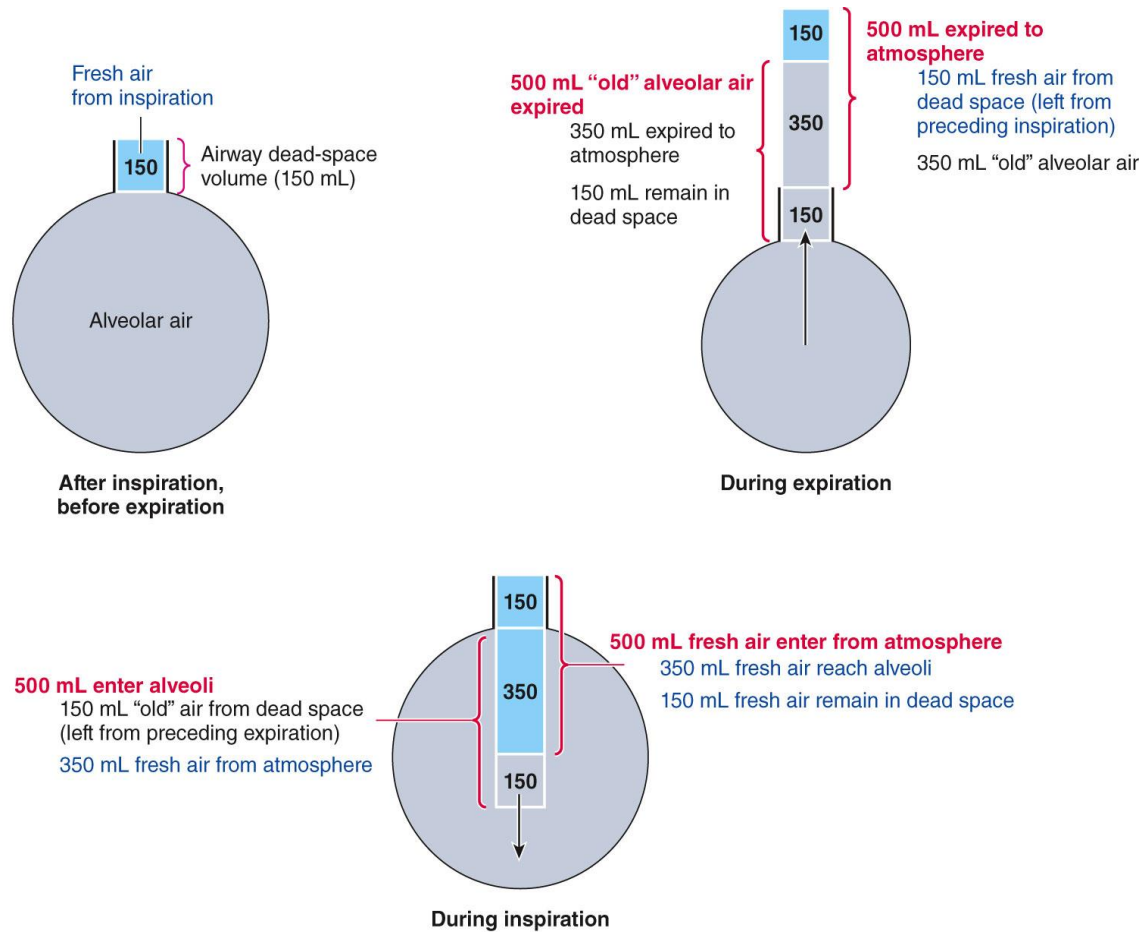


▪ Alveolar ventilation

- When increasing pulmonary ventilation (e.g. during activity), it is advantageous to have a **greater increase in tidal volume** than respiratory rate
 - Not all inspired air reaches the alveoli for gas exchange
 - **Anatomic dead space** = Volume of conducting passages (~0.15 L)
 - **Alveolar ventilation** = Volume of air exchanged between the atmosphere and alveoli per minute

$$\text{Alveolar ventilation} = (\text{TV} - \text{dead space}) \times \text{RR}$$

11.6 Breathing: Lung Volumes in Mammals

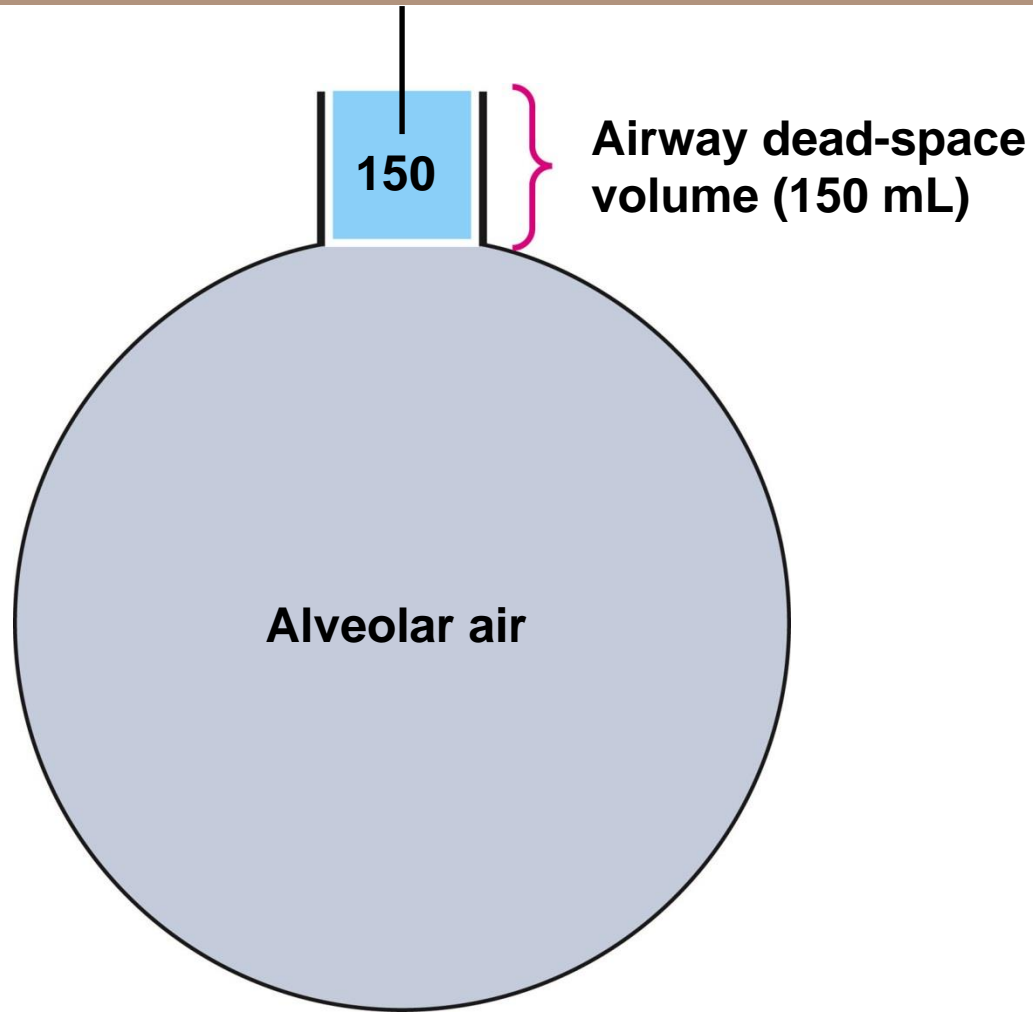


The numbers in the figure represent ml of air.

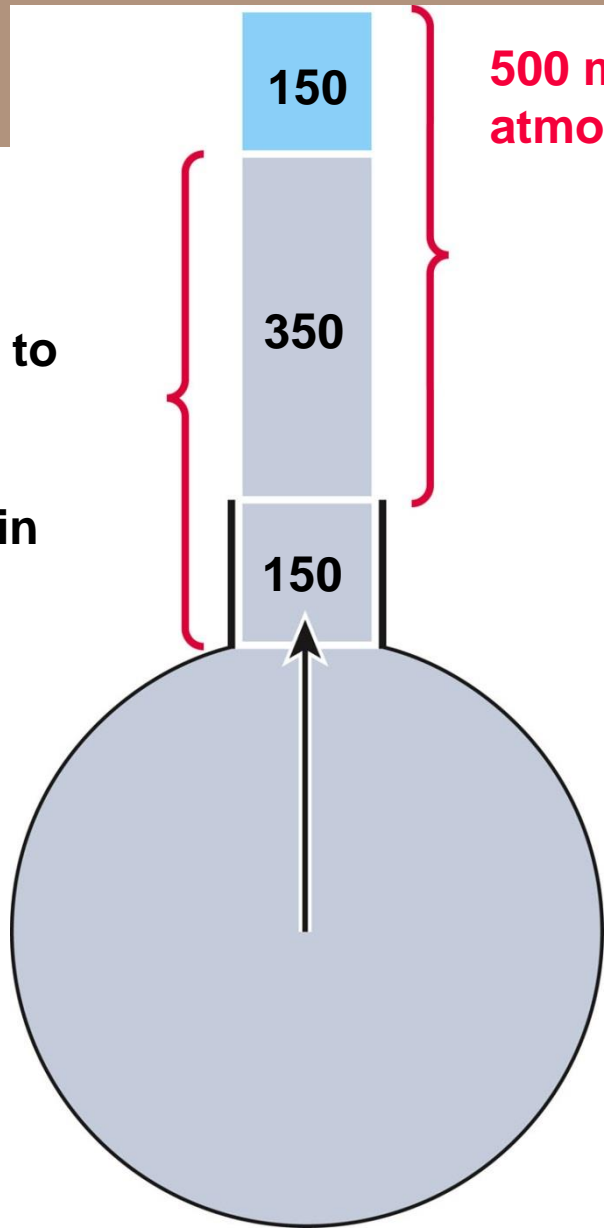
KEY

- "Old" alveolar air that has exchanged O_2 and CO_2 with the blood
- Fresh atmospheric air that has not exchanged O_2 and CO_2 with the blood

Fresh air
from inspiration



After inspiration,
before expiration



500 mL “old” alveolar air expired

350 mL expired to atmosphere

150 mL remain in dead space

500 mL expired to atmosphere

150 mL fresh air from dead space (left from preceding inspiration)

350 mL “old” alveolar air

During expiration

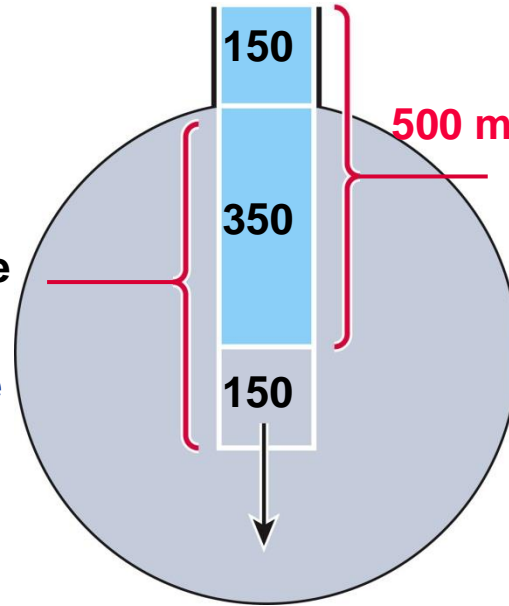




500 mL enter alveoli

**150 mL “old” air from dead space
(left from preceding expiration)**

350 mL fresh air from atmosphere



500 mL fresh air enter from atmosphere

350 mL fresh air reach alveoli

**150 mL fresh air remain in dead
space**

During inspiration

11.7 Breathing: Flow-through versus Tidal Respirers



- Comparative efficiency
 - **Flow-through systems** (e.g. fishes) have much **lower dead-space** volumes than tidal systems
 - **Partial flow-through systems** in **birds** have **higher dead-space volumes**
 - Due to the larger size of the trachea
 - To compensate, a bird has a **higher TV** and **lower RR** than a mammal of comparable size
 - Only **2% of total energy** is expended on quiet breathing in mammals
 - 25-fold **increase in energy requirement** for pulmonary ventilation during **strenuous activity** increases percentage to 5%
 - ~20% of total energy is expended on respiration in **fish**

11.7 Breathing: Flow-through versus Tidal Respirers



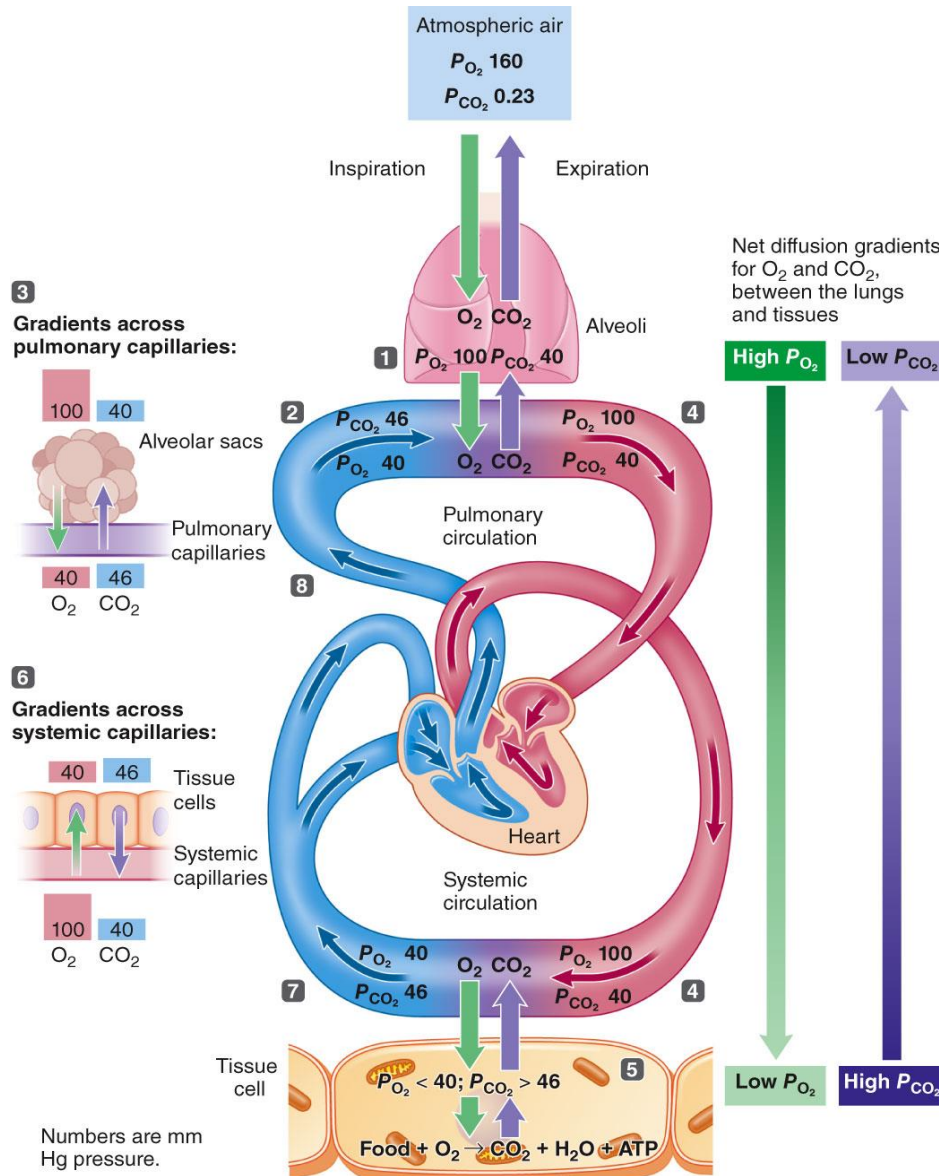
- Comparative efficiency
 - The tidal lung of mammals can only achieve a blood P_{O_2} equal to that of expired air
 - **25% efficiency** of O_2 extraction from air
 - In **birds** (partially tidal with dead spaces and crosscurrent blood flow), efficiency is 30 - 40%
 - Countercurrent blood flow in **fish, crustaceans and amphibians** yields **90% O_2 extraction efficiency** from water (however, O_2 content is lower in water)

11.8 Gas Exchange at Vertebrate Respiratory Organs and Body Tissues



- Lung air P_{O_2} is lower than inspired atmospheric air
 - **Saturated with water** (partial pressure of water vapor is 47 mmHg at body temperature)
 - Inspired air is **mixed with old air** in dead space
 - Average **alveolar P_{O_2} is 100 mmHg**
 - O_2 diffuses into pulmonary capillary blood about as fast as it is inhaled
 - P_{CO_2} is higher in lung air than in inspired air
 - Average alveolar P_{CO_2} is 40 mmHg

11.8 Gas Exchange at Vertebrate Respiratory Organs and Body Tissues



1 Alveolar P_{O_2} remains relatively high and alveolar P_{CO_2} remains relatively low because a portion of the alveolar air is exchanged for fresh atmospheric air with each breath.

2 In contrast, the systemic venous blood entering the lungs is relatively low in O_2 and high in CO_2 , having given up O_2 and picked up CO_2 at the systemic capillary level.

3 The partial pressure gradients established between the alveolar air and pulmonary capillary blood induce passive diffusion of O_2 into the blood and CO_2 out of the blood until the blood and alveolar partial pressures become equal.

4 The blood leaving the lungs is thus relatively high in O_2 and low in CO_2 . It arrives at the tissues with the same blood-gas content as when it left the lungs.

5 The partial pressure of O_2 is relatively low and that of CO_2 is relatively high in the O_2 -consuming, CO_2 -producing tissue cells.

6 Consequently, partial pressure gradients for gas exchange at the tissue level favor the passive movement of O_2 out of the blood into non-circulatory cells to support their metabolic requirements and also favor the simultaneous transfer of CO_2 into the blood.

7 Having equilibrated with the tissue cells, the blood leaving the tissues is relatively low in O_2 and high in CO_2 .

8 The blood then returns to the lungs to once again fill up on O_2 and dump off CO_2 .

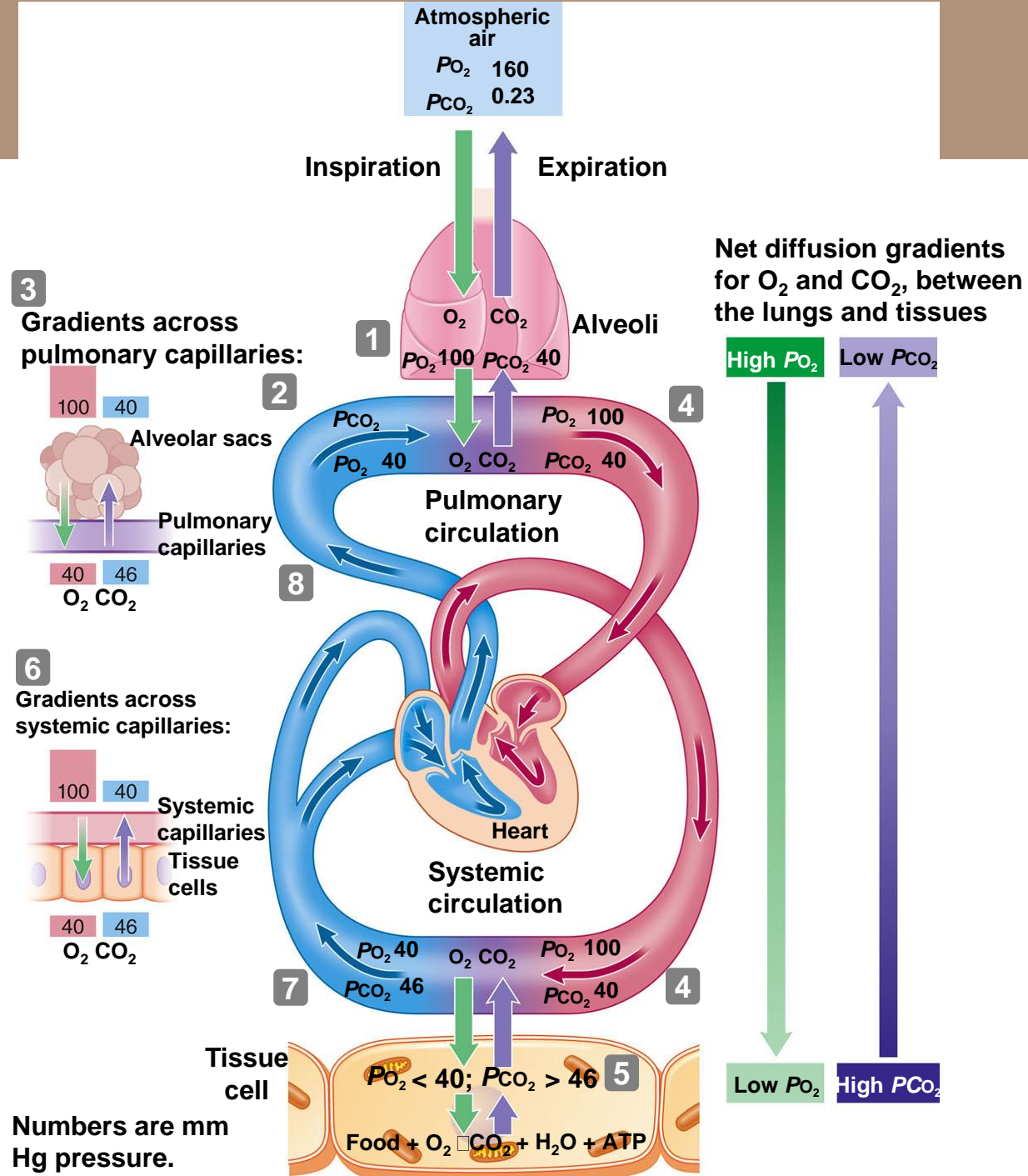


Figure 11-27 p528

11.8 Gas Exchange at Vertebrate Respiratory Organs and Body Tissues



- Gas exchange in the lungs
 - **O₂ diffuses from alveolar air into capillary blood**, equilibrating at P_{O₂} of 100 mmHg
 - **CO₂ diffuses from capillary blood into alveolar air**, equilibrating at P_{CO₂} of 40 mmHg
 - **Increased perfusion** of lung or gill capillaries improves gas exchange
 - **Increased thickness** of gas exchange barriers slows diffusion and **reduces gas exchange**
 - Low or high environmental pH causes **mucification** and **inflammation** of gill epithelium
 - **Pulmonary edema, pulmonary fibrosis** and **pneumonia** interfere with gas exchange in air breathers

11.8 Gas Exchange at Vertebrate Respiratory Organs and Body Tissues



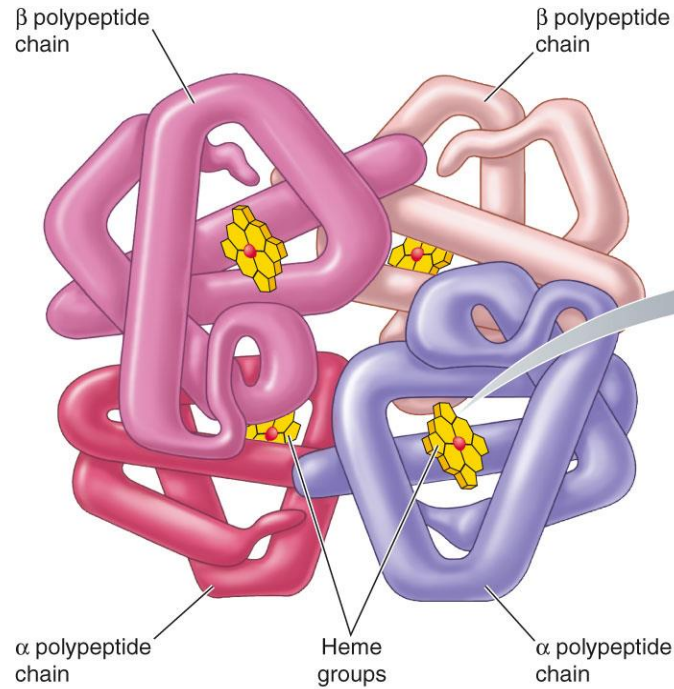
- Gas exchange in the tissues
 - **Cellular P_{O_2} is 40 mmHg and P_{CO_2} is 46 mmHg**
 - **O_2 diffuses from systemic capillary blood into cells, equilibrating at 40 mmHg**
 - **CO_2 diffuses from cells into capillary blood, equilibrating at 46 mmHg**
 - **Increased metabolic activity** will lower capillary blood and tissue P_{O_2} and raise blood and tissue P_{CO_2}

11.9 Circulatory Transport and Gas Exchange

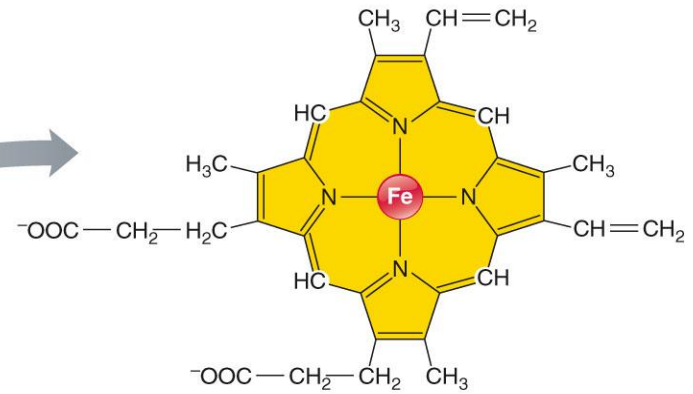


- O_2 is transported in blood bound to **metal-containing respiratory pigments**
 - **Hemoglobin**
 - Annelids, mollusks, crustaceans, vertebrates
 - Highly folded polypeptide chain (**globin**) and iron-containing **heme** group
 - Red when oxygenated; blue when deoxygenated
 - **Hemocyanin**
 - Arthropods, annelids, mollusks
 - Large proteins bound to copper ions
 - Blue when oxygenated; colorless when deoxygenated
 - **Hemerythrin**
 - Brachiopods, sipunculids, one annelid
 - Red iron pigment, not in heme complex
 - <https://en.wikipedia.org/wiki/Hemerythrin>
 - **Chlorocruorin** and **erythrocrutorin**
 - Some annelids
 - Large iron/heme proteins; green or red
 - <https://en.wikipedia.org/wiki/Chlorocruorin>

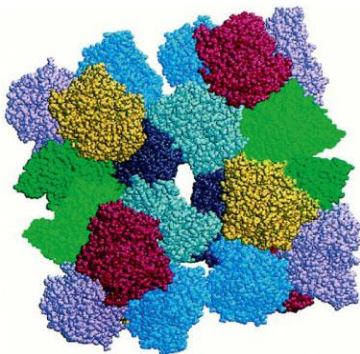
11.9 Circulatory Transport and Gas Exchange



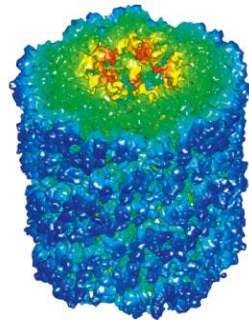
(a) Hemoglobin molecule



(b) Iron-containing heme group



(c)

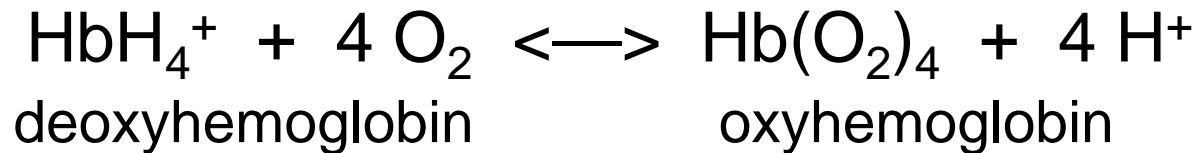


(d)

11.9 Circulatory Transport and Gas Exchange



- O_2 transport in vertebrates
 - Amount of **O_2 dissolved** is **proportional to P_{O_2}** of blood (3 ml O_2 /liter of blood at P_{O_2} of 100 mmHg)
 - The majority of O_2 is **bound to hemoglobin**
 - Most vertebrate hemoglobin is **tetrameric** and capable of binding to four O_2 molecules

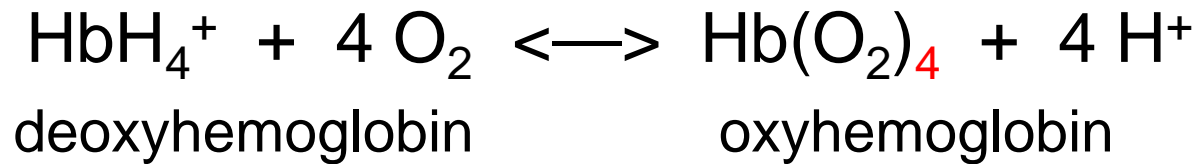


- **Myoglobin** is a monomer that stores O_2 in muscle cells
- **Neuroglobin** (neurons) and **cytoglobin** (fibroblasts)

11.9 Circulatory Transport and Gas Exchange



- Please note another significant error on page 532

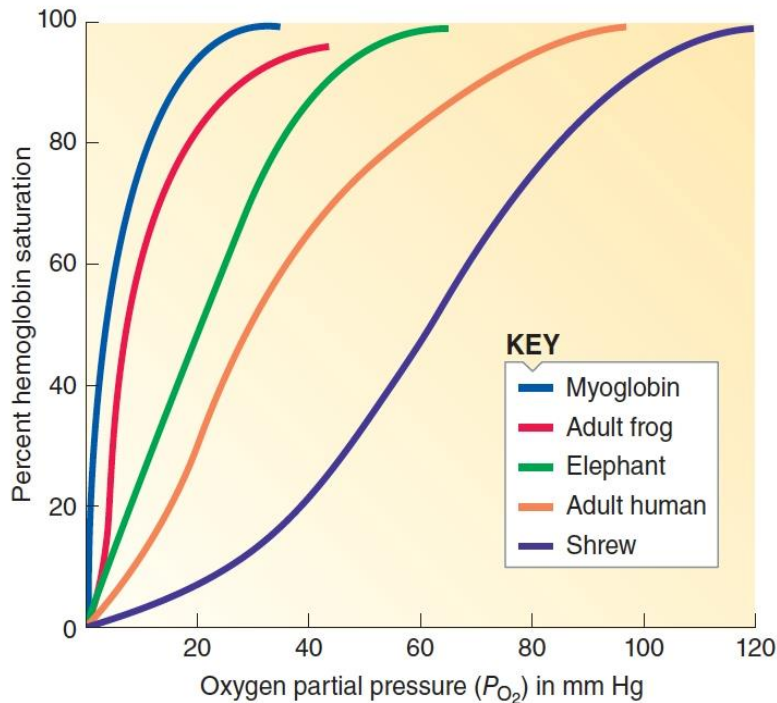


11.9 Circulatory Transport and Gas Exchange

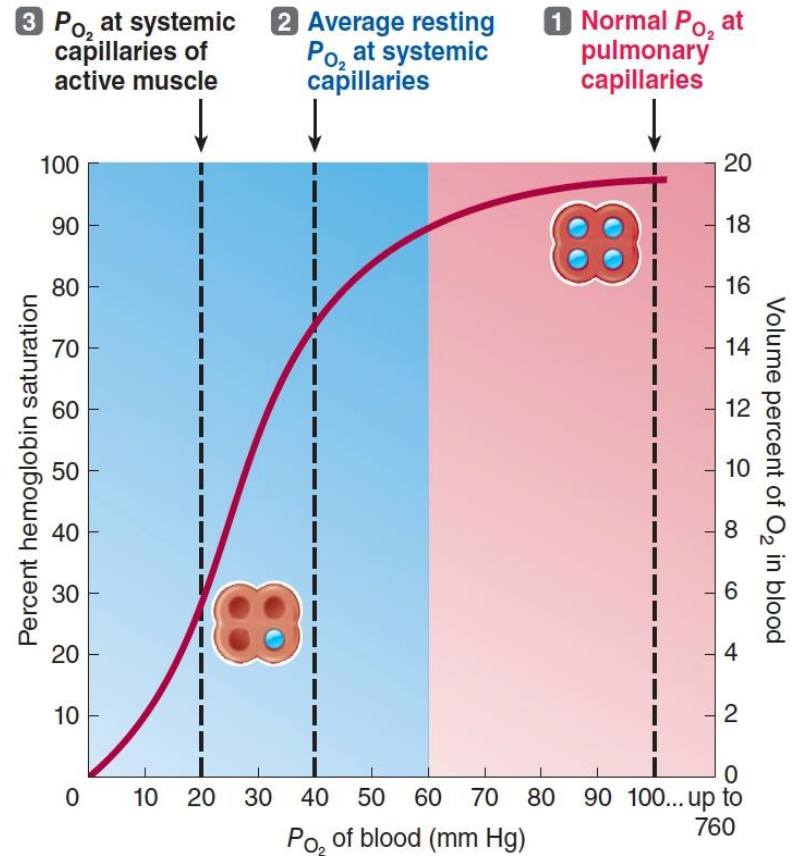


- Hemoglobin saturation
 - Binding of O_2 to hemoglobin is **reversible** and subject to the **law of mass action**
 - The most important factor determining **% hemoglobin saturation** is **P_{O_2}**
 - Hemoglobin **binds O_2 in the lungs** and **unloads O_2 in the tissues**
 - **Affinity** of hemoglobin for O_2 (measured as **P_{50}**) **increases with body size** and is higher in animals adapted to **high altitude** or **low oxygen** environments

11.9 Circulatory Transport and Gas Exchange



(a)



KEY

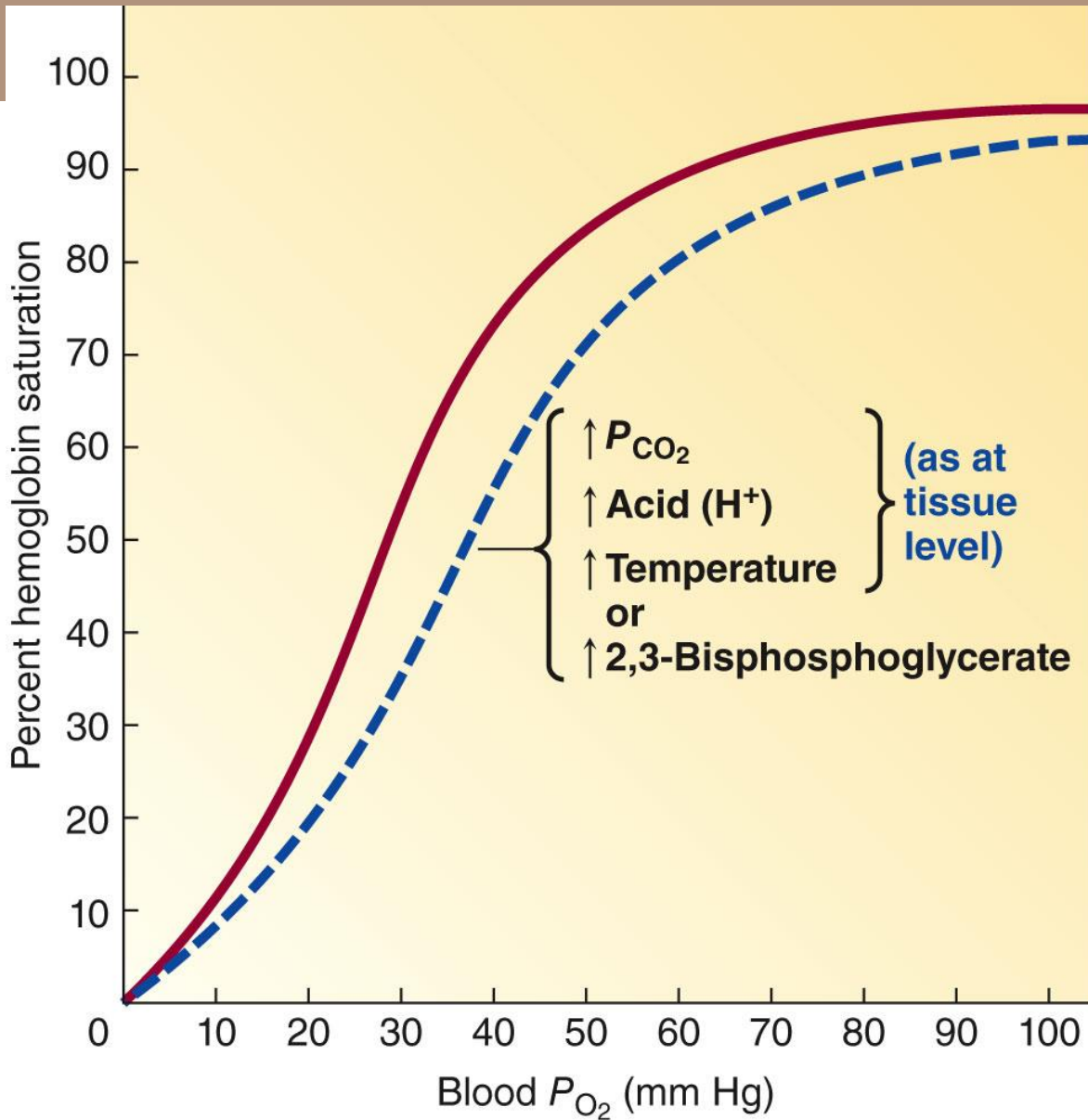


(b)

11.9 Circulatory Transport and Gas Exchange



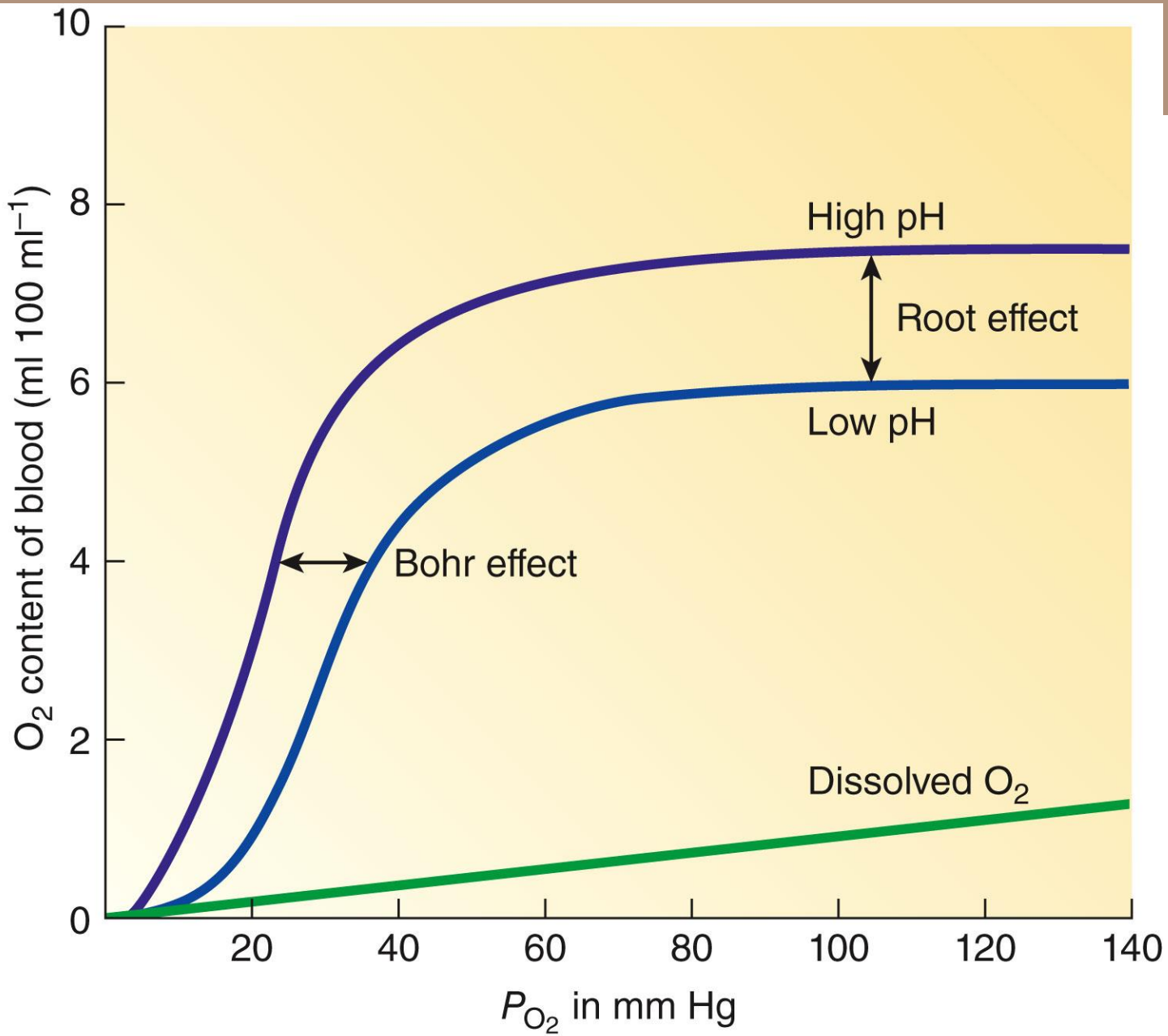
- Factors that **decrease affinity** of Hb for O₂ promote **greater unloading** of O₂ in the tissues
 - Increased **Pco₂**
 - Increased **acidity** (Bohr effect)
 - Acidity also lowers **maximal O₂-binding capacity** (Root effect)
 - Increased **temperature**
 - **Organic phosphates**
 - 2,3-diphosphoglycerate (DPG) in most mammals
 - Inositol pentaphosphate (IPP) in birds
 - Nucleoside triphosphates in fishes



Arterial P_{CO_2} and acidity, normal body temperature (as at pulmonary level)

↑ P_{CO_2}
 ↑ Acid (H^+)
 ↑ Temperature
 or
 ↑ 2,3-Bisphosphoglycerate
 (as at tissue level)

(a)



(b)

11.9 Circulatory Transport and Gas Exchange

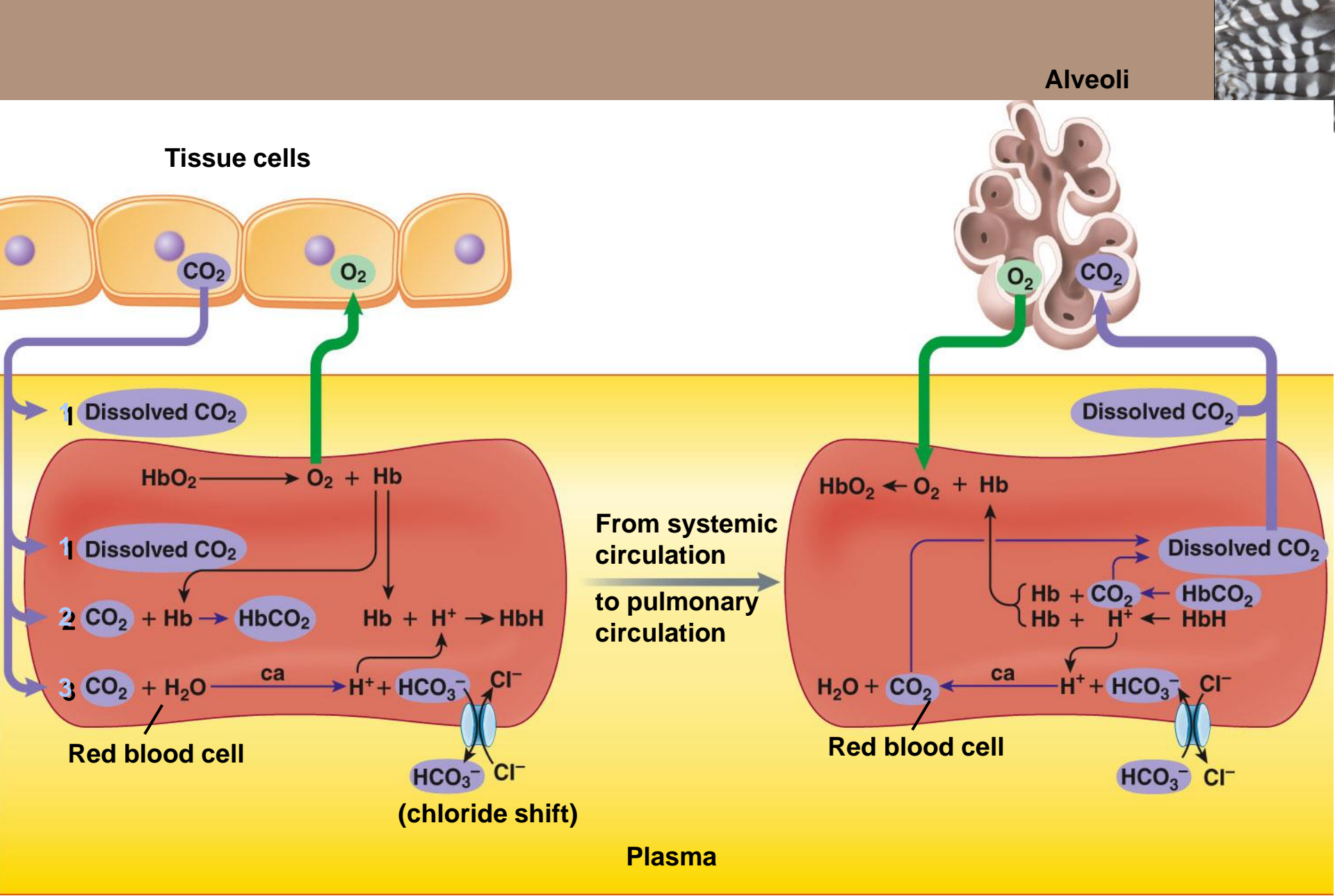


■ Carbon dioxide transport in blood

- **Dissolved** (5 - 10%)
- **Bound to hemoglobin** (25 - 30%)
 - Forms **carbaminohemoglobin** (HbCO₂)
 - Binds with the globin
- **Bicarbonate ion (HCO₃⁻)** (60 - 70%)



- Enzyme for the first step is **carbonic anhydrase** found in lungs, kidneys and gills
- Chloride ions enter red blood cells in exchange for efflux of bicarbonate ion (**chloride shift**)
- Deoxygenated hemoglobin picks up CO₂ and H⁺ (**Haldane effect**)



ca = Carbonic anhydrase

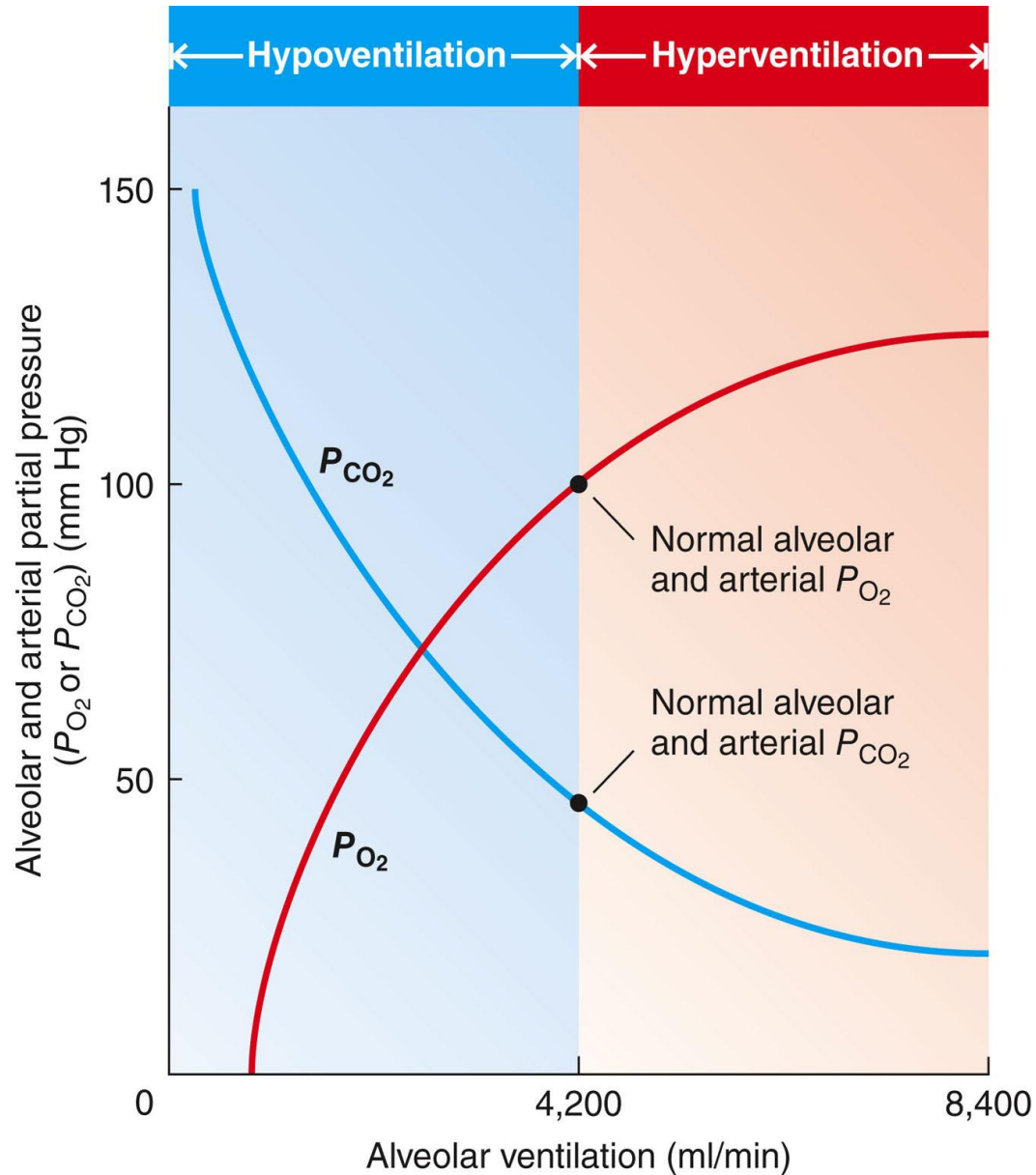
11.9 Circulatory Transport and Gas Exchange



- Abnormalities in arterial P_{O_2}
 - **Hypoxic hypoxia** (e.g. high altitude)
 - **Anemic hypoxia** (e.g. carbon monoxide poisoning)
 - **Circulatory hypoxia** (e.g. congestive heart failure)
 - **Histotoxic hypoxia** (e.g. cyanide poisoning)

- Abnormalities in arterial P_{CO_2}
 - **Hypercapnia** = excess CO_2 in arterial blood
 - Caused by **hypoventilation**
 - **Hypocapnia** = below normal arterial P_{CO_2}
 - Caused by **hyperventilation**
 - Changes in blood CO_2 mainly affect **acid-base balance**

11.9 Circulatory Transport and Gas Exchange



11.10 Control of Respiration

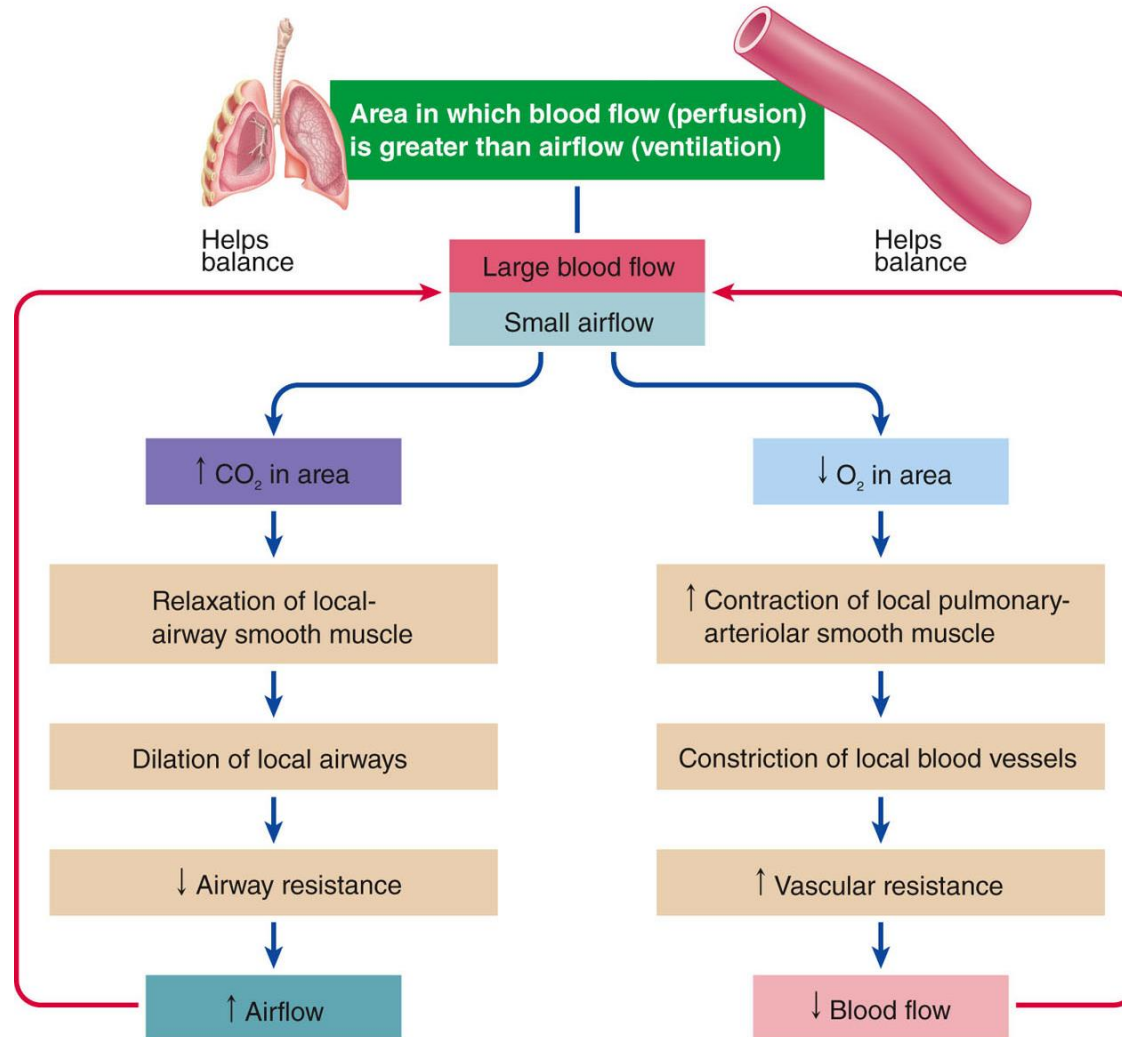


- Control of respiration in insects
 - **Metathoracic ganglia** control **closer muscles** which reduce opening of spiracles

- Extrinsic regulation of airways in mammals
 - **Parasympathetic** stimulation promotes **bronchoconstriction**, increasing airway resistance
 - **Sympathetic** stimulation promotes **bronchodilation**, decreasing airway resistance

- Intrinsic regulation of airways in mammals
 - **Ventilation rates match perfusion rates** by adjustment of airway smooth muscle and arterioles
 - **Local increase in CO₂** induces **relaxation** of airway smooth muscle
 - **Local decrease in O₂** causes **vasoconstriction** of pulmonary arterioles

11.10 Control of Respiration



(a) Local controls to adjust ventilation and perfusion to lung area with large blood flow and small airflow

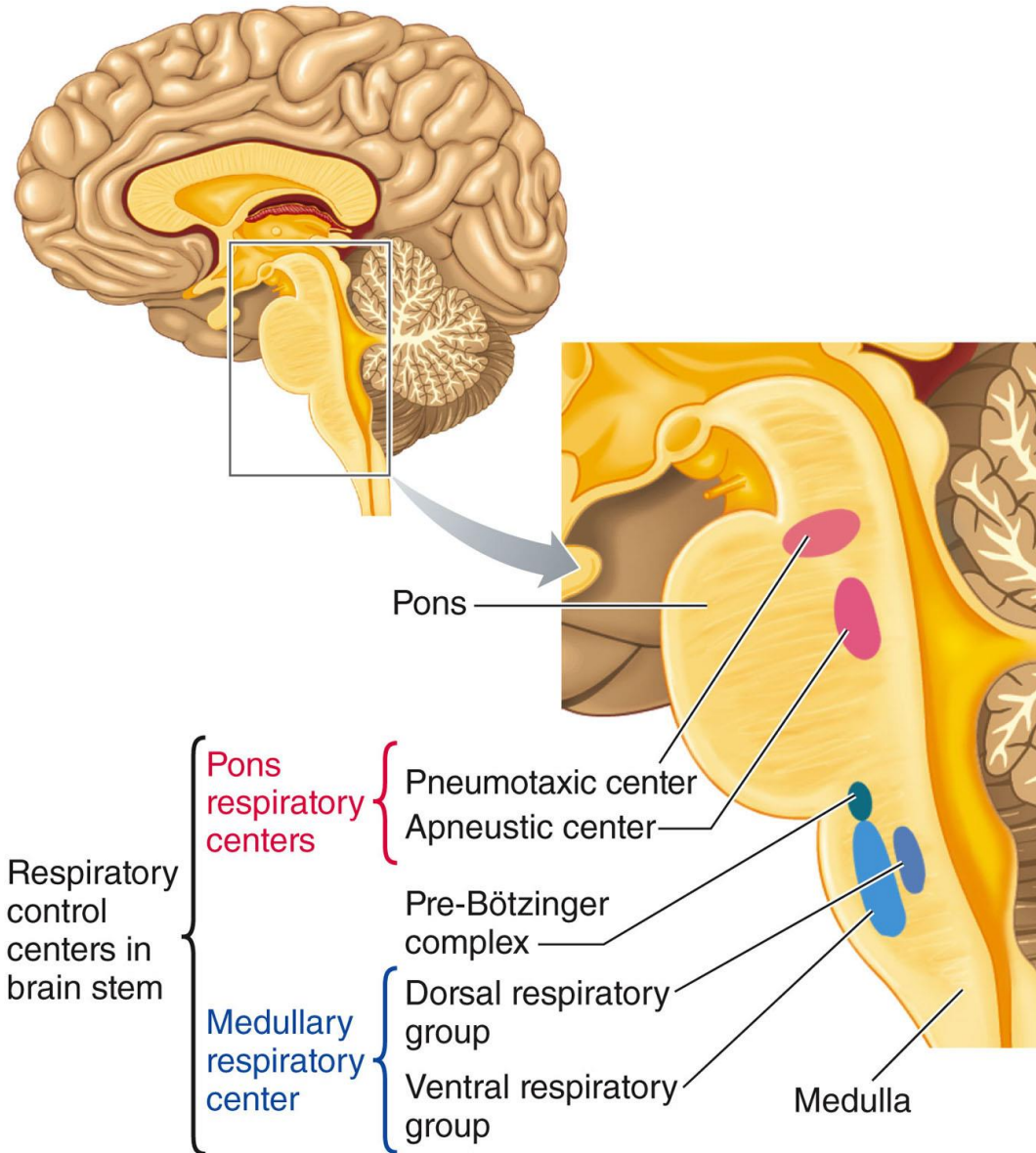
11.10 Control of Respiration



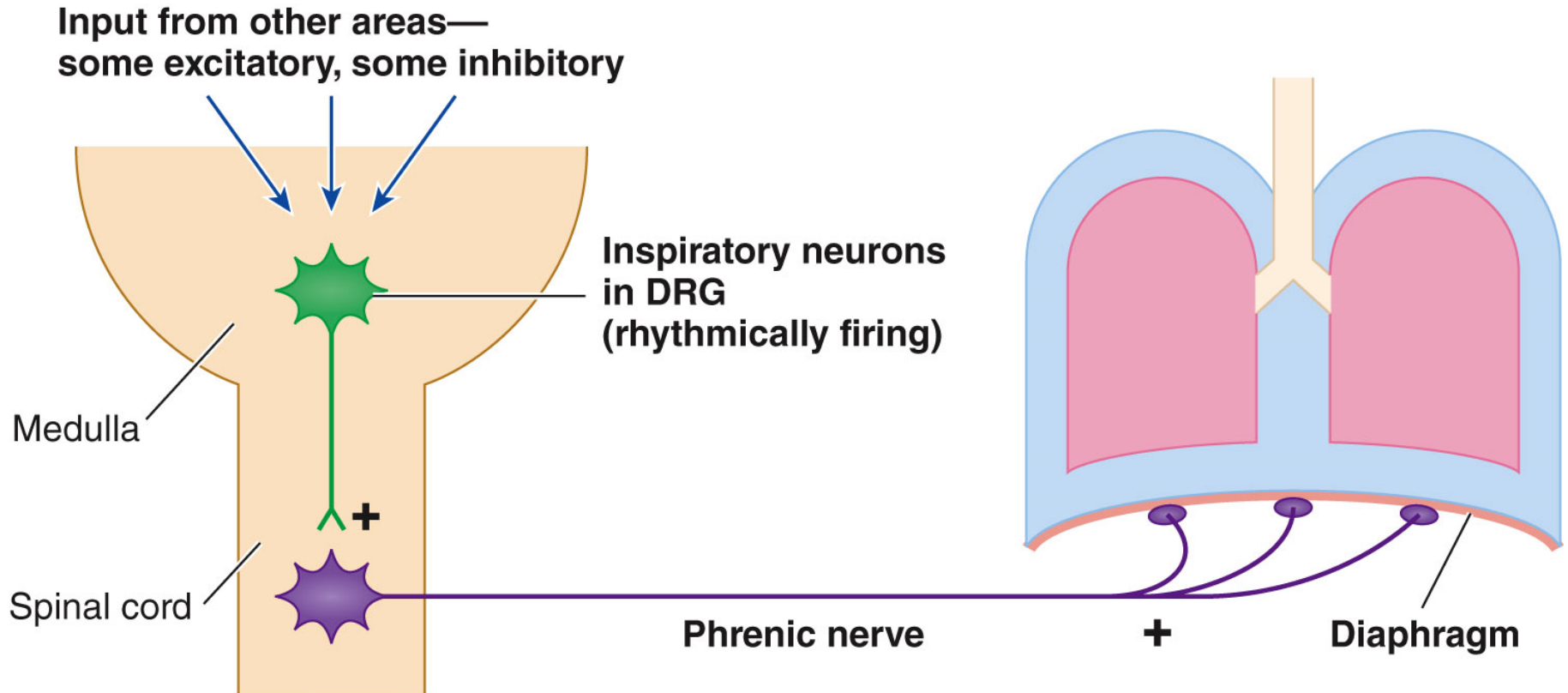
▪ **Medullary respiratory center**

- **Dorsal respiratory group (DRG)** contains **inspiratory neurons** that terminate on motor neurons supplying inspiratory muscles
- **Ventral respiratory group (VRG)** contains **inspiratory neurons** and **expiratory neurons**
 - Utilized only during **active breathing** when demands for ventilation increase
- Generation of a **respiratory rhythm** lies in the **pre-Botzinger complex**
 - Neurons display **pacemaker** activity
- **Pneumotaxic center** and **apneustic center** in the **pons** fine tune the breathing pattern

11.10 Control of Respiration



11.10 Control of Respiration



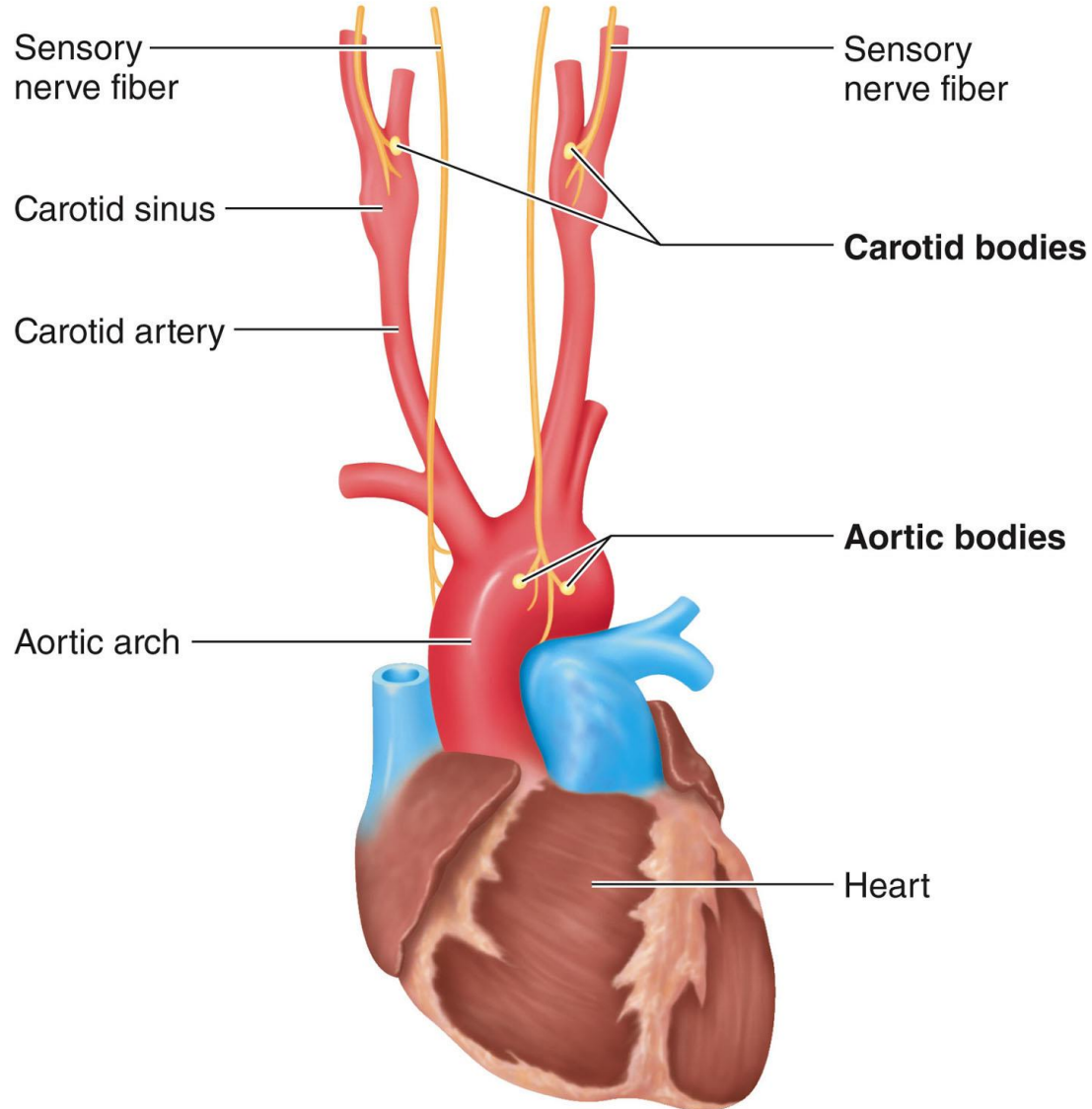
Not shown are intercostal nerves to external intercostal muscles.

11.10 Control of Respiration

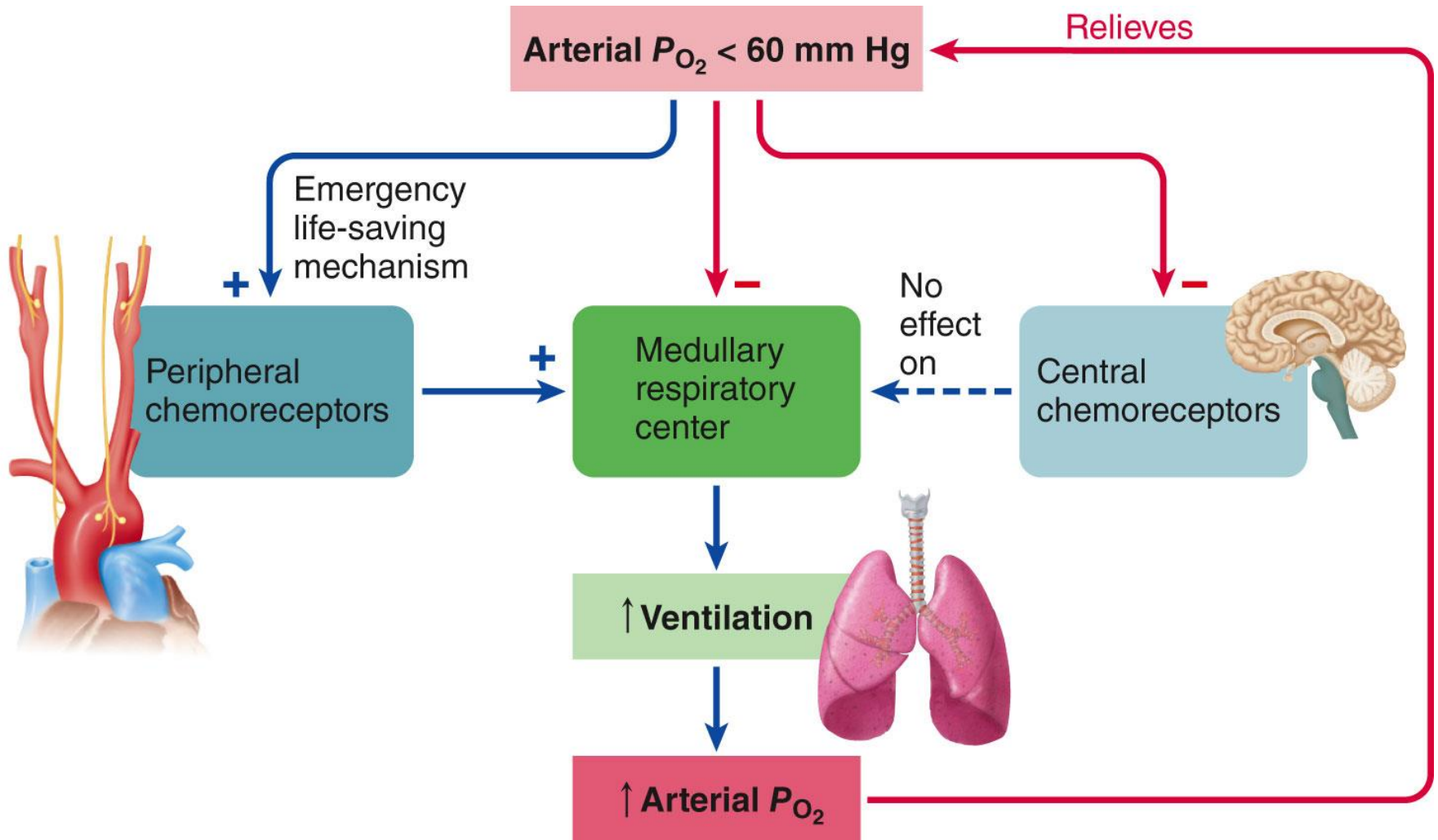


- Arterial blood gases are precisely regulated.
 - The **medullary respiratory center** adjusts rate and depth of ventilation in response to inputs from **central** and **peripheral chemoreceptors**.
 - Arterial P_{O_2} is monitored by **peripheral chemoreceptors** in **carotid** and **aortic bodies**
 - In **water-breathing vertebrates**, P_{O_2} is the **primary homeostatic variable**
 - Increased arterial P_{CO_2} , detected by **central chemoreceptors**, is the most powerful stimulus to breathing in air-breathers

11.10 Control of Respiration



11.10 Control of Respiration

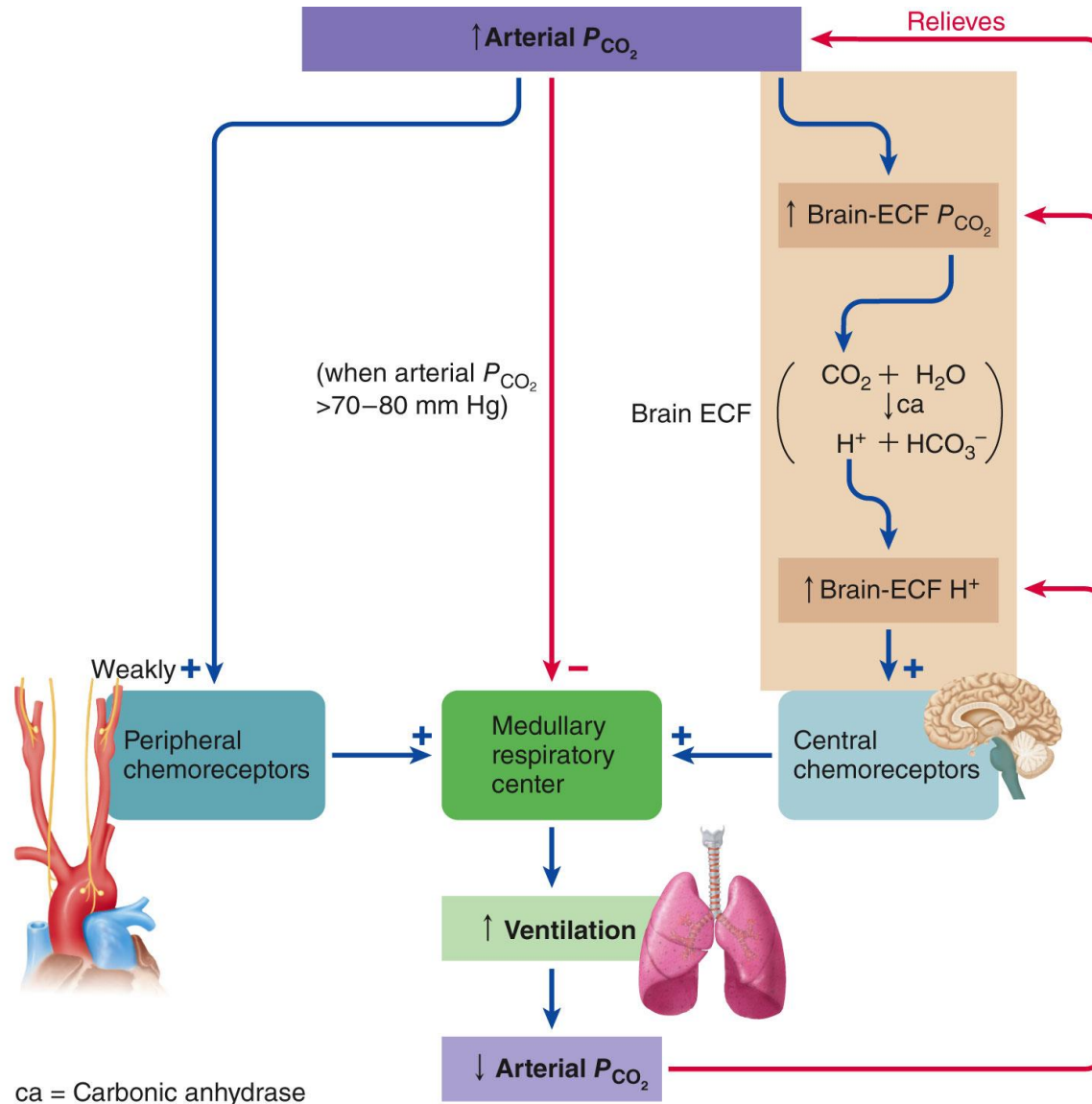


11.10 Control of Respiration

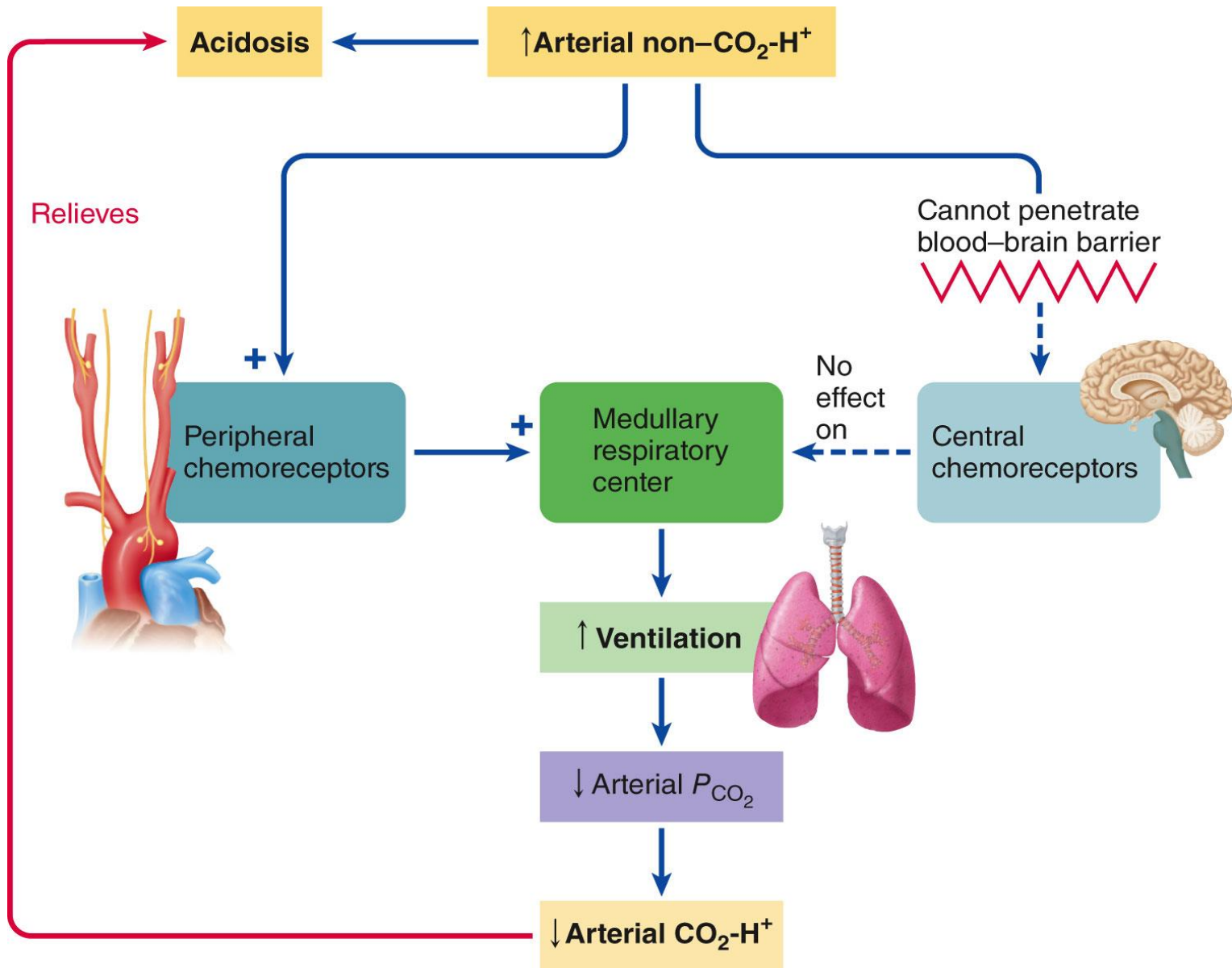


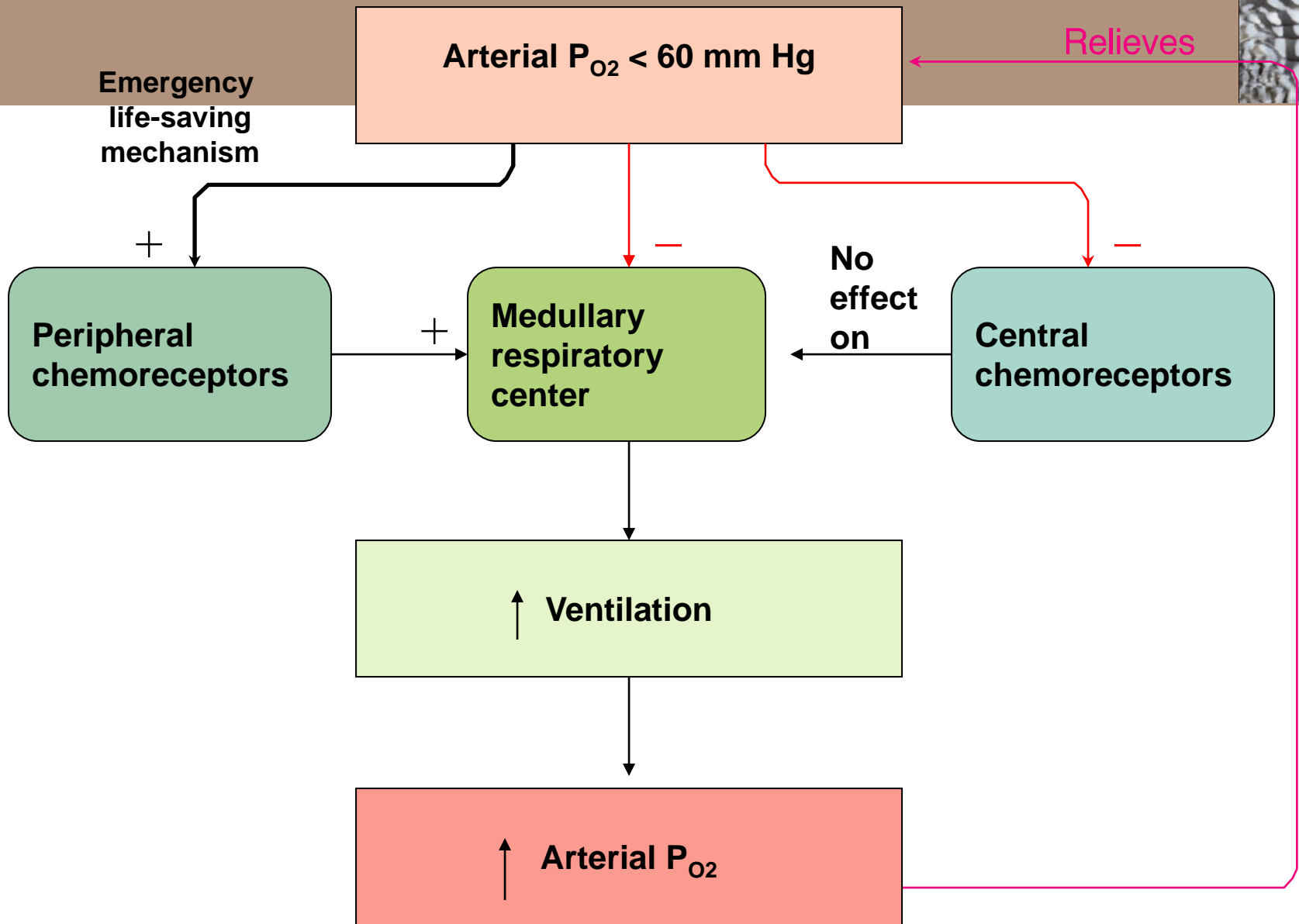
- Role of H^+ in respiratory control
 - Central chemoreceptors are **most sensitive** to CO_2 -induced **H^+ production** in the brain **extracellular fluid**
 - **Peripheral chemoreceptors** are also highly responsive to **arterial H^+ concentration**
 - Major role in response to changes in H^+ unrelated to P_{CO_2} (e.g. lactate or keto acids)
 - Important in regulating **acid-base balance**

11.10 Control of Respiration



11.10 Control of Respiration





11.10 Control of Respiration

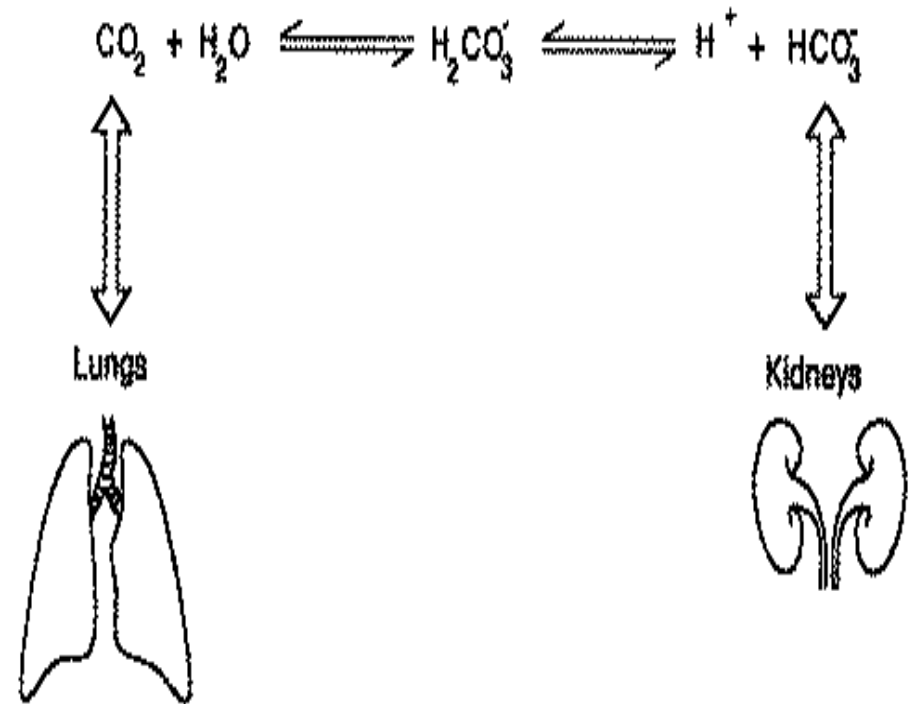


- Ventilation increases abruptly at the onset of **exercise**.
 - Occurs **without** changes in arterial P_{O_2} or P_{CO_2}
 - Possible factors increasing ventilation during exercise
 - **Reflexes** originating from **body movements**
 - Anticipatory activation by **epinephrine**
 - Anticipatory activation by the **cerebral cortex**

ABGs

■ Base Excess

- Amt of blood buffer
- Normal +/- 2 mEq/L
- High value—alkalosis
 - Citrate excess from rapid blood transfusions
 - IV HCO₃ infusion
 - DKA
 - Ingestion large amt bicarb solutions (antacids)



ABGs



- Base excess
 - Low value—acidosis
 - Lg amts of bicarb ion excretion
 - ie: diarrhea
 -

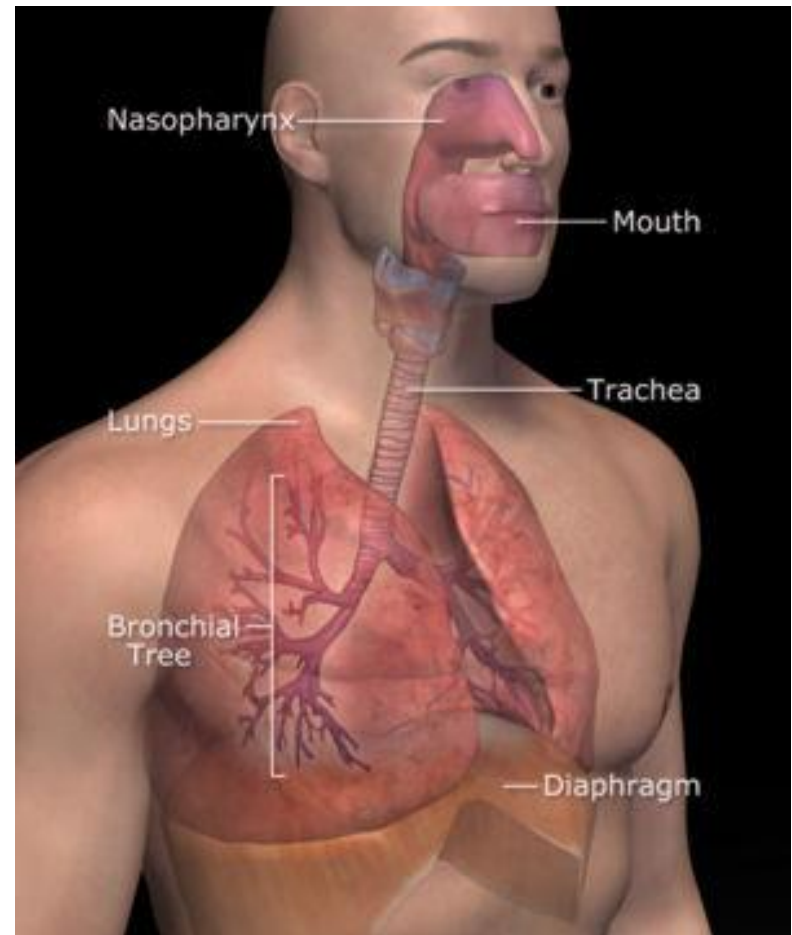
ABGs

- Bicarbonate
 - Major renal component
 - Kidneys excrete & retain to maintain normal balance
 - Principal buffer ECF
 - Normal 22-26 mEq/L
 - Metabolic acidosis < 22 mEq/L
 - Metabolic alkalosis > 26 mEq/L



Acid-Base Imbalances

- Either respiratory or metabolic, depend on their underlying cause
- Corrects AB imbalances through process known as compensation



Respiratory Acidosis

pH < 7.35

PaCO₂ >45 mm Hg

PaO₂ < 80 mm Hg

Bicarb level normal if
uncompensated

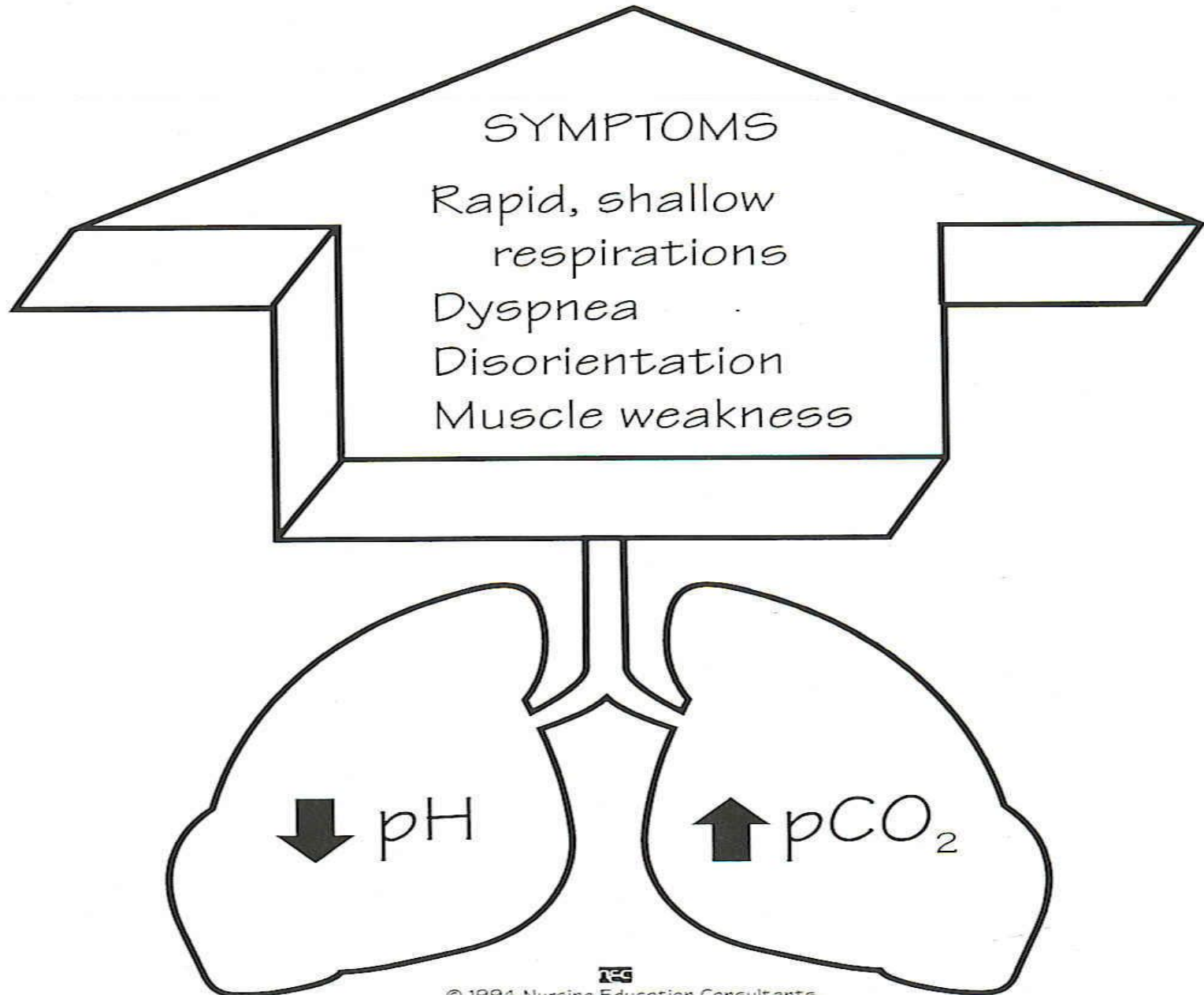
Bicarb level > 26 mEq/L
if compensated

Hypoventilation → CSF
& brain cells become
acidic → neurological
changes →
hypoxemia → further
neurological impairment
Hyperkalemia &
hypercalcemia can
occur
Kidneys hold to bicarb &
release hydrogen ions
UA—may take 24 hrs

Respiratory Acidosis Causes

- Hypoventilation resulting primary respiratory problems
 - Chest wall injury
 - Respiratory failure
 - Cystic fibrosis
 - Pneumonia
 - Atelectasis (obstruction of small airways often caused by mucus)
- Hypoventilation resulting from factors other than resp system
 - Obesity
 - Head injury
 - Drug overdose (OD) with resp depressant
 - Paralysis of resp muscles caused by neurological alterations

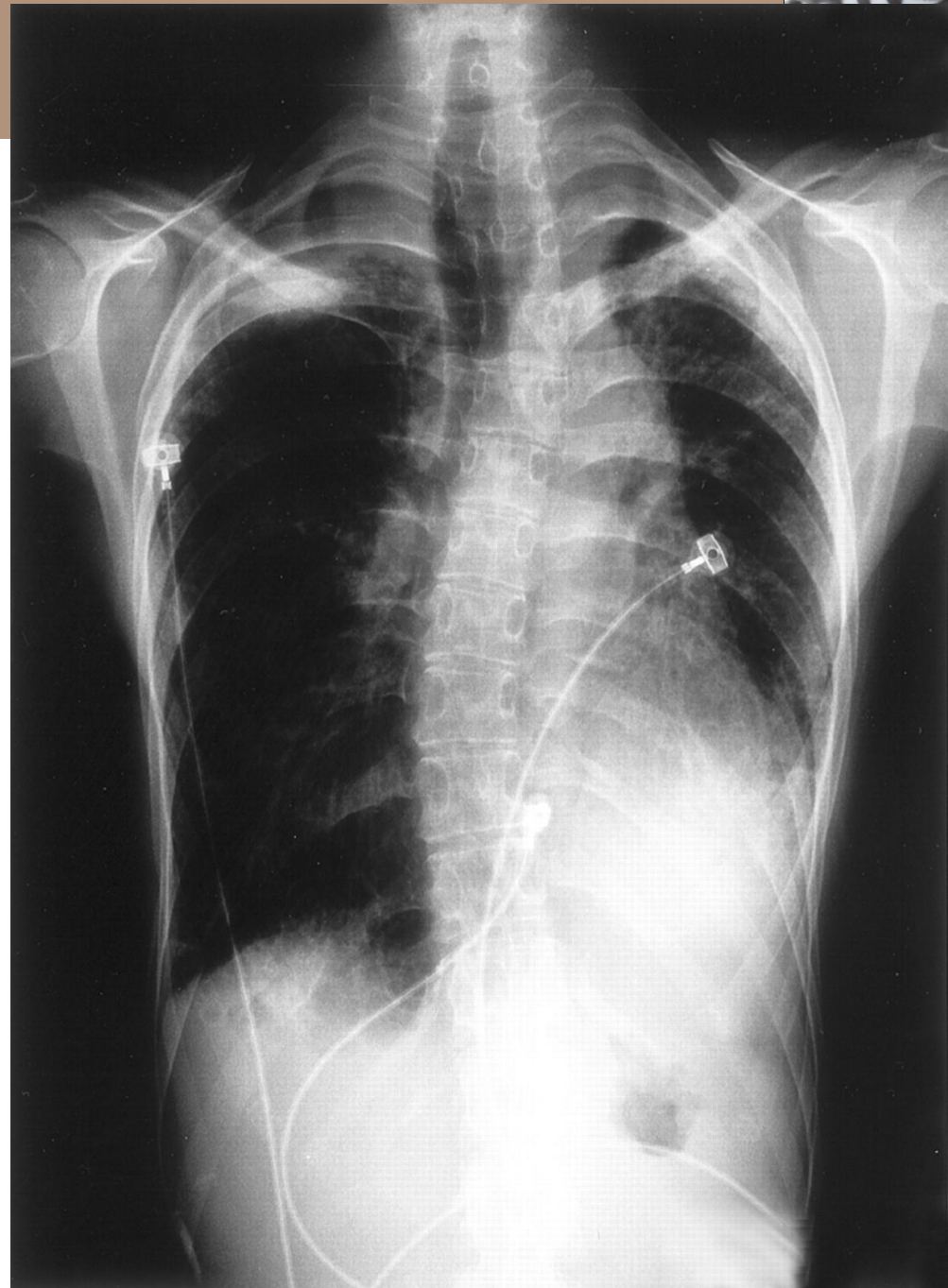
RESPIRATORY ACIDOSIS



Respiratory Acidosis

S/S

- Convulsion
- Coma
- Muscular twitching
- Confusion
- Dizziness
- Lethargy
- HA
- Warm flushed skin
- Ventricular dysrhythmia



Respiratory Alkalosis

- pH >7.45
- PaCO₂ <35 mm Hg
- PaO₂ normal
- HCO₃ nl if short-lived or uncompensated
- HCO₃ <22 mm Hg if compensated
- Begins outside resp system ie: anxiety, panic attack OR within resp system ie: initial phase of asthma attack
- Body does not usually compensate because pH returns to nl before kidneys can respond

Respiratory Alkalosis

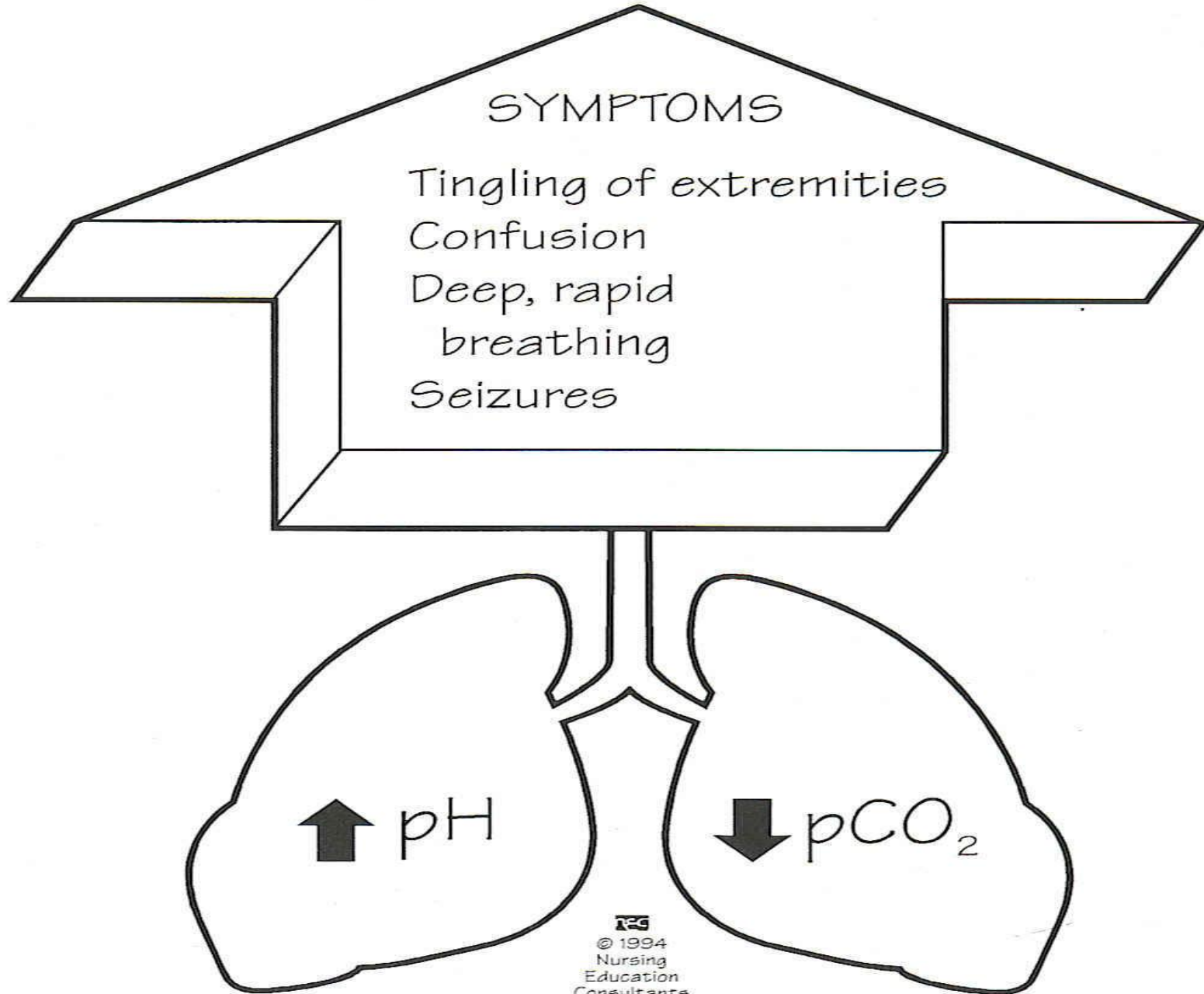
Causes

- Salicylate overdoses
- Anxiety
- Hypermetabolic states
ie: fever, exercise
- CNS disorders ie: head
injury, infections
- Asthma
- Pneumonia
- Inappropriate vent
settings

S/S

- Confusion
- Dizziness
- Convulsions
- Coma
- Tachypnea
- Numbness/tingling of
extremities
- dysrhythmias

RESPIRATORY ALKALOSIS



Metabolic Acidosis

High acid content of bld
Loss of HCO_3

pH < 7.35

PaCO_2 normal if
uncompensated

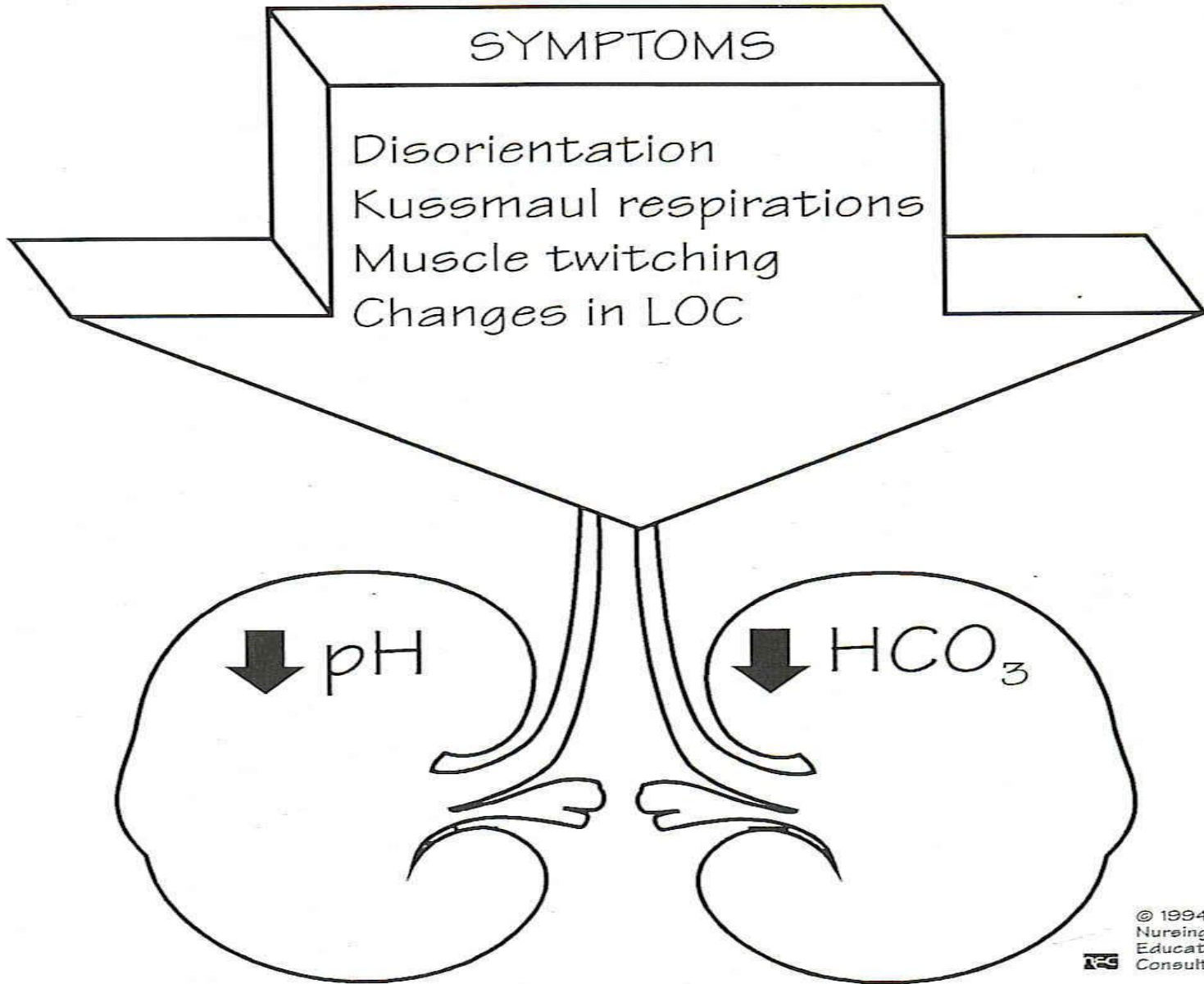
< 35 mm Hg if
compensated

PaO_2 normal or
increased

$\text{HCO}_3 < 22$ mEq/L

O_2 Sat normal

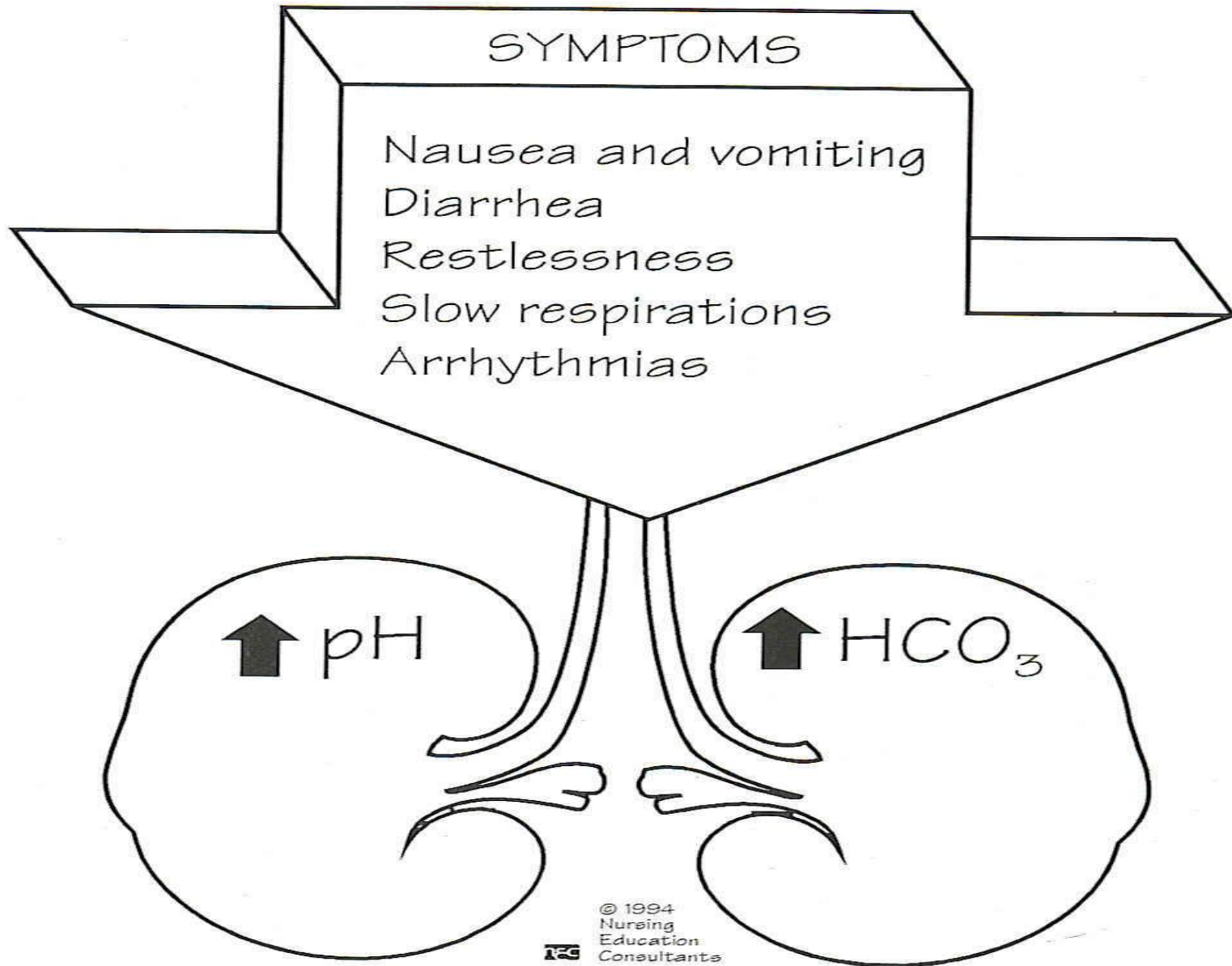
METABOLIC ACIDOSIS



Metabolic Alkalosis

- pH >7.45
 - PaCO₂ normal if uncompensated
 - PaCO₂ >45 mm Hg if compensated (occurs by decreasing RR & no renal disease)
 - PaO₂ normal
 - HCO₃ > 26 mEq/L
- Causes
 - Excessive vomiting
 - Prolong gastric sx
 - Excess aldosterone
 - Hypokalemia
 - Hypercalcemia
 - Use of drugs ie: steroids, diuretics, sodium bicarb

METABOLIC ALKALOSIS



Normal blood gas in an artery for humans:

pH 7.35–7.45

PaCO₂ 35–45 mmHg

PaO₂ 80–100 mmHg

HCO₃⁻ 22–26 mmol/L

<https://www.rccc.eu/ppc/calculadoras/ABG%20interpreter%20-%20calculator.htm>