

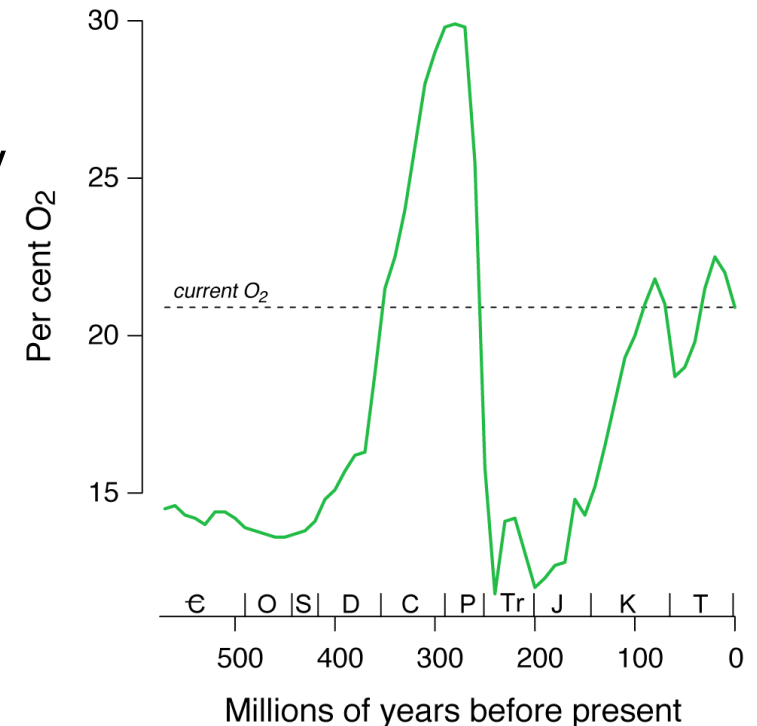
Respiration

- Cellular respiration: $\text{C}_6\text{H}_{12}\text{O}_6 + \text{O}_2 = \text{CO}_2 + \text{H}_2\text{O}$
 - Respiratory gases: O_2 , CO_2
- Organismal respiration
 - Exchange of respiratory gases between cells/tissues and environment
 - Gas exchange
 - Passive (diffusion)
 - Active (breathing, transport)
- SO: cellular respiration relies on both gas exchange mechanisms and environmental respiratory gas features

Air and Water

O₂ and CO₂ in the environment

- Dry gas* composition of present day Earth's atmosphere: *water vapor removed
 - 21% O₂ (20.95%)
 - 78% N₂ (78.09%)
 - 0.93% Ar (noble gases)
 - 0.03% CO₂
- O₂ content of Earth's atmosphere has varied over geological time
 - Largest shift: from Carboniferous-Permian (~30 % O₂) to start of Triassic (~10% O₂)
 - During time of elevated O₂, organisms first invaded terrestrial realm, and there were many giant insects (dragonflies with 70cm wingspans)
- CO₂ content has been rising since start of industrial age and burning of fossil fuels
 - Svante Arrhenius (1859-1927) predicted greenhouse effect global warming as a result, and we are now seeing these predictions hold true.

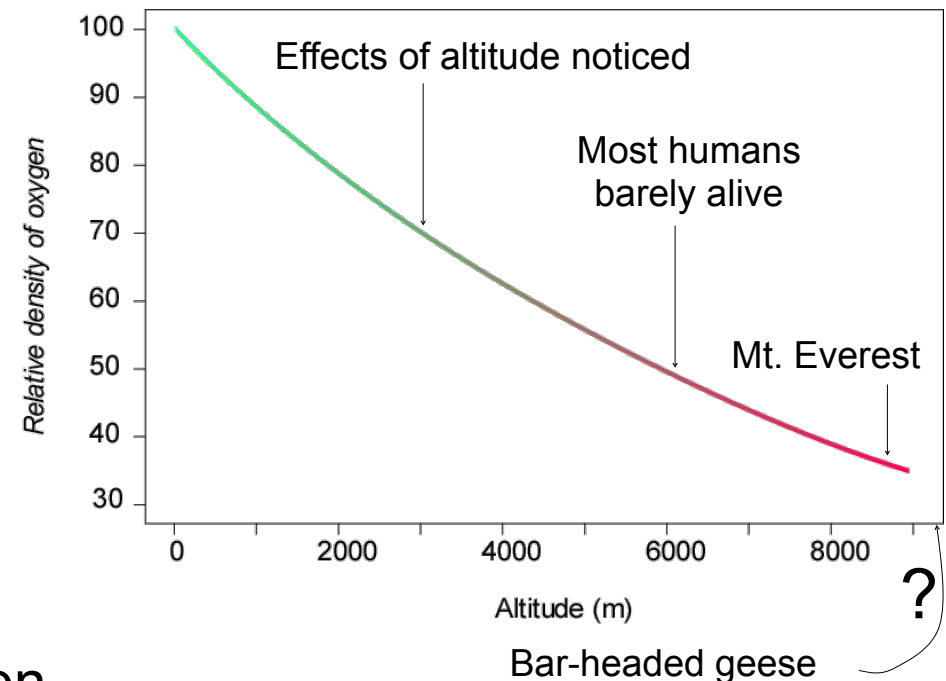


based on R. Berner (2001)

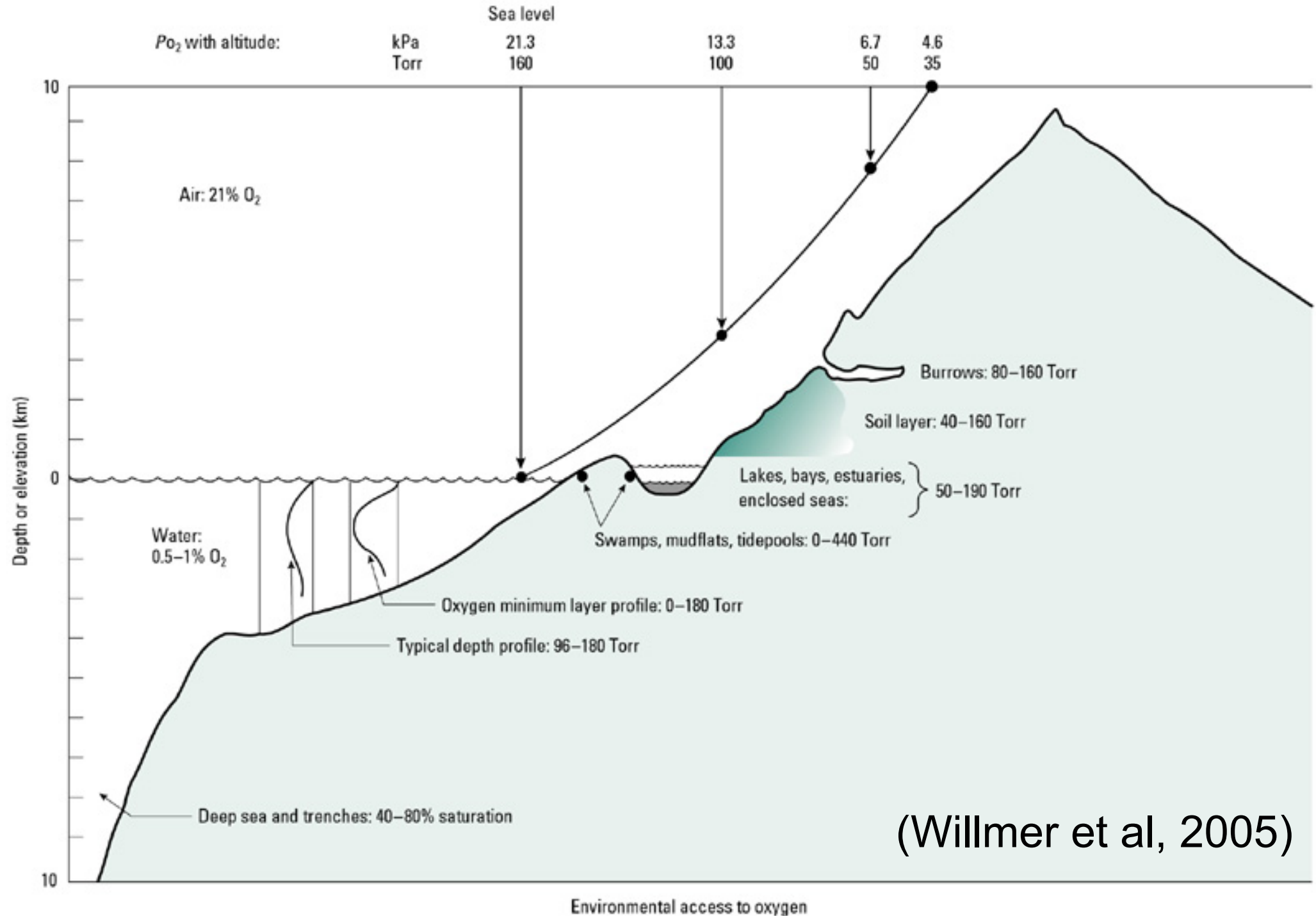
O₂ and CO₂ in the environment

- Dry gas* composition of present day Earth's atmosphere:
 - 21% O₂ (20.95%)
 - 78% N₂ (78.09%)
 - 0.93% Ar (noble gases)
 - 0.03% CO₂
- Concentrations of gases in air do not change with altitude
 - however the amount of air present per volume decreases with altitude
 - < 1 ATM pressure
 - Thus, there is less oxygen in a given volume of air at high altitude than at low altitude

based on J. West (1996)



Oxygen across the Earth's surface



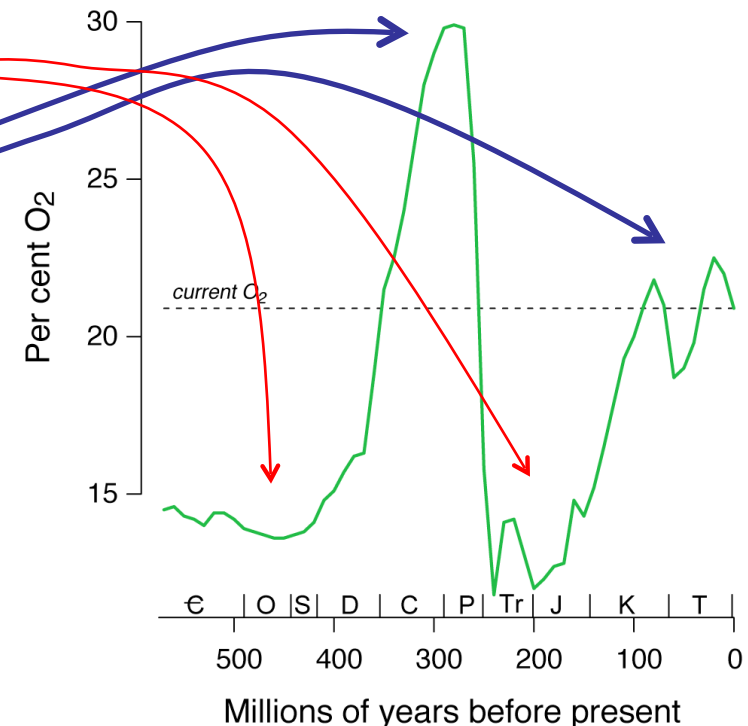
Paleo-atmosphere and flight dynamics

- High atmospheric O_2 in Permian would have resulted in a hyperdense atmosphere
 - O_2 is heavier than N_2 (32 vs. 28 g/mol)
- Did hyperdense atmosphere favor the evolution of flight?
 - Biomechanically, flight is easier in denser atmospheres

No new flying organisms evolved

Evolution of flight occurred
Insects, pterosaurs (C-P)
Birds, bats (K-T)

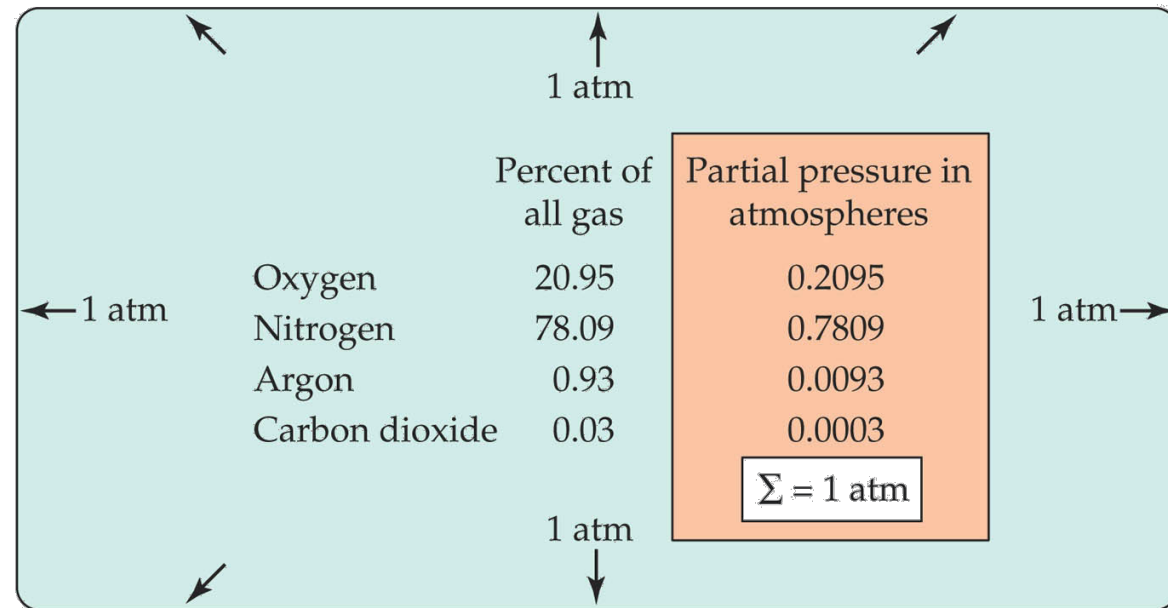
Dudley, *J. Exp. Biol.* 1998. 201: 1043-1050



Gases in air

Dry air in a box at sea level

- Universal Gas Law:
 $PV=nRT$
P = pressure
V = volume
n = quantity (moles) of gas
R = gas constant
(8.314 J/mol•K)
T = temperature



	Percent of all gas	Partial pressure in atmospheres
Oxygen	20.95	0.2095
Nitrogen	78.09	0.7809
Argon	0.93	0.0093
Carbon dioxide	0.03	0.0003
		$\Sigma = 1 \text{ atm}$

- Partial Pressure: the individual pressure of each gas in a mixture
- Dalton's Law: The partial pressure of each gas is independent of the other gases
 - Total Pressure = Sum Partial Pressures
- Partial pressure and concentration (percentage, mole fraction) of gases in a mixture of gas are proportional in the gas phase, but not necessarily when gases are in solution.

Wet Gases in air

- When gases in are are in contact with wet surfaces, such as biological tissues, they will become in equilibrium with the water
- Thus, air inside an organism (in our lungs) is saturated with water vapor
 - 100% relative humidity (rh)
- At normal body temperature (37°C), water vapor partial pressure is about 0.062 atm, or 6.2% of the percent of all of the gases
 - 1 L of exhaled air contains about 44 mg H₂O
- The amount of water dissolved in air is positively correlated with the temperature of the air.
 - 1 L of Hawaii beach air (100% rh) at 30°C contains about 30 mg H₂O
 - 1 L of air on the summit of Mauna Kea at 0°C contains about 5 mg H₂O
 - 1 L of steam contains about 600 mg H₂O (= 0.6 ml)

Gases in water

- In equilibrium, $P_{O_{2air}} = P_{O_{2water}}$
- Although $P_{O_{2air}}$ is proportional to concentration of the O_2 in air, $P_{O_{2water}}$ is not necessarily proportional to the concentration of the O_2 in water.
 - This is because water temperature and salinity affect how gases are dissolved
- Diffusion of gas into water is inversely proportional to the square root of the molecular weight of the gas
 - O_2 diffuses from gas to liquid faster than CO_2
- Henry's Law: $C = AP$
 - C = concentration
 - A = absorption coefficient (solubility) In the gas phase, $A=1$, so $C=P$
 - P = partial pressure.
- A varies among gases:
 - $A_{CO_2} = 77 \text{ mmol L}^{-1}$ (High CO_2 solubility is why bubbles
 - $A_{O_2} = 2.2 \text{ mmol L}^{-1}$ in your soda are CO_2 and not O_2)
 - $A_{N_2} = 1.1 \text{ mmol L}^{-1}$
- A is inversely proportional to temperature:
 - Higher T = lower A (That's why you chill your fizzy drink before opening it!)
- A is inversely proportional to salinity:
 - Higher salinity = lower A (That's why salt makes your soda bubble)

oxygen solubility in air & water

	Concentration of O ₂ (mL O ₂ at STP/L) at specified temperature		
	0°C	12°C	24°C
Air	210	200	192
Freshwater	10.2	7.7	6.2
Seawater ^a	8.0	6.1	4.9

STP: Standard
Temperature and
Pressure
(0°C, 1 atm)

- Warm air carries less oxygen at STP because it is less dense
- Warm water carries less oxygen at STP because hydrogen bonds between H₂O and O₂ molecules are weaker at higher temperatures
- Saltier water carries less oxygen at STP because hydrogen bonds between H₂O and salt ions form and these exclude possible hydrogen bonds between H₂O and O₂ molecules.
- Dramatically lower O₂ content of water compared to air means that water-breathing organisms must work much harder to obtain an equivalent amount of O₂.

	Water	Air	Ratio: Water / air
O ₂ concentration (liter / liter)	0.007	0.209	~1:30
Density, ρ (kg / liter)	1	0.0013	~800:1
Dynamic viscosity, (cP)	1	0.02	50:1
Heat capacity (cal / liter °C)	1000	0.31	~3000:1
Heat conductivity (cal / s cm °C)	0.0014	0.000 057	~25:1
Diffusion coefficient, D_{O_2} (cm ² / s)	0.000 025	0.198	~1:8000
D_{CO_2} (cm ² / s)	0.000 018	0.155	~1:9000
Diffusion constant, K_{O_2} (cm ² / atm min)	34×10^{-6}	11	~1:300 000
K_{CO_2} (cm ² / atm min)	850×10^{-6}	9.4	~1:11 000
Liters of medium per liter O ₂	143	4.8	~30:1
Kilograms of medium per liter O ₂	143	0.0062	~23 000:1

Table 1.5 Comparison of air and water as respiratory medium. Schmidt-Neilsen (1997)

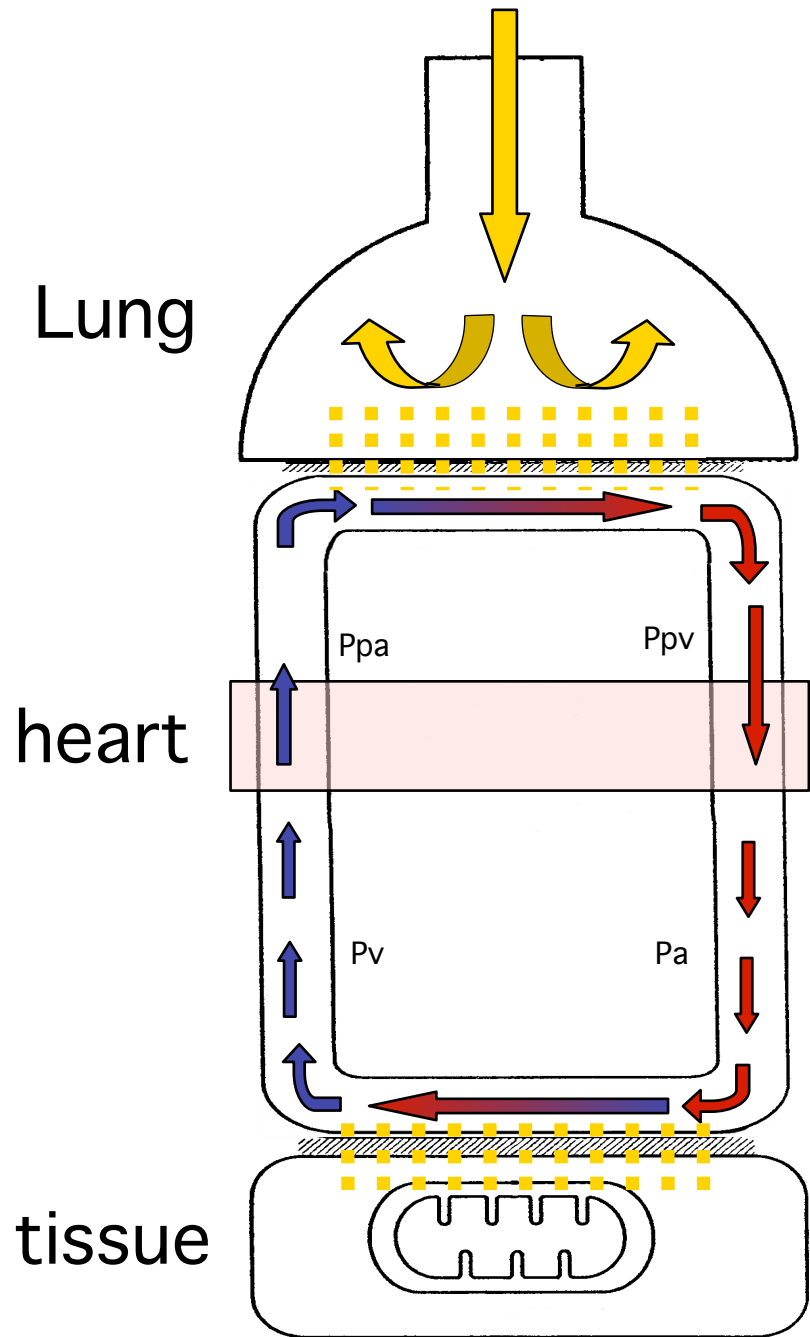
Temperature (C°)	Fresh water (ml O ₂ liter ⁻¹ water)	Sea water (ml O ₂ liter ⁻¹ water)
0	10.29	7.97
10	8.02	6.35
15	7.22	5.79
20	6.57	5.31
30	5.57	4.46

Table 1.4 The temperature effect on the amount of oxygen dissolved in fresh water and in sea water in equilibrium with atmospheric air. [Krogh 1941]

Gas Exchange Models

Oxygen Cascade

Oxygen Cascade



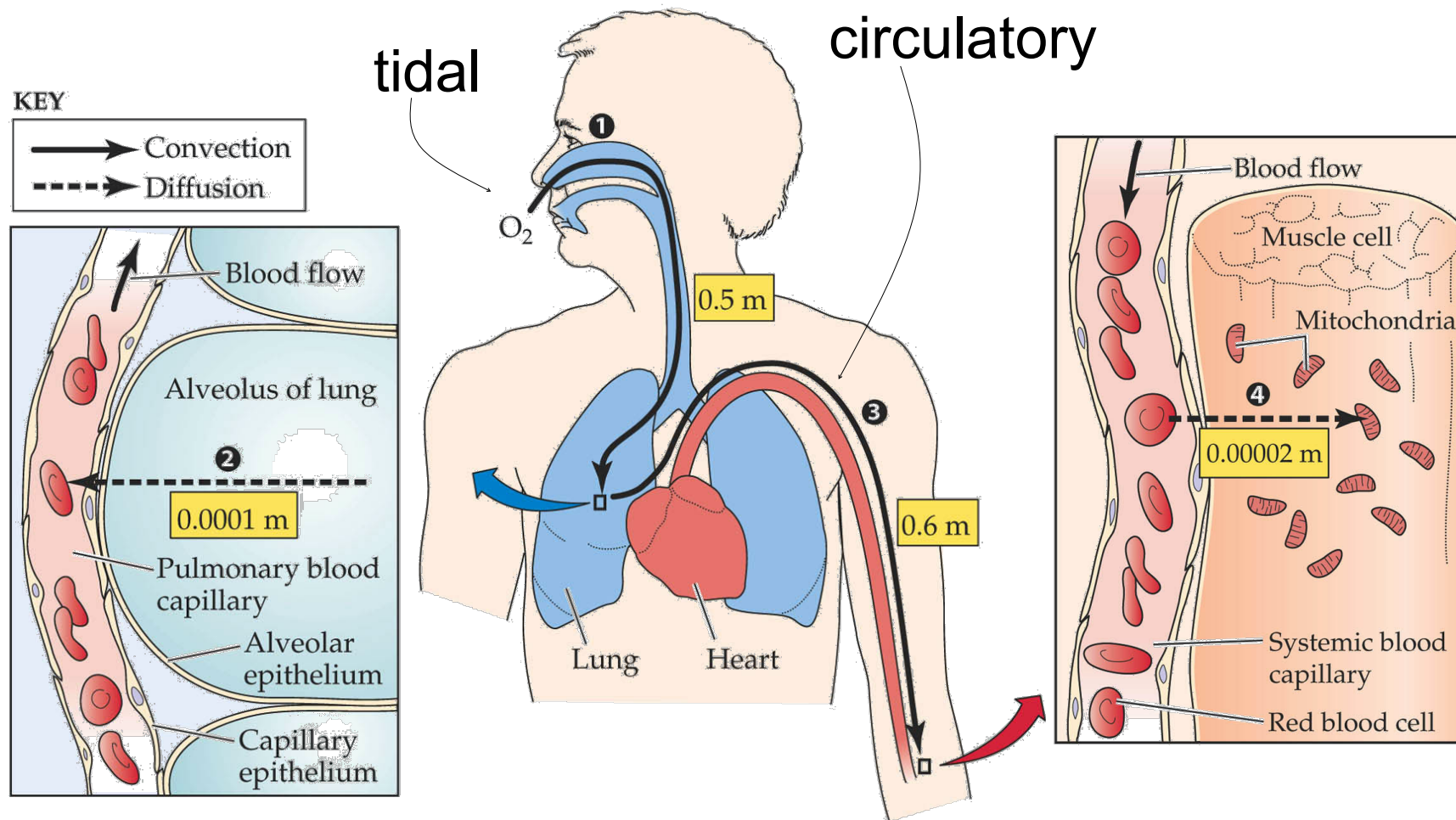
1. convection

2. diffusion

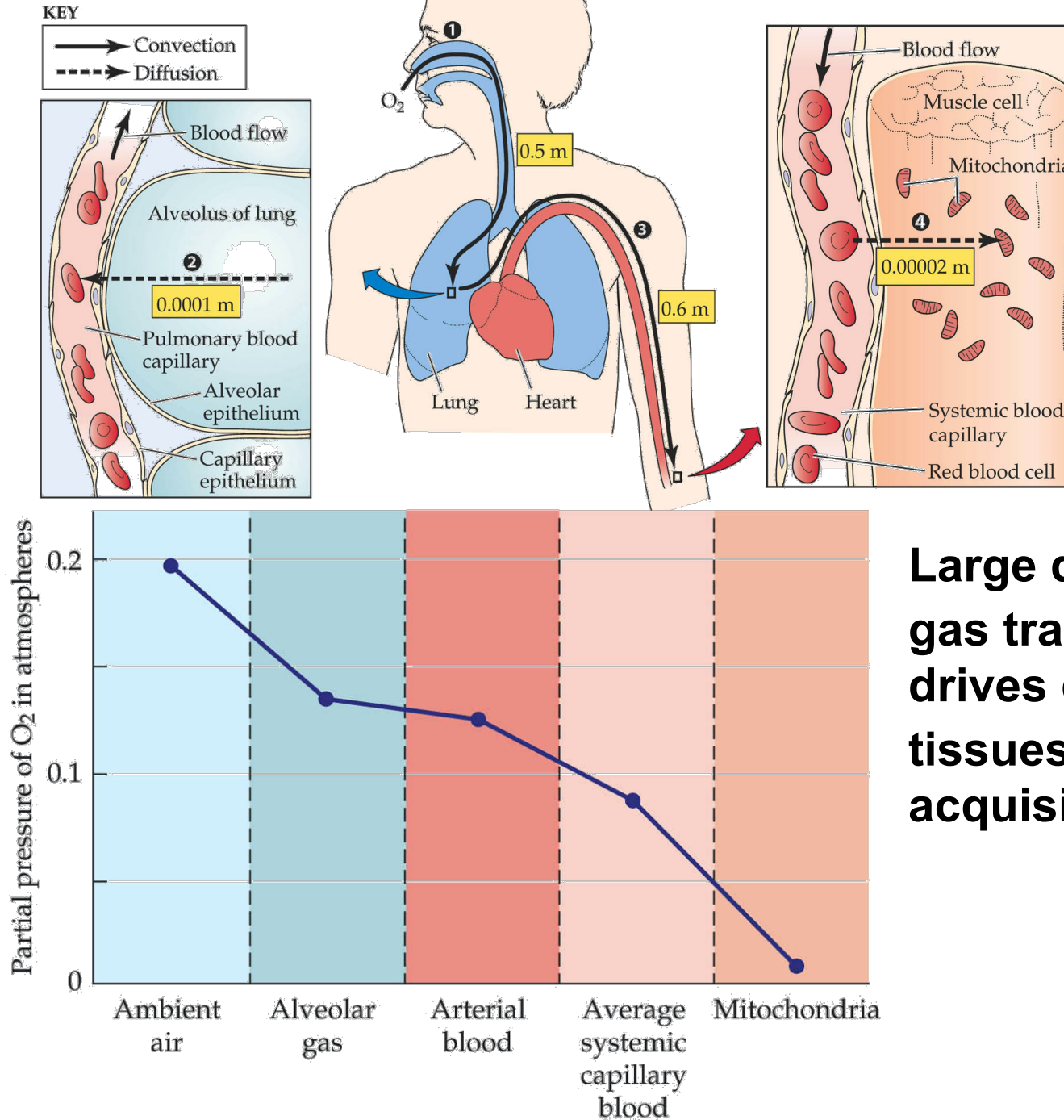
3. convection

4. diffusion

Tidal and Circulatory Convection



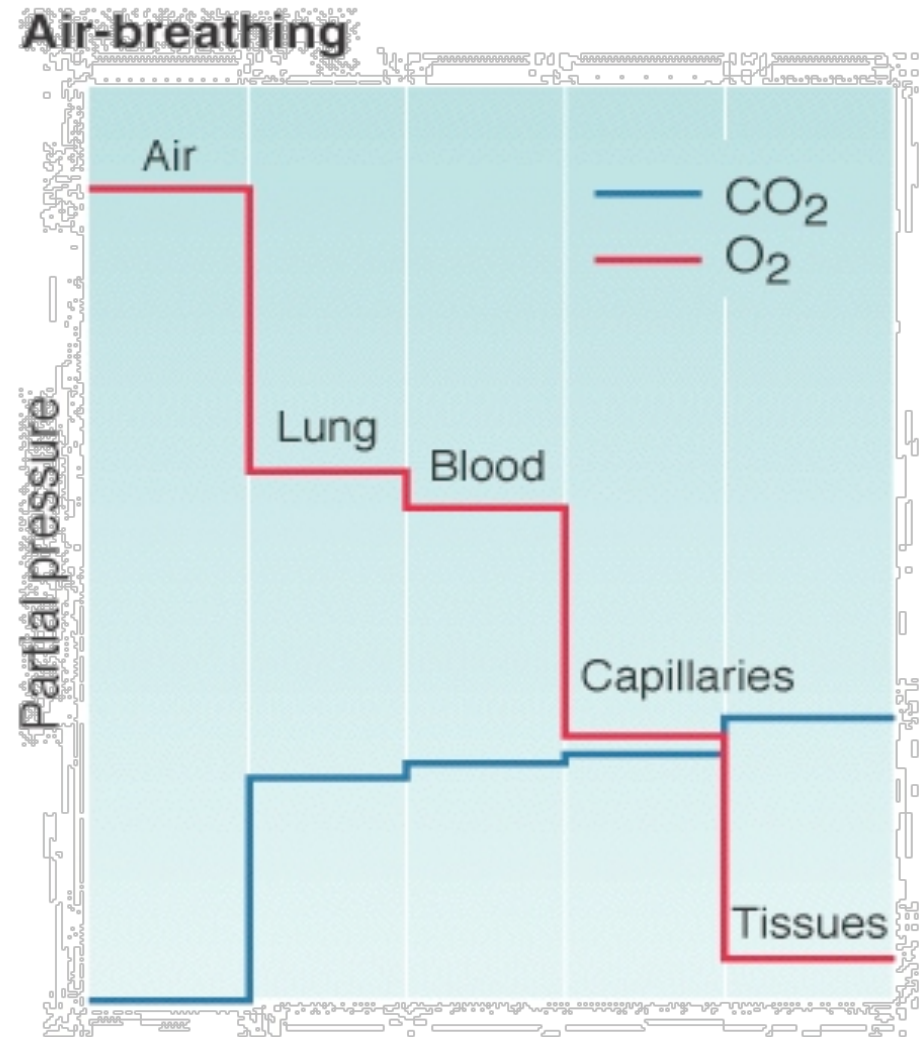
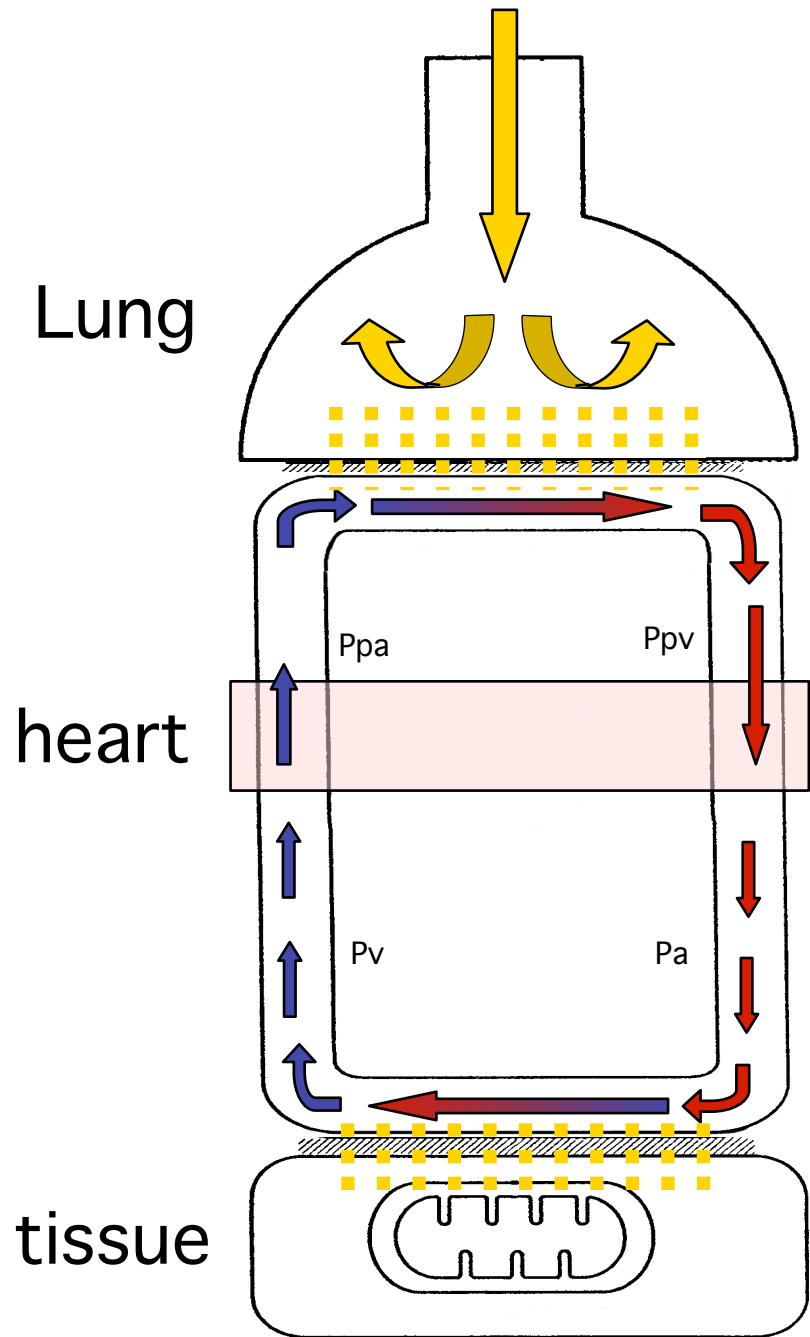
Convection/Diffusion: O₂ cascade



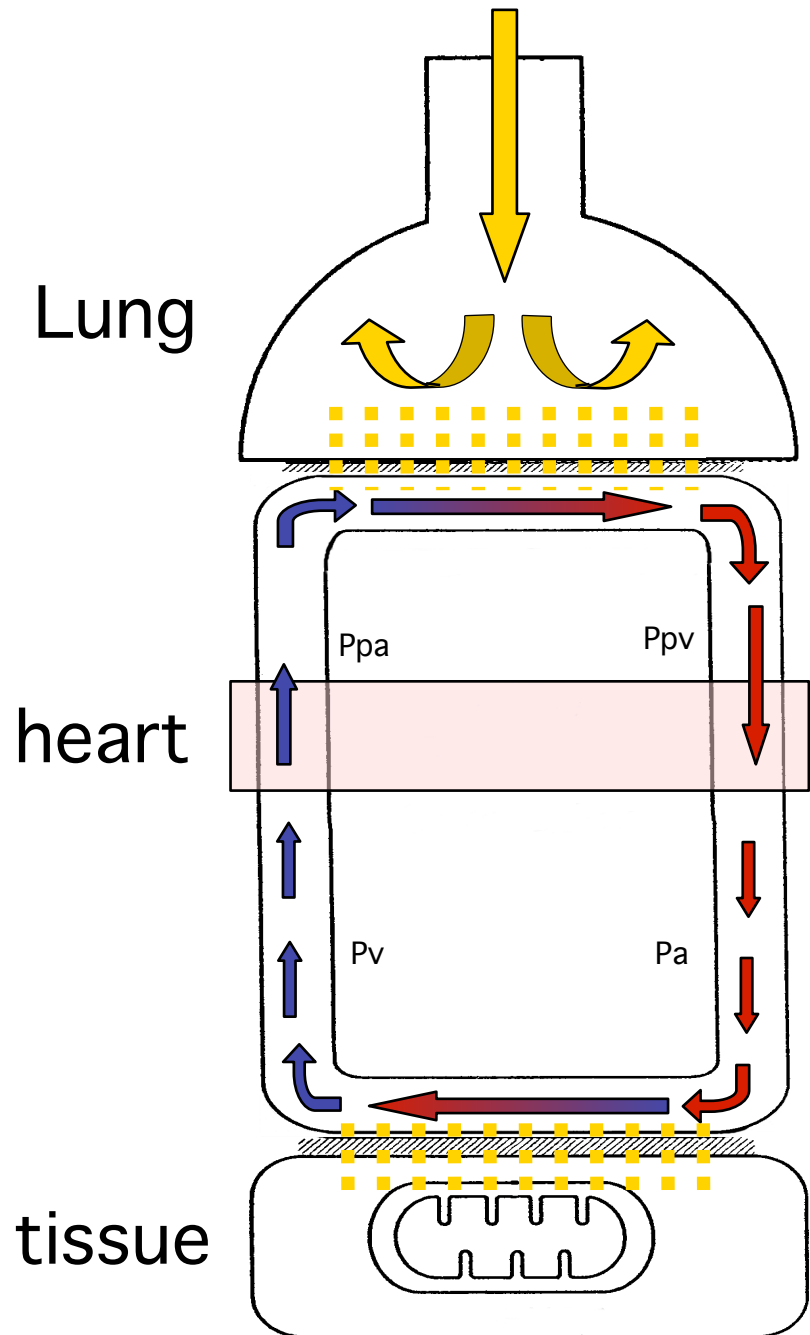
Large differences in PO₂ at gas transport boundaries drives diffusion of O₂ into tissues from site of acquisition to site of usage

Oxygen Cascade

Passive! Requires favorable gradients



Oxygen Cascade



1. convective

$$V_{O_2} = V\beta_{\text{gas}}(P_{I_{O_2}} - P_{E_{O_2}}) = G_{\text{vent}}(\Delta P_{O_2})$$

2. diffusive

$$V_{O_2} = DL_{O_2} (P_{A_{O_2}} - P_{\text{cap}_{O_2}}) = G_{\text{diff}}(\Delta P_{O_2})$$

3. convective

$$V_{O_2} = Q\beta_{\text{blood}}(P_{a_{O_2}} - P_{v_{O_2}}) = G_{\text{perf}}(\Delta P_{O_2})$$

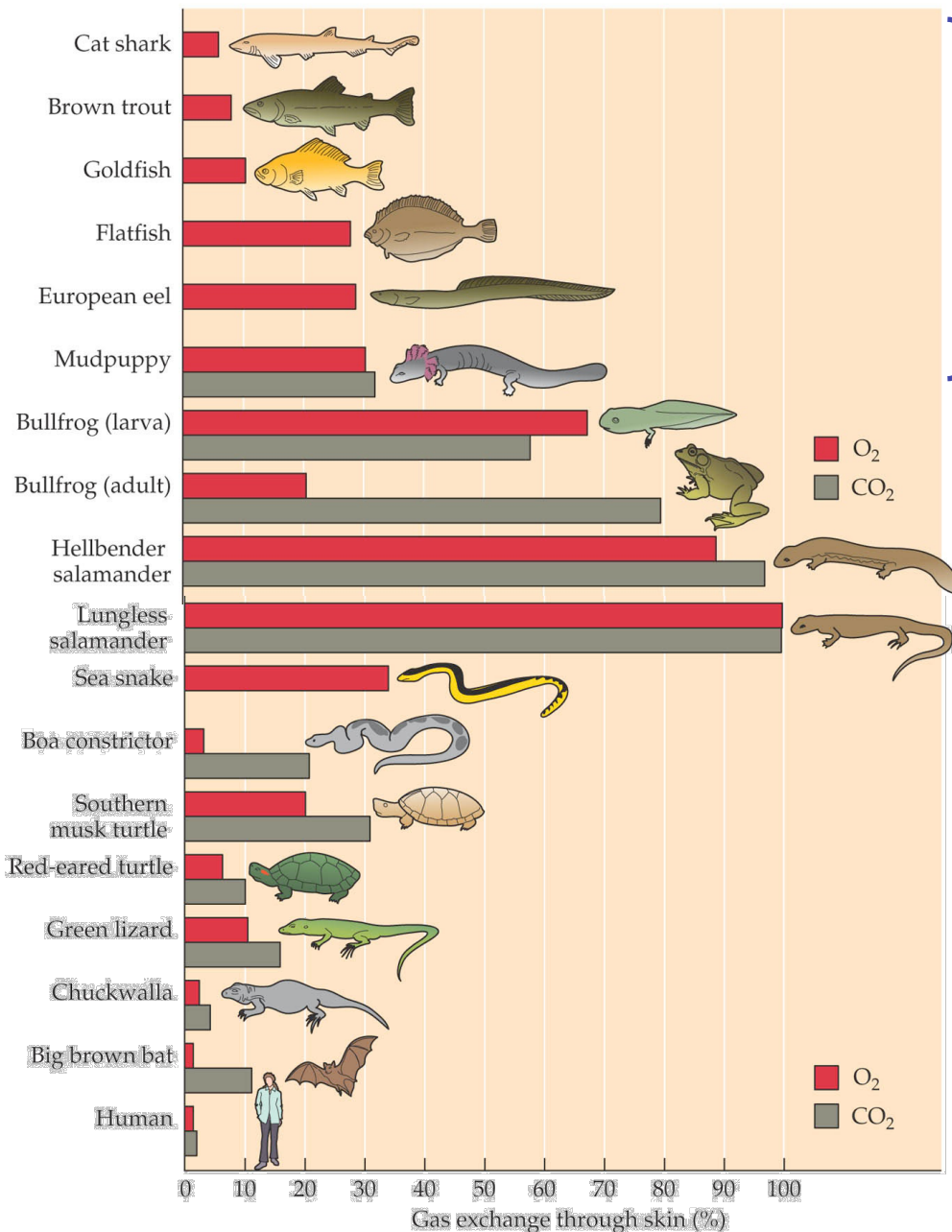
4. diffusive

$$V_{O_2} = DM_{O_2}(P_{a_{O_2}} - P_{\text{mit}_{O_2}}) = G_{\text{diff}}(\Delta P_{O_2})$$

Gas Exchange Surfaces and Surface Area

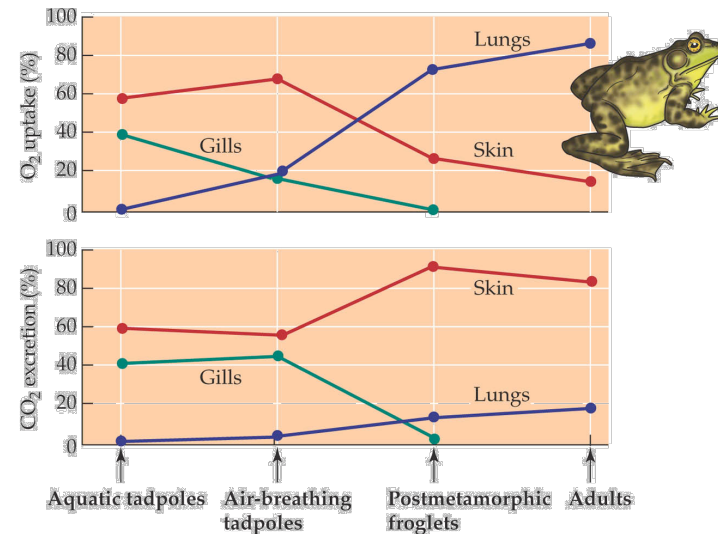
- Skin
- Gills
- Lungs

Gas exchange through skin



Fully aquatic organisms:

Amphibious organisms:



Adult bullfrogs use skin for CO₂ exchange and lungs for O₂ exchange

Seasonal variation: underwater overwintering

Terrestrial organisms:

Surface Area/Volume relationships

- Gas exchange is limited by area of surfaces contacting environment
 - Skin: low surface area, limited potential to increase



Lake Titicaca
frog,
Talmatobius
culeus



©K.-H. Junger

Ventilation Patterns

Gills

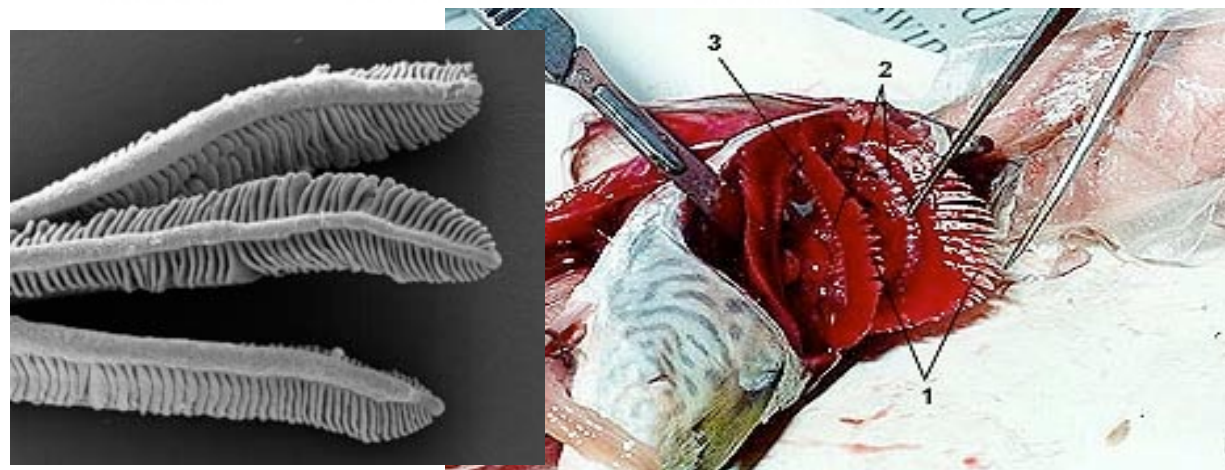
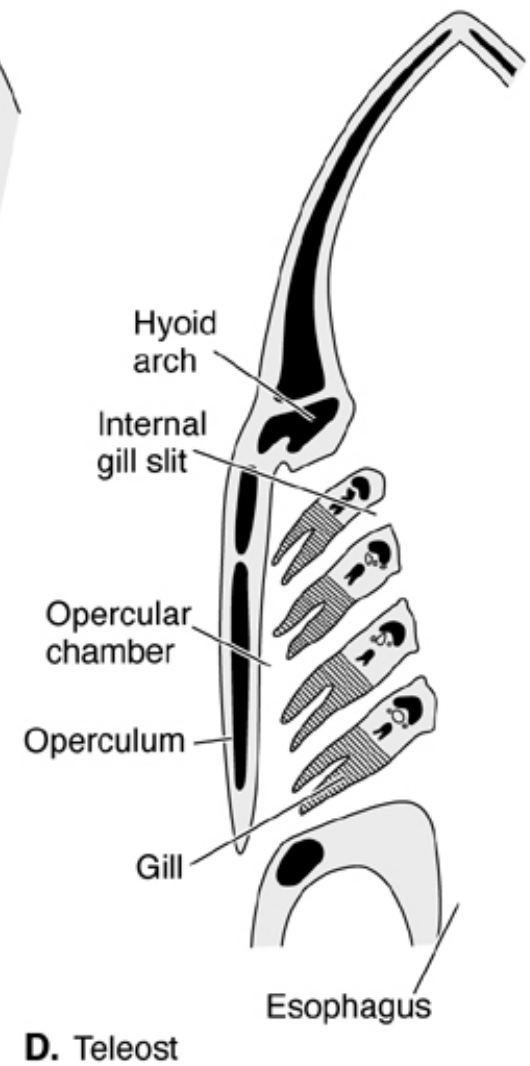
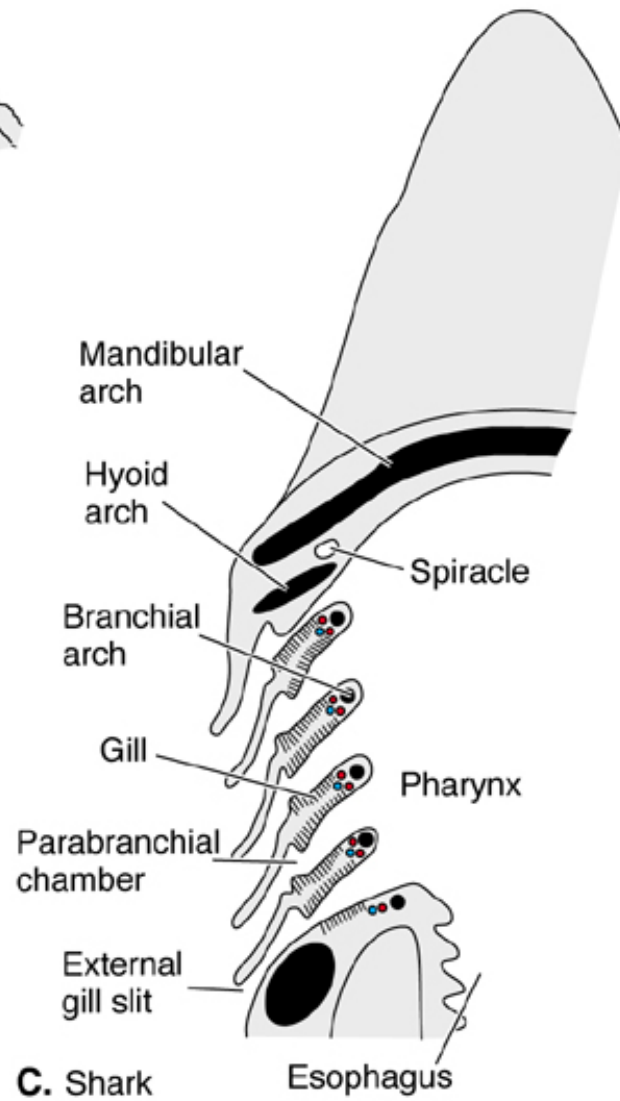
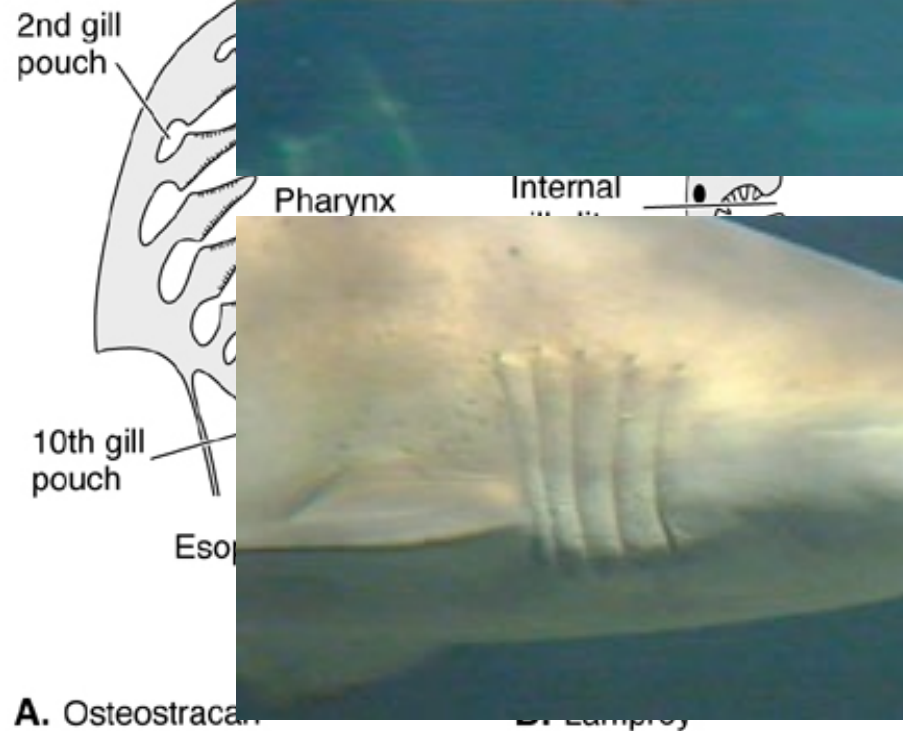
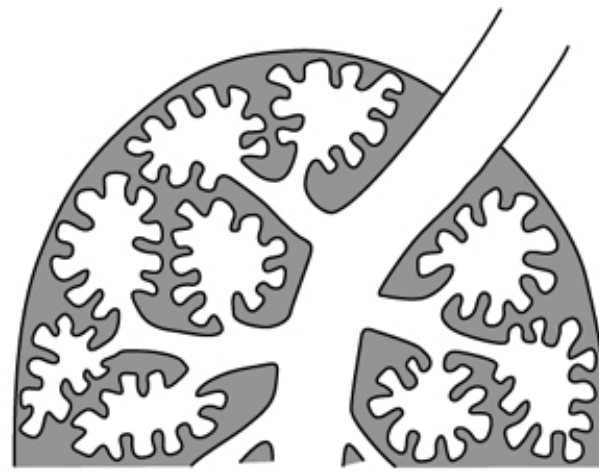
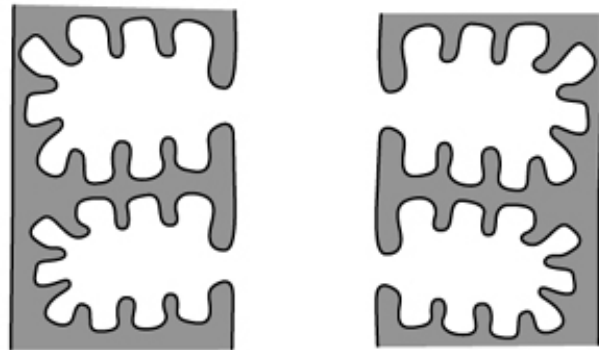


Fig. 18.2

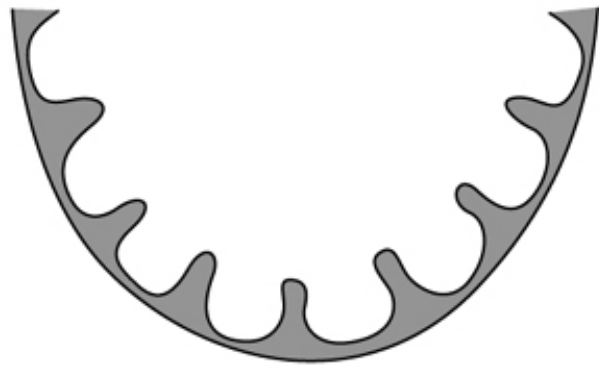
Vertebrate Lungs increase in SA



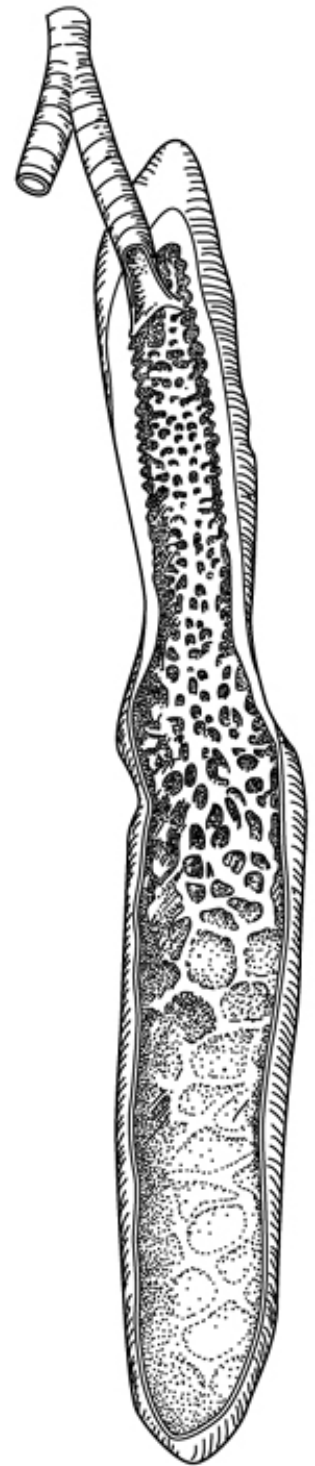
C. Mammal



B. "Reptile"



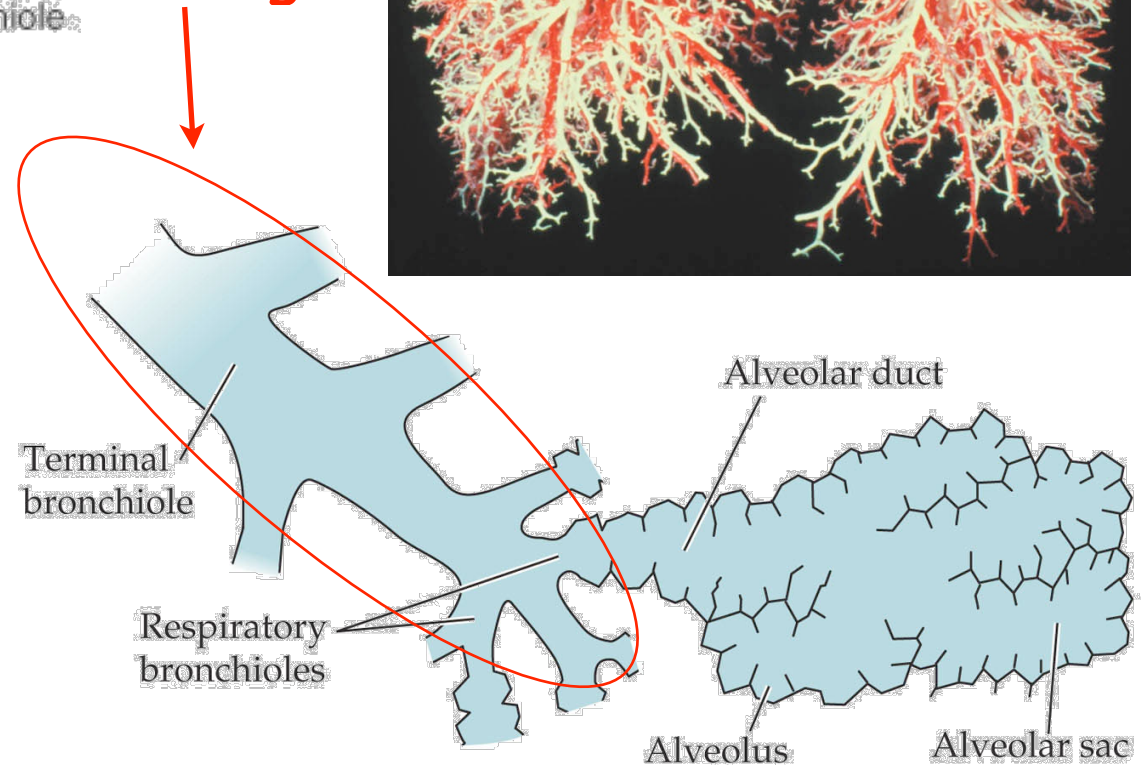
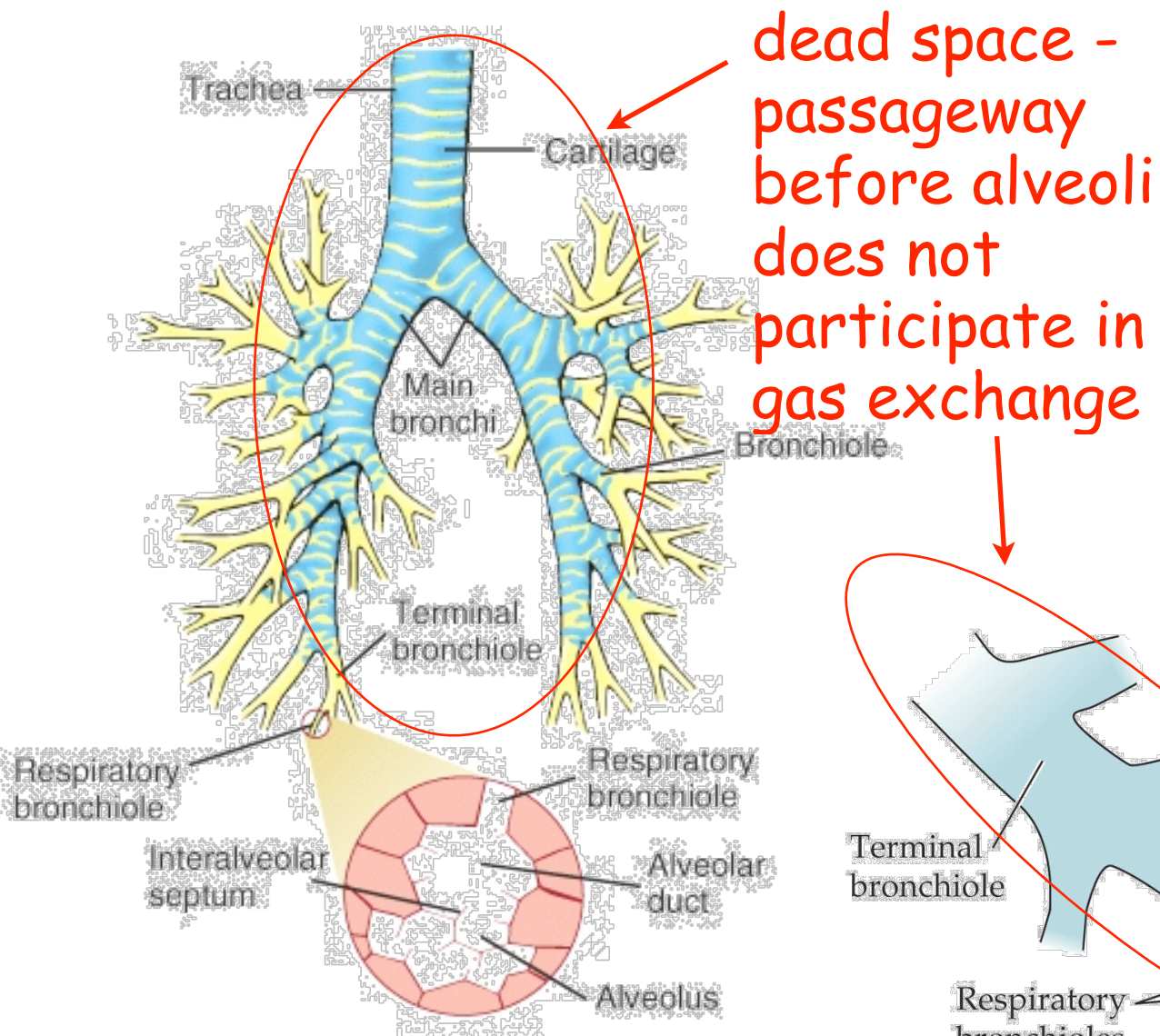
A. Amphibian



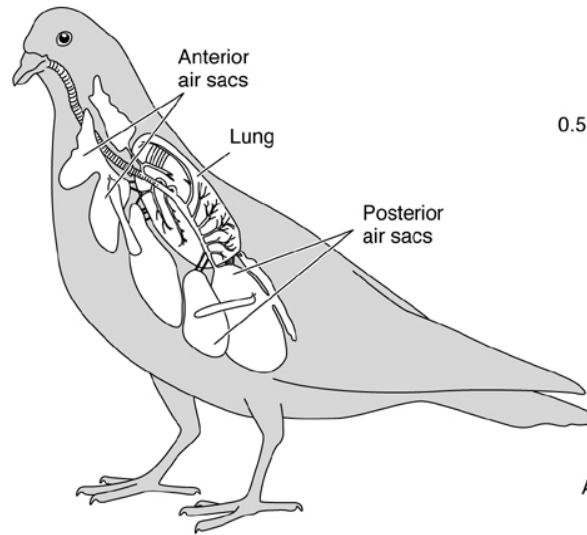
D. Ophiosaurus

Fig. 18.15

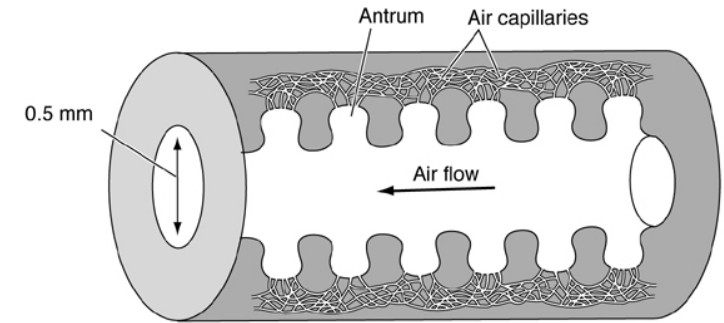
Mammal Lungs: Alveolar surfaces are sites of gas exchange



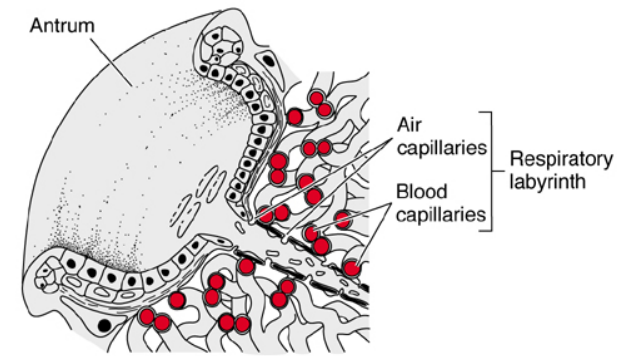
Bird Lungs



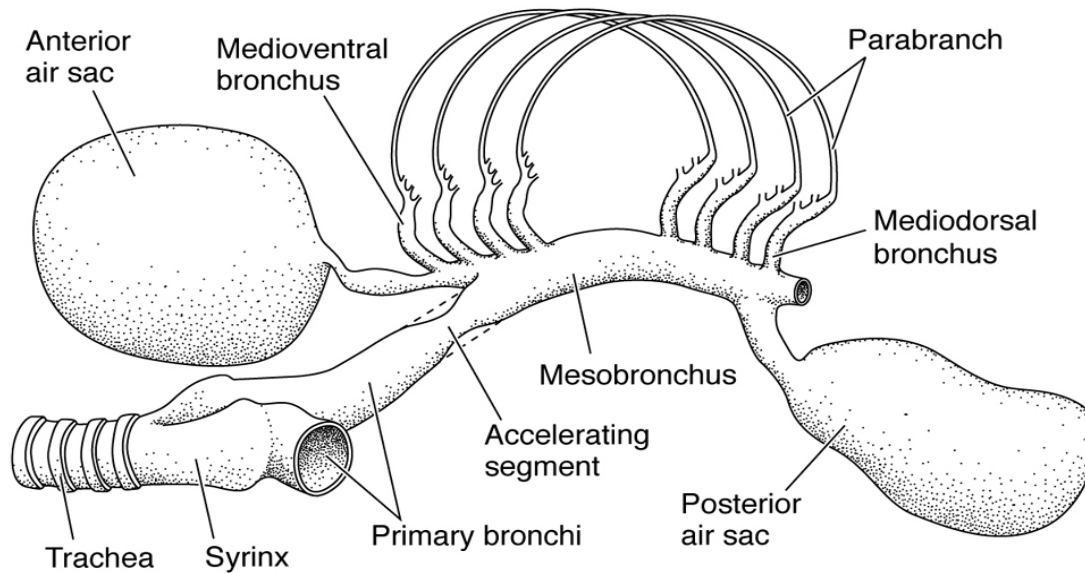
A. Lungs and air sacs



B. Parabronchus and air capillaries

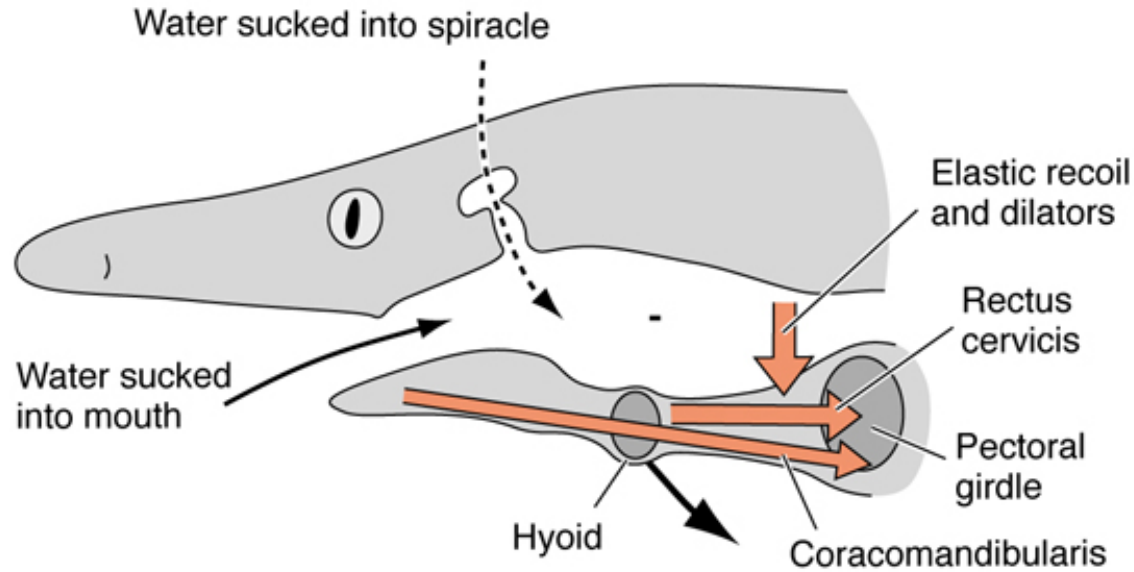


C. Antrum and respiratory labyrinth

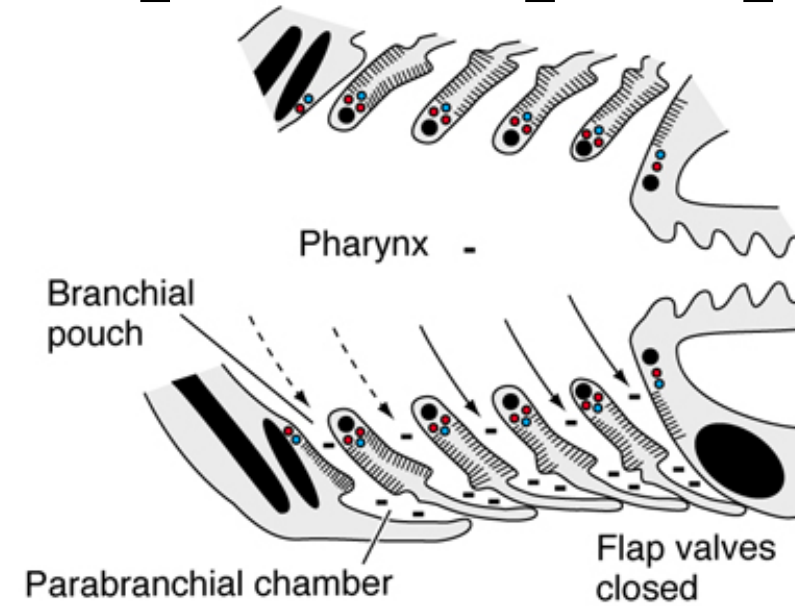


Fish Pumps & Gills

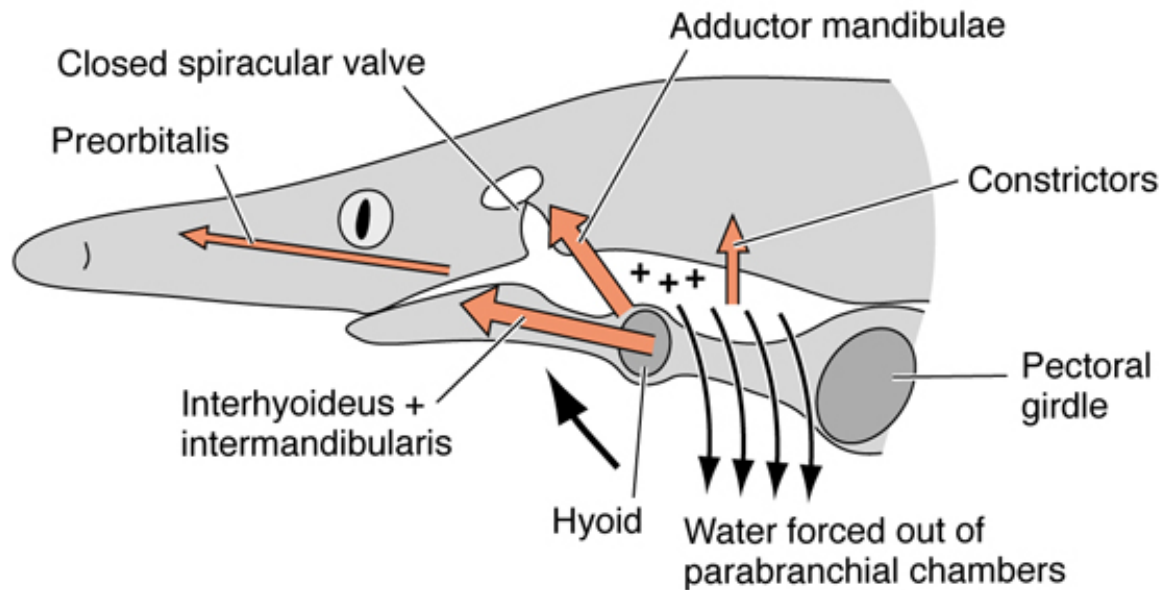
Elasmobranchs: suction pump-force pump



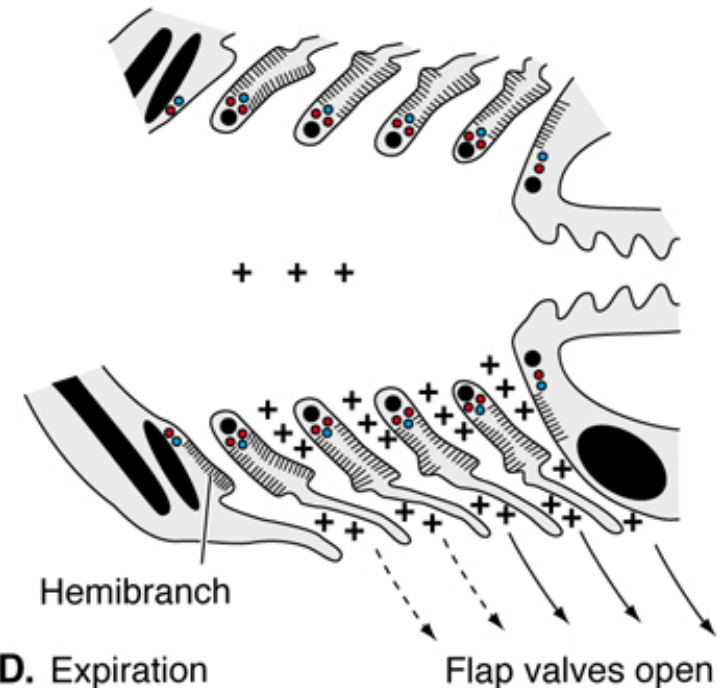
A. Suction pump



B. Inspiration



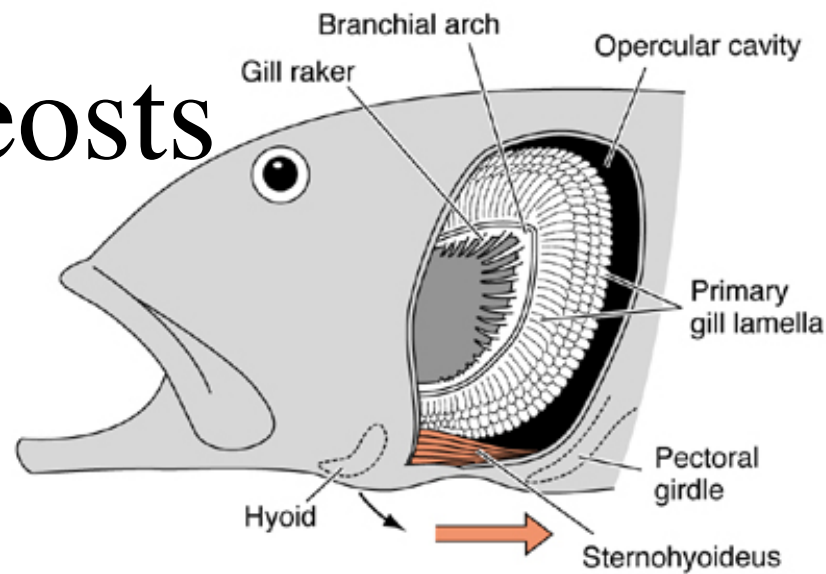
C. Force pump



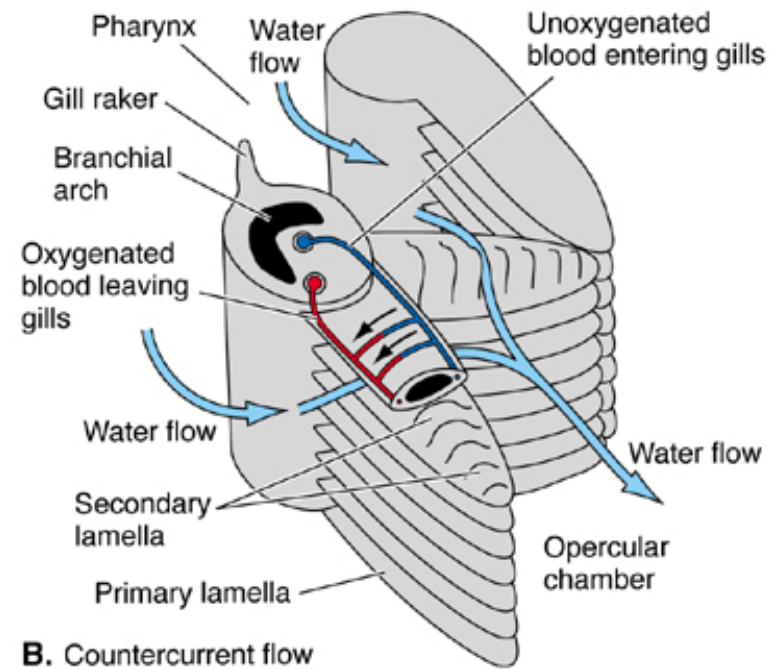
D. Expiration

Fig. 18.5

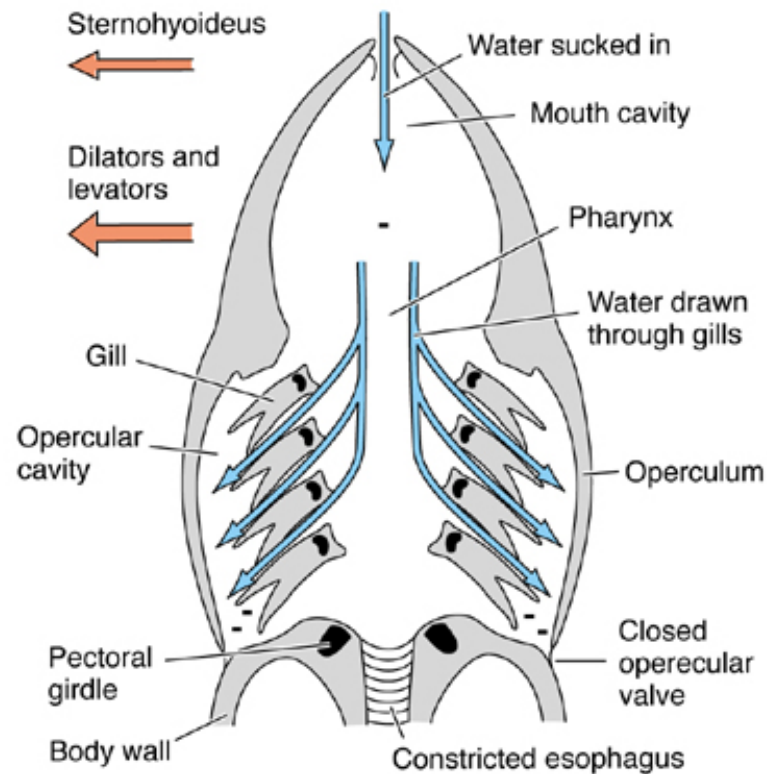
Teleosts



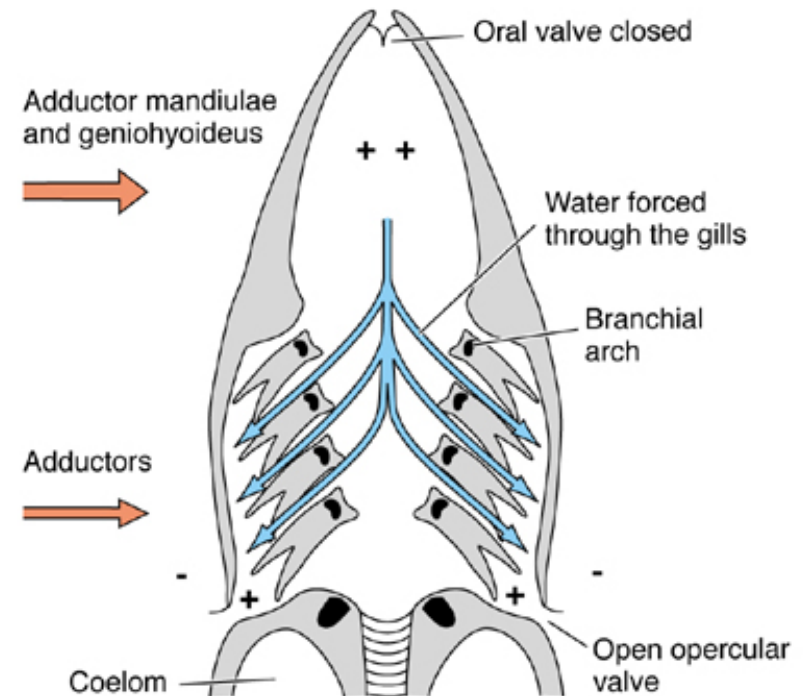
A. Lateral view



B. Countercurrent flow



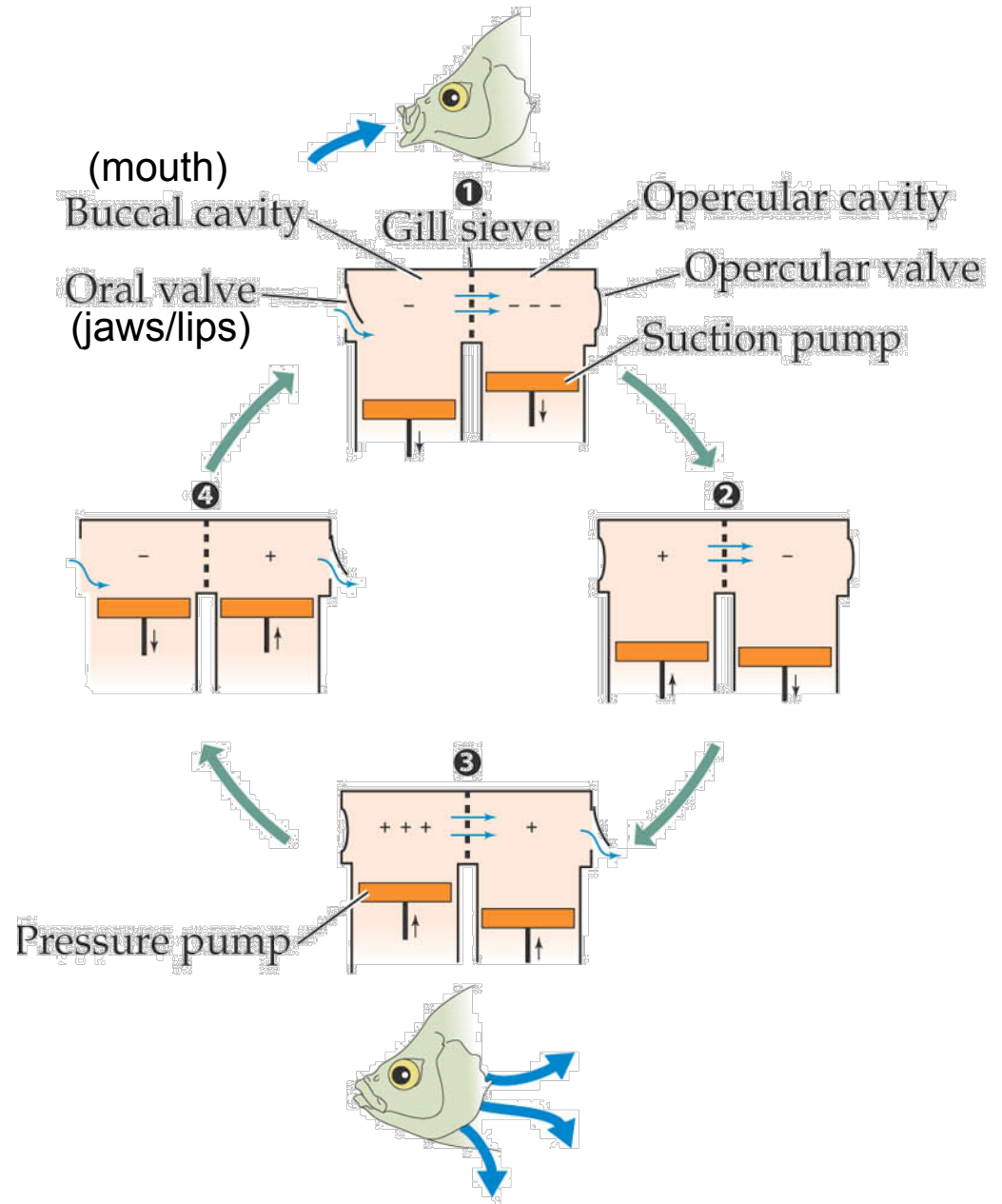
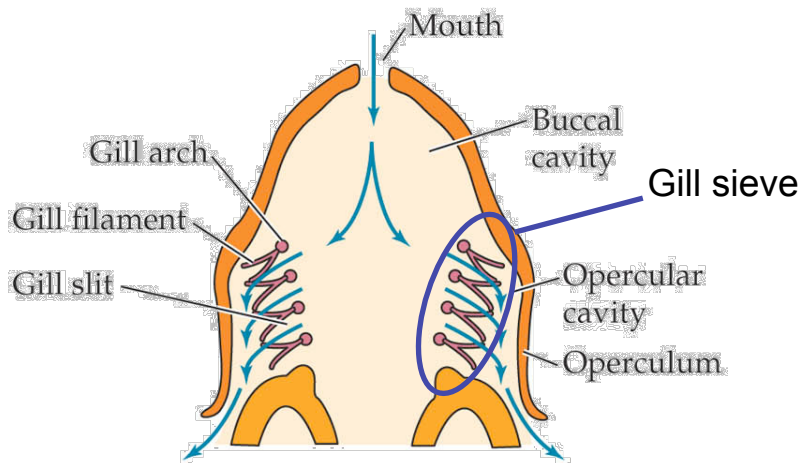
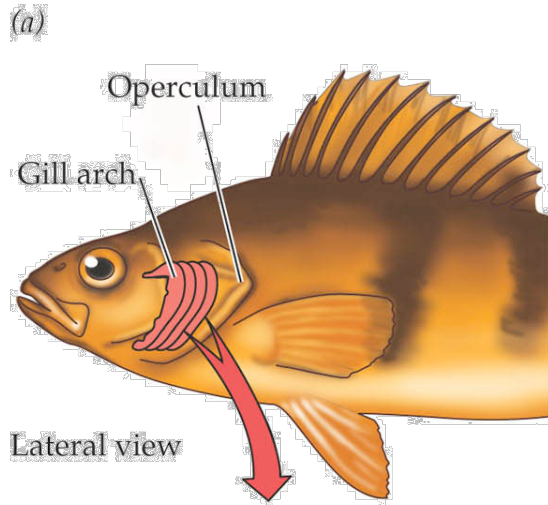
C. Inspiration (expansion stage)



D. Inspiration (compression stage)

Fig. 18.6

Fish gills: opercular breathing



Gill “Sieve”

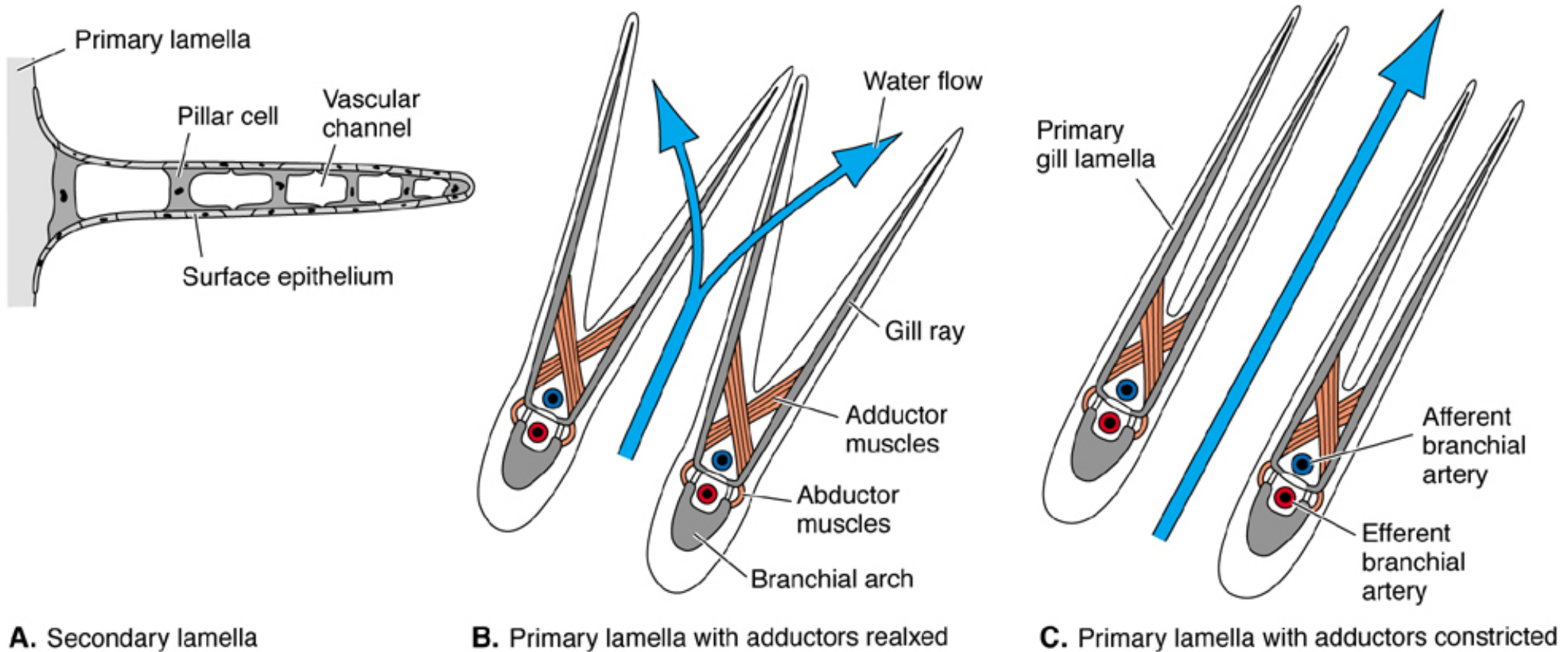
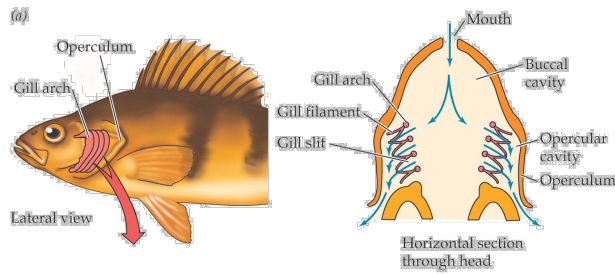


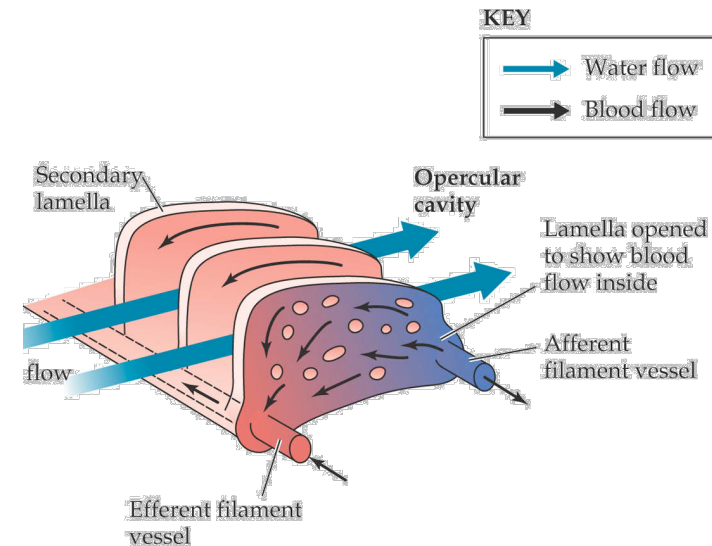
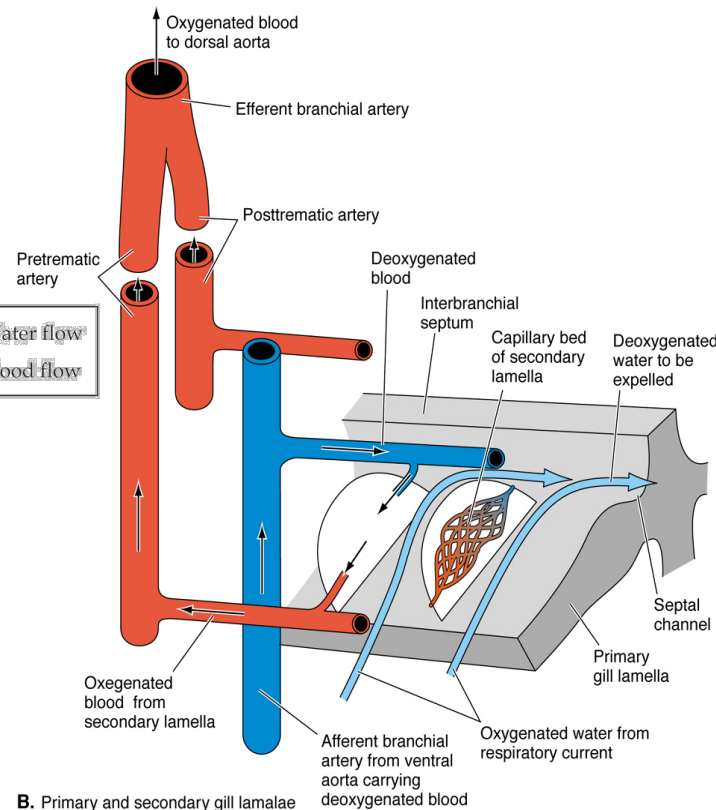
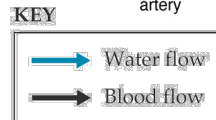
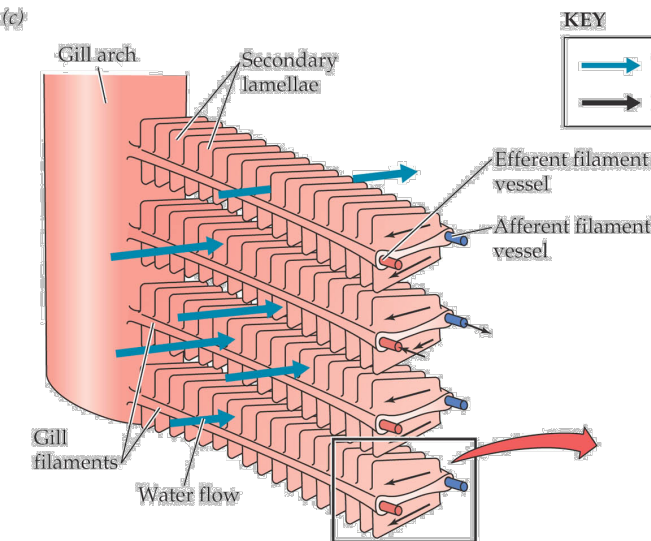
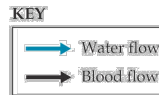
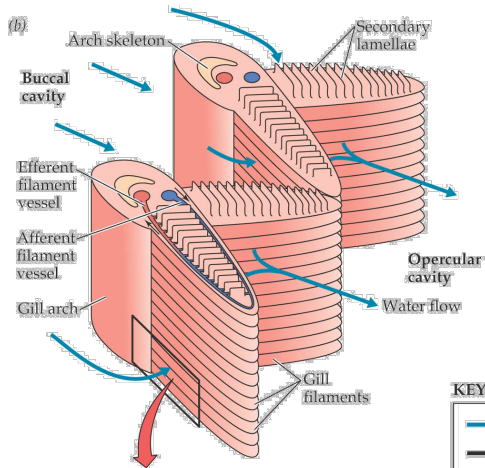
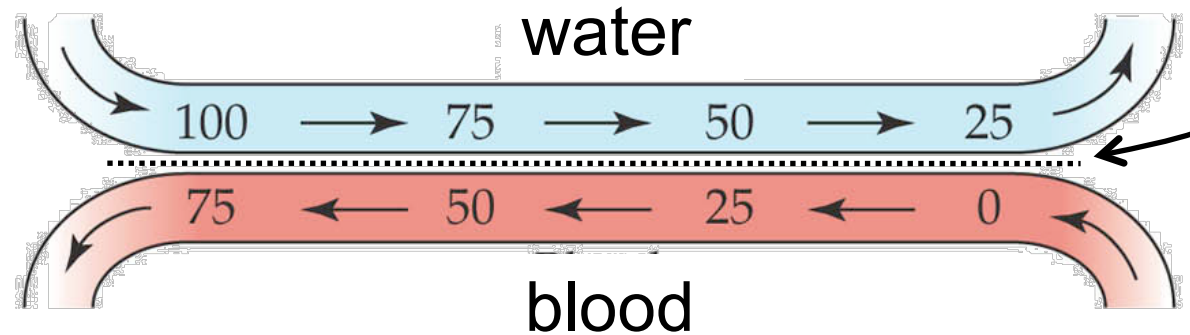
Fig. 18.7

Gill function



Gill surface

(b) Countercurrent gas exchange



Gas Exchange Models

Lung Air Flow Patterns

Pump Evolution (Lungs)

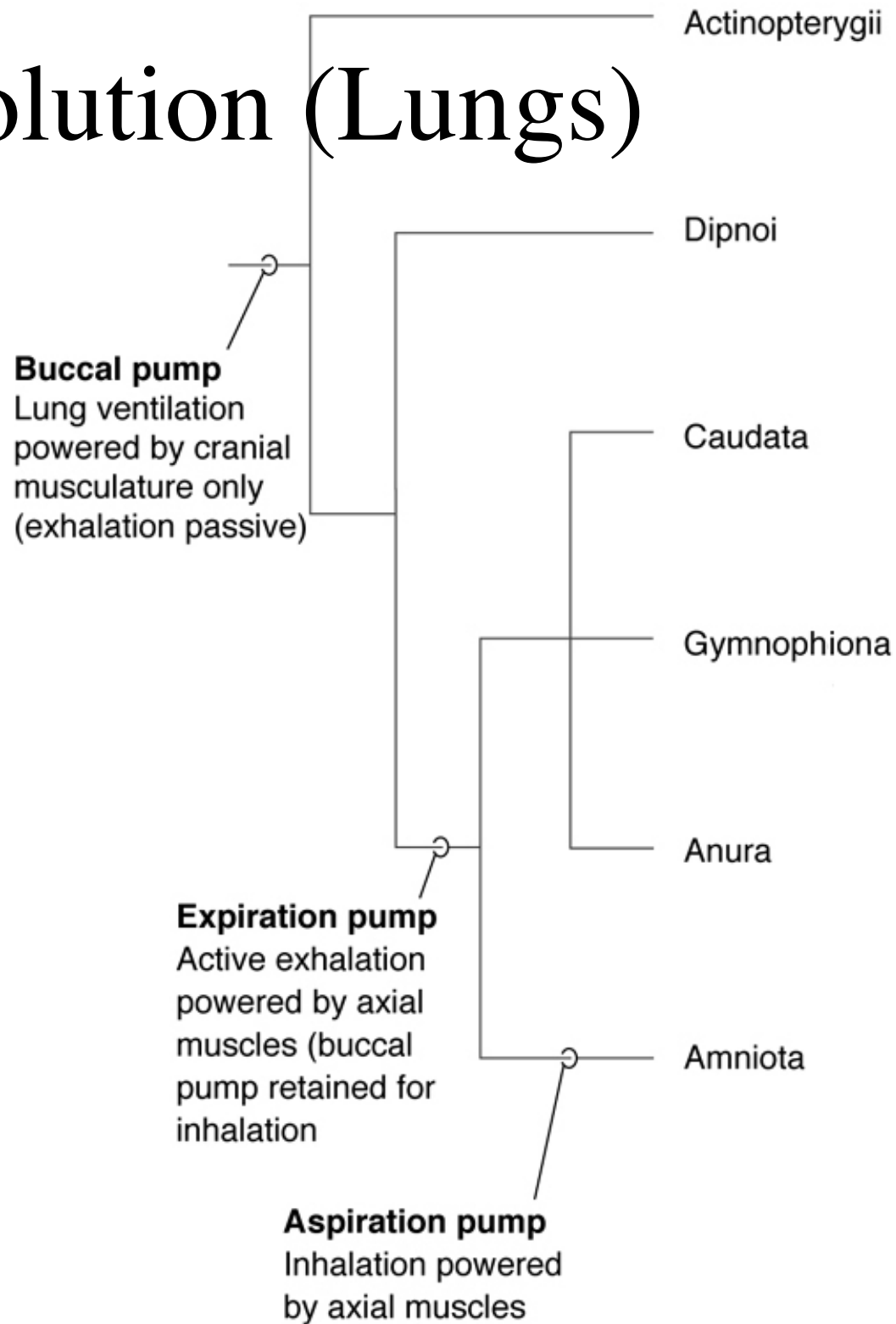
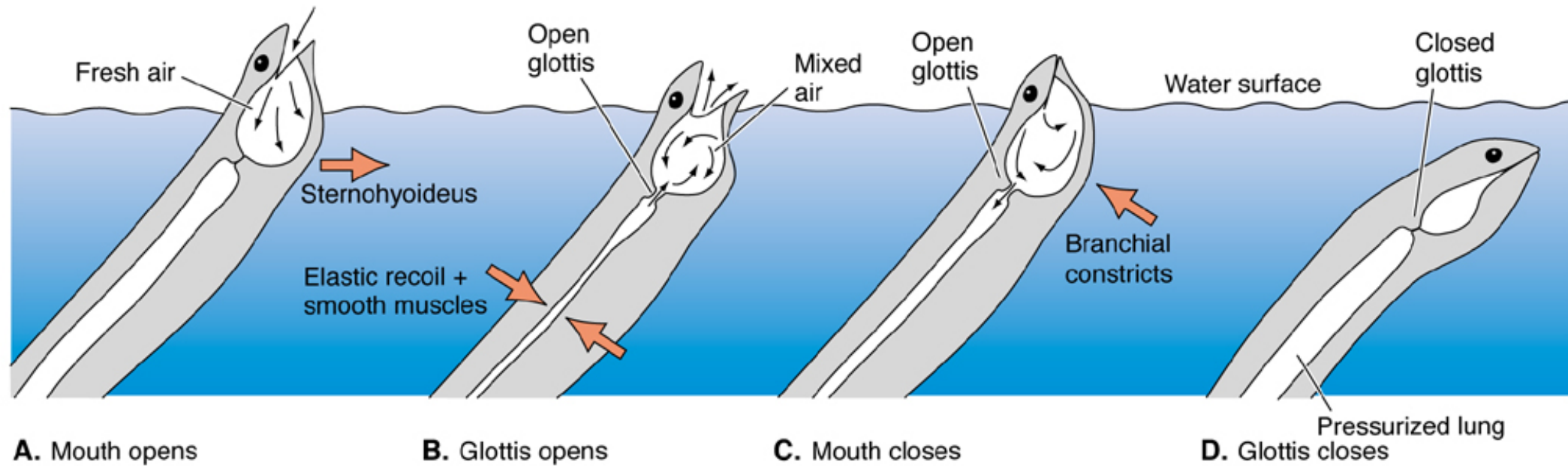


Fig. 18.23

PUMPS: Lungfish: Buccal Pump



Inspiration: Buccal pump

Expiration: passive

Fig. 18.10

Amphibian: Buccal Pump

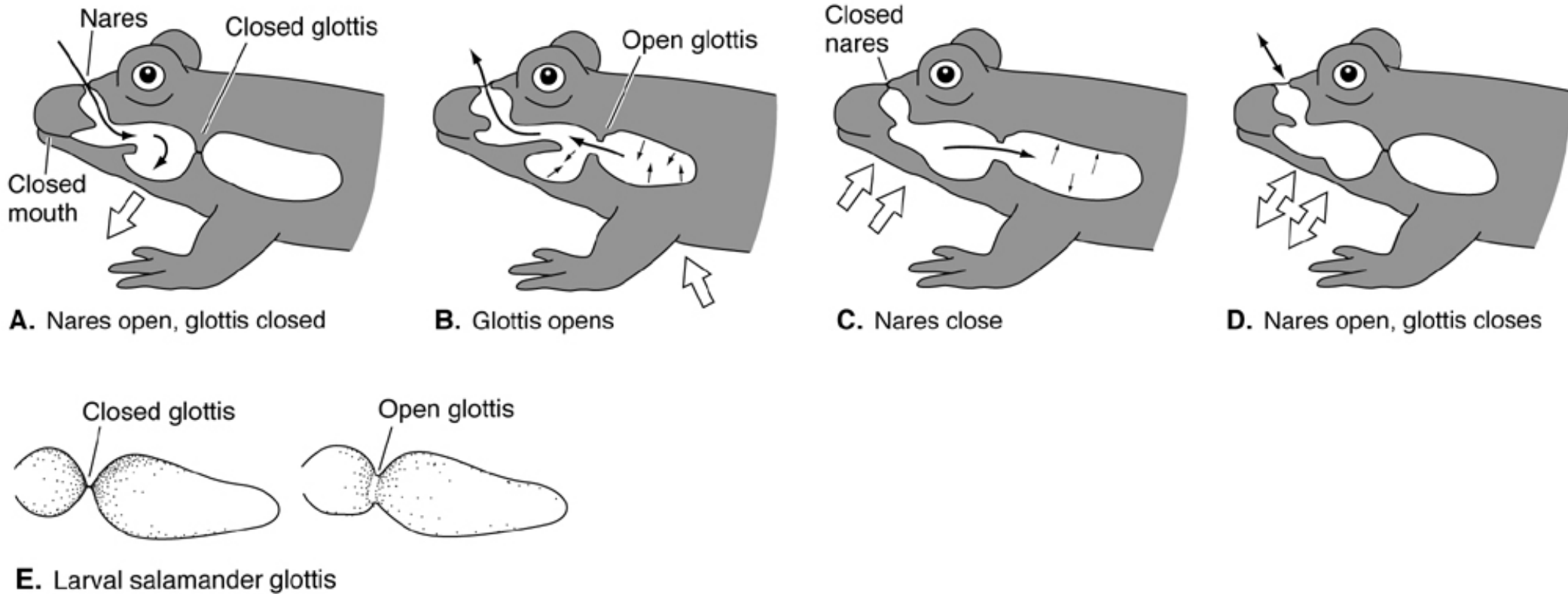
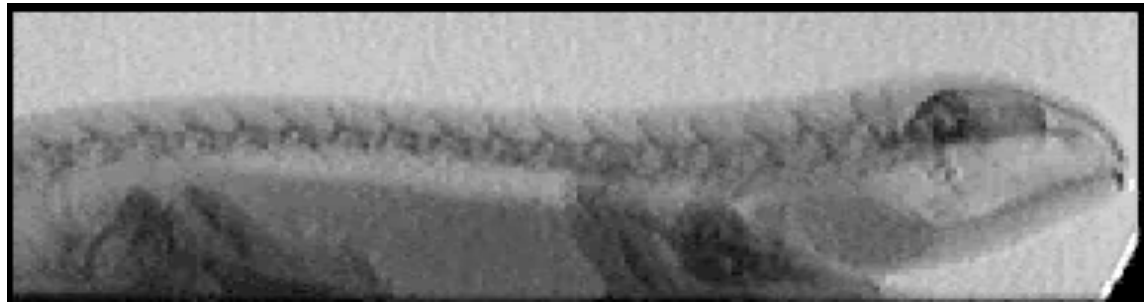
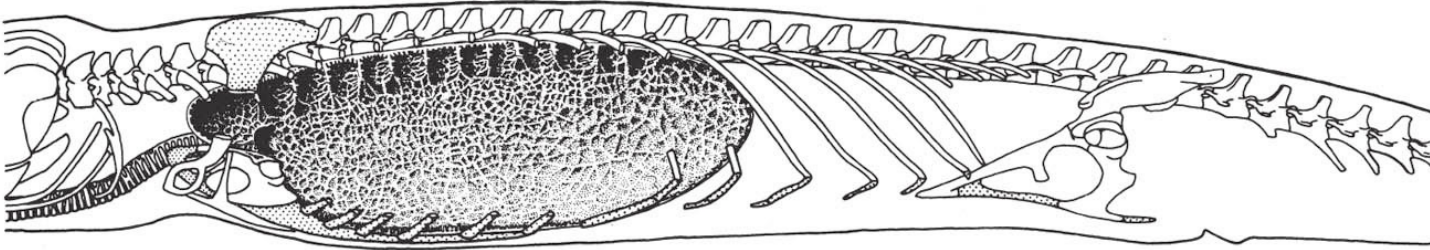


Fig. 18.14



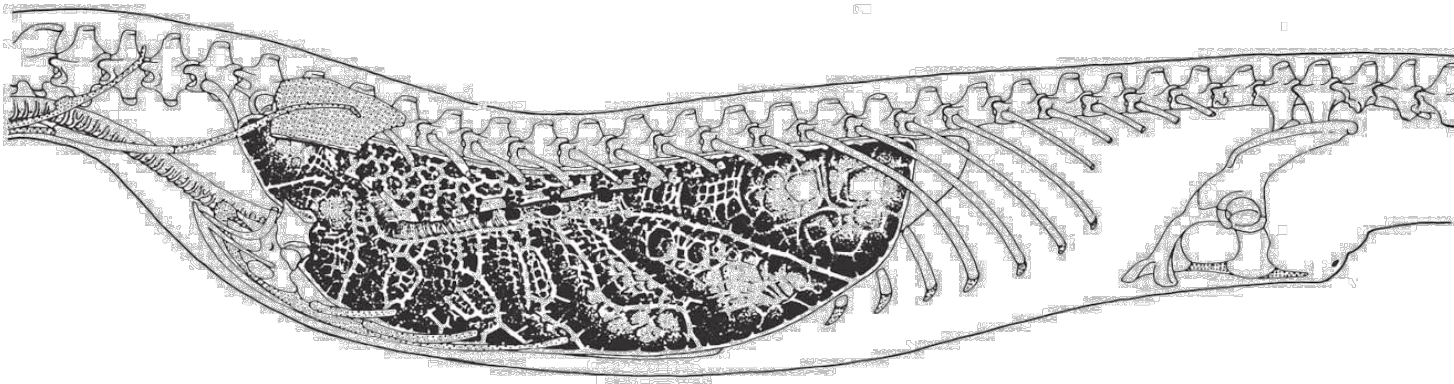
Vertebrate Lungs: Reptiles

(a) A unicameral lung in a lacertid lizard



Courtesy of Hans-Rainer Dunder

(c) A multicameral lung in a monitor lizard



Courtesy of Hans-Rainer Dunder

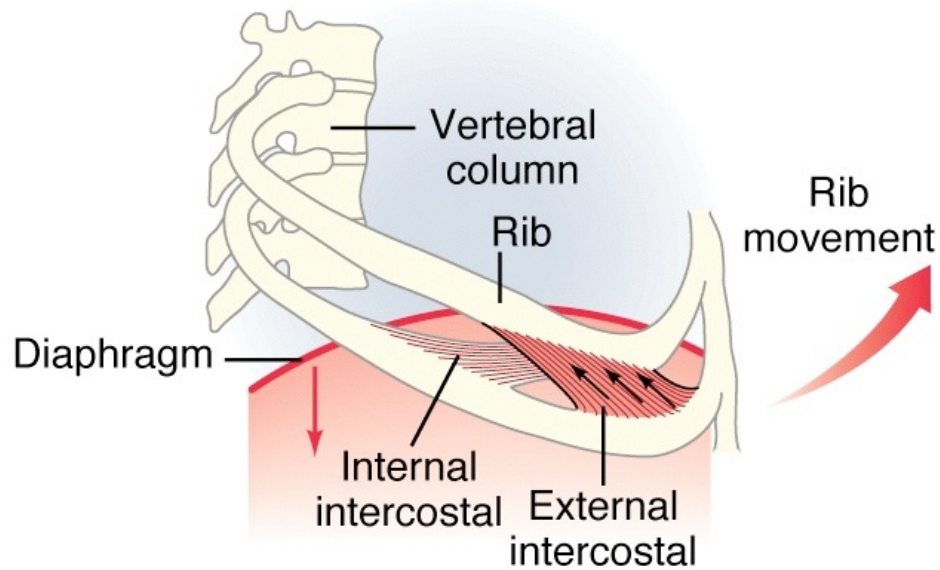
Tracheal
reinforcement

Increased surface
area

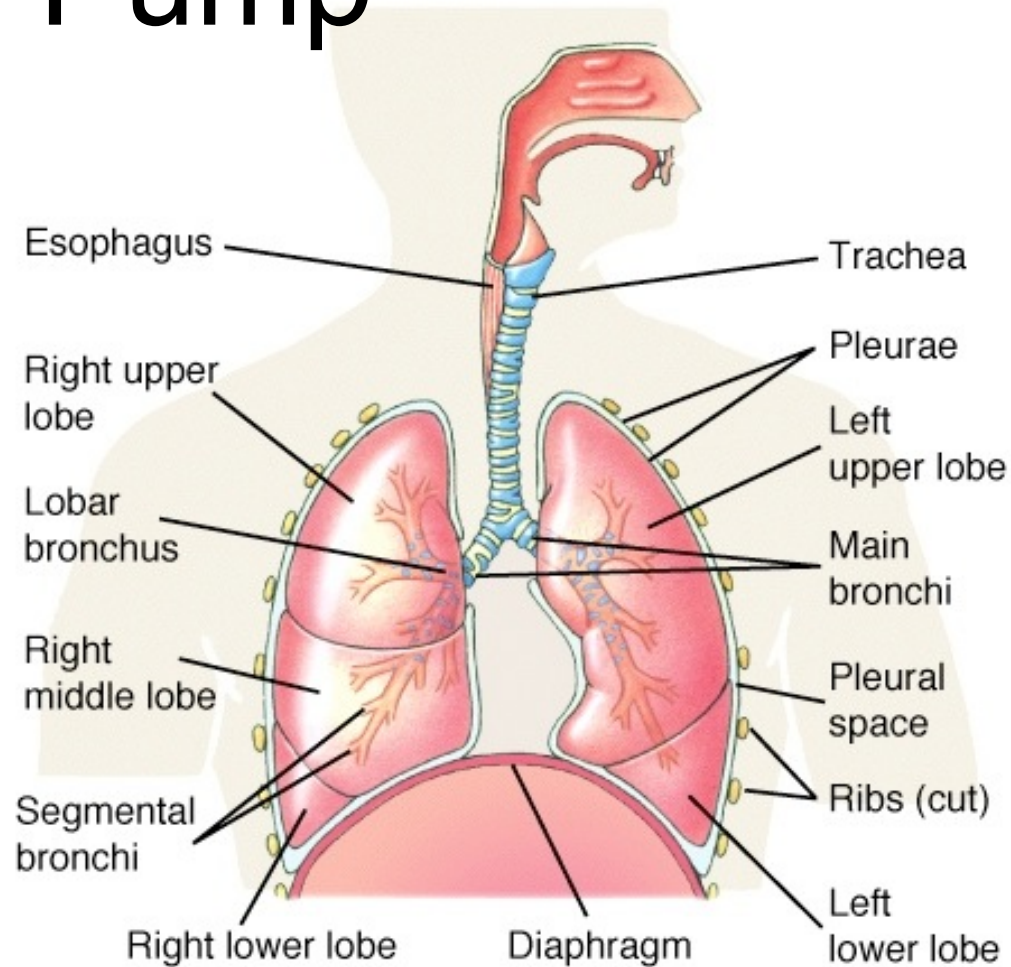
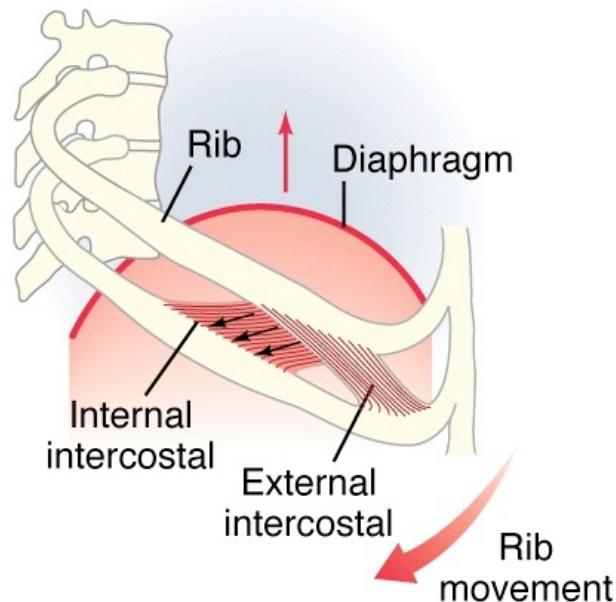
Higher metabolic rate
supported

Aspiration Pump: Intercostal Suction Pump

(a) **Inhalation**



(b) **Exhalation**



Mammals have diaphragm

All amniotes (birds, reptiles, mammals) have aspiration pump



Crocodilians: Diaphragmatic Muscle!

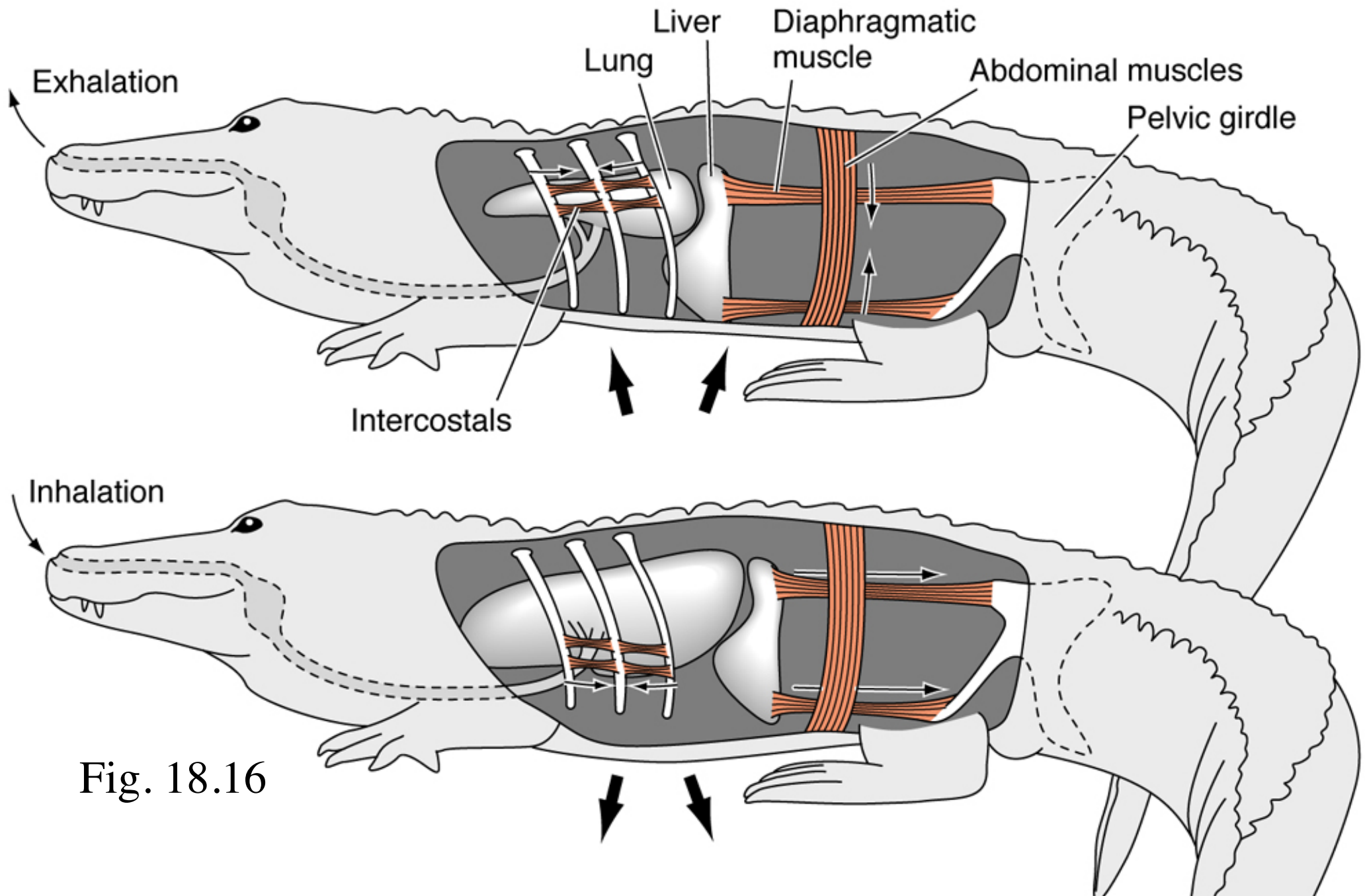
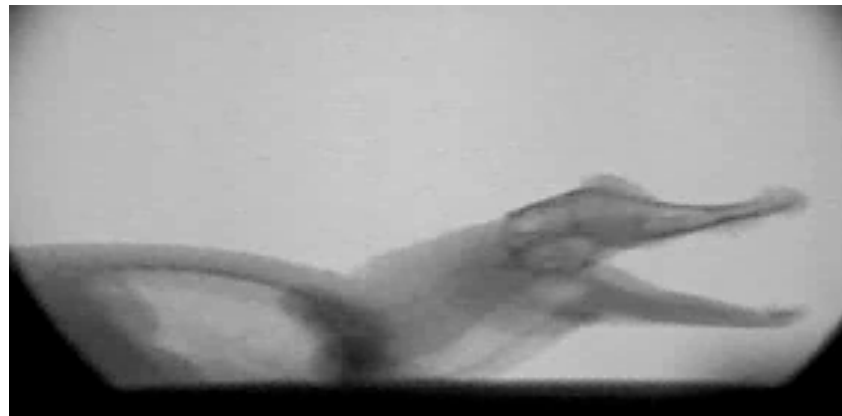
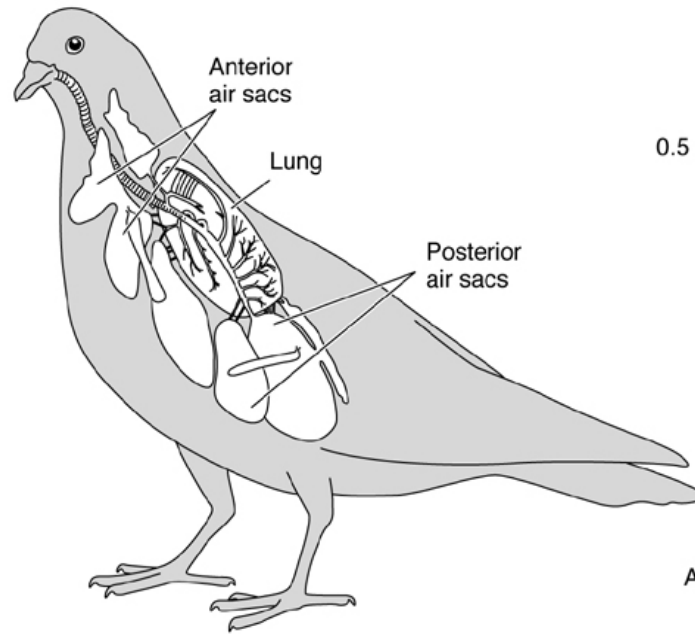
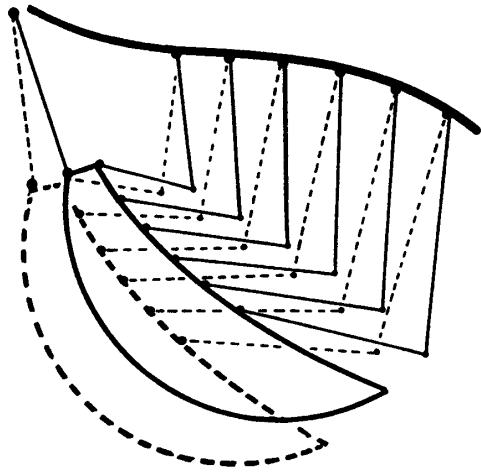
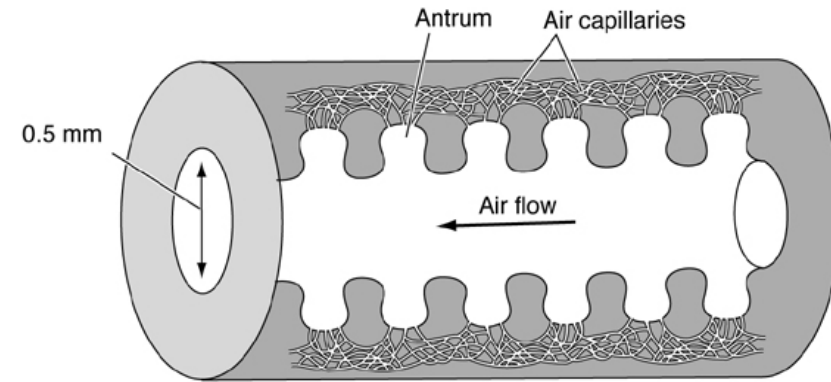


Fig. 18.16

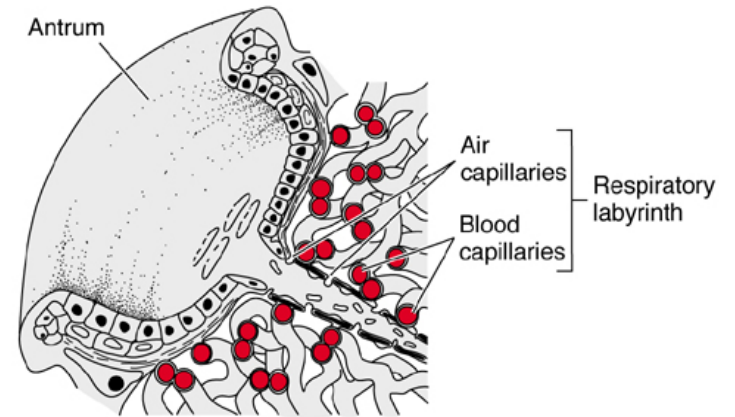




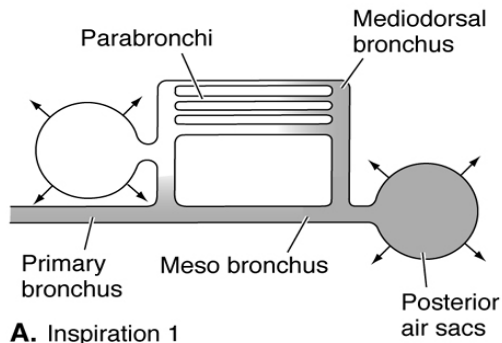
A. Lungs and air sacs



B. Parabronchus and air capillaries

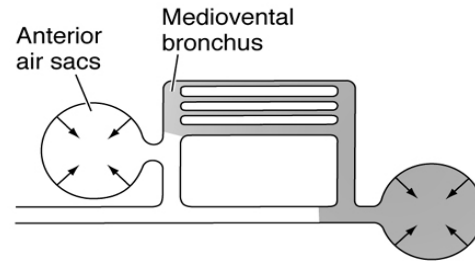


C. Antrum and respiratory labyrinth

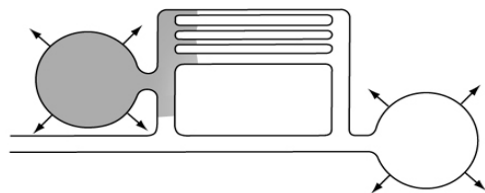


A. Inspiration 1

Cycle 1

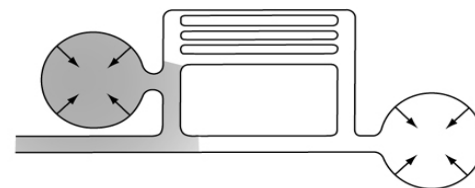


B. Expiration 1



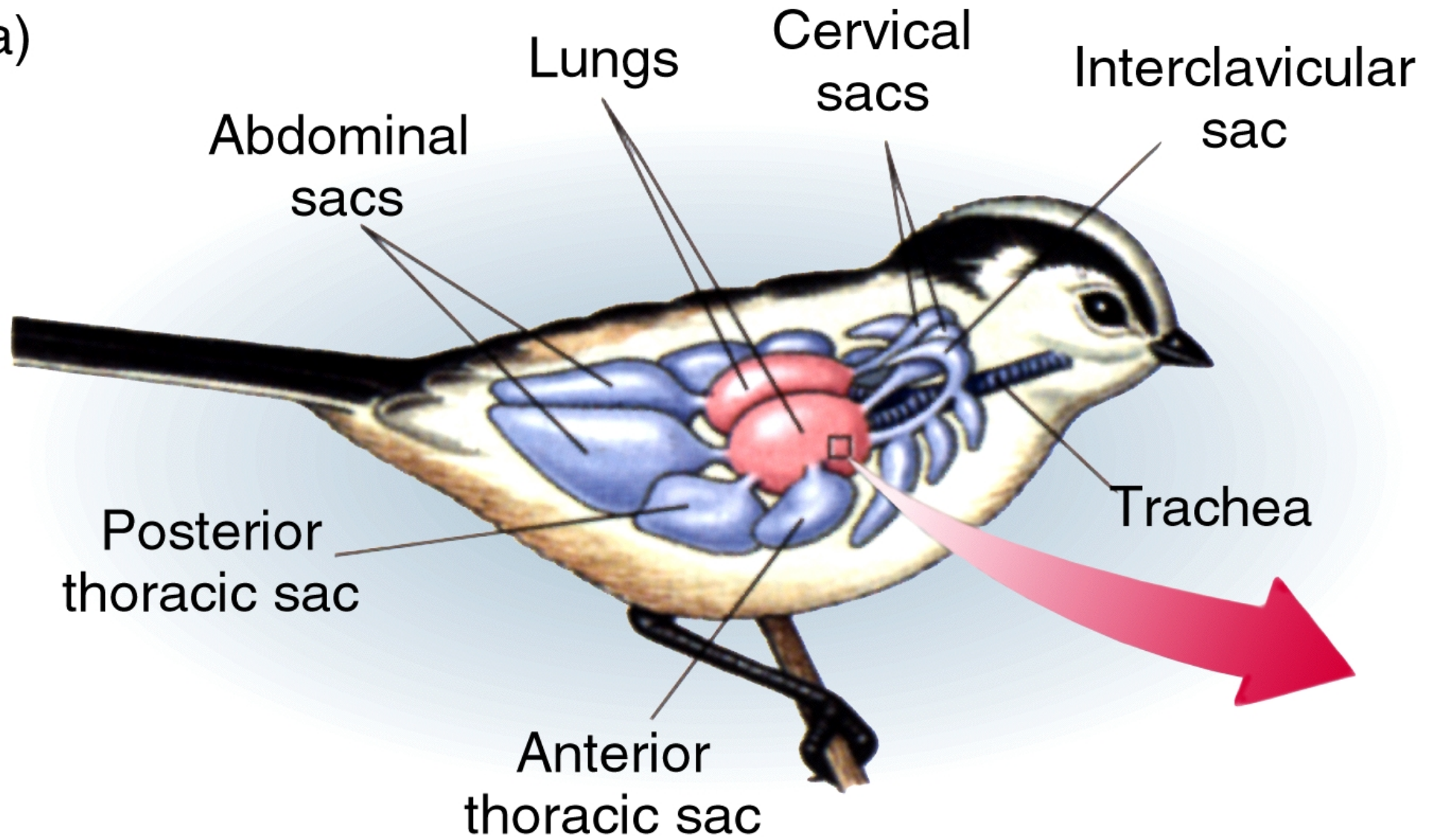
C. Inspiration 2

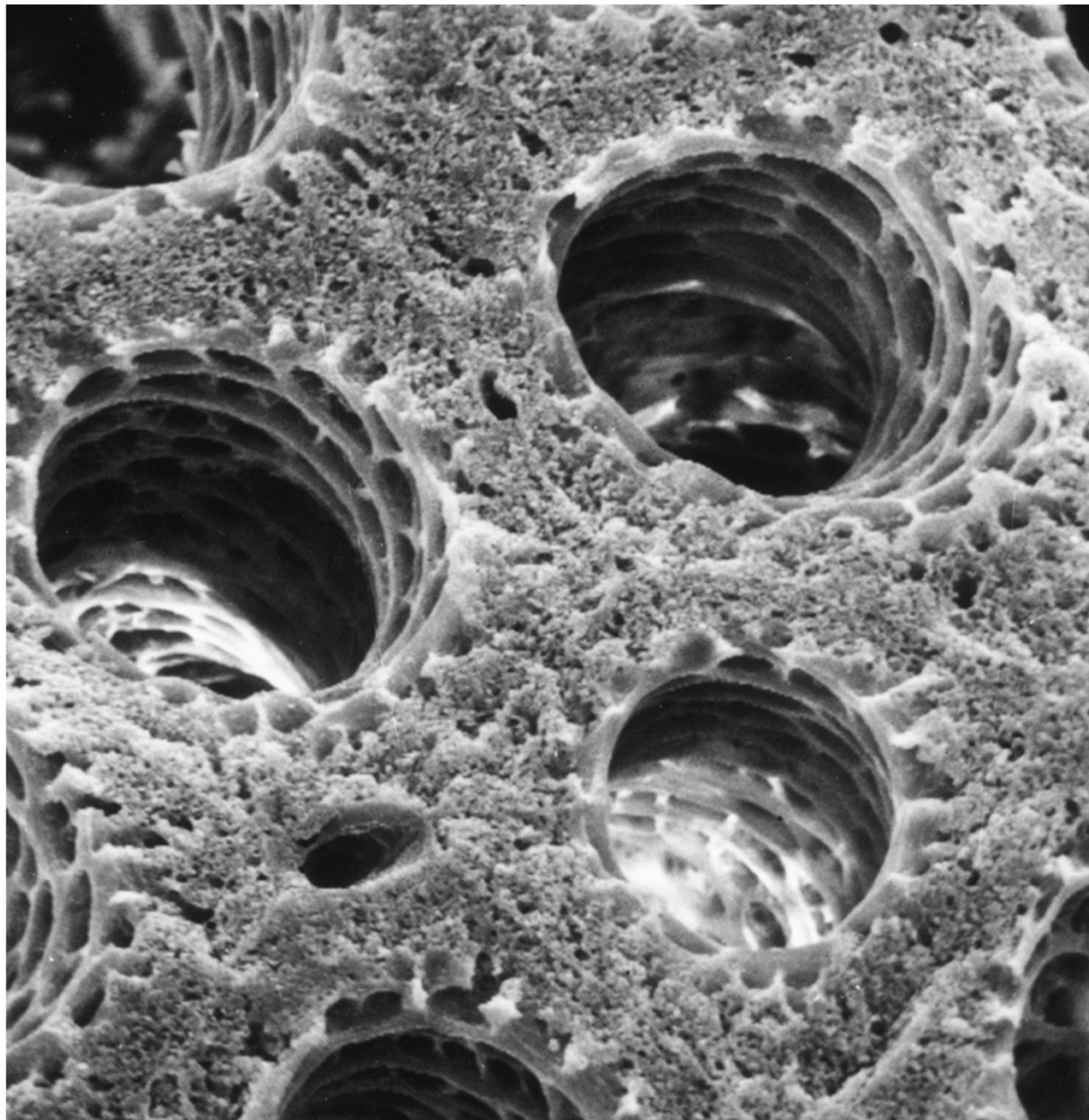
Cycle 2



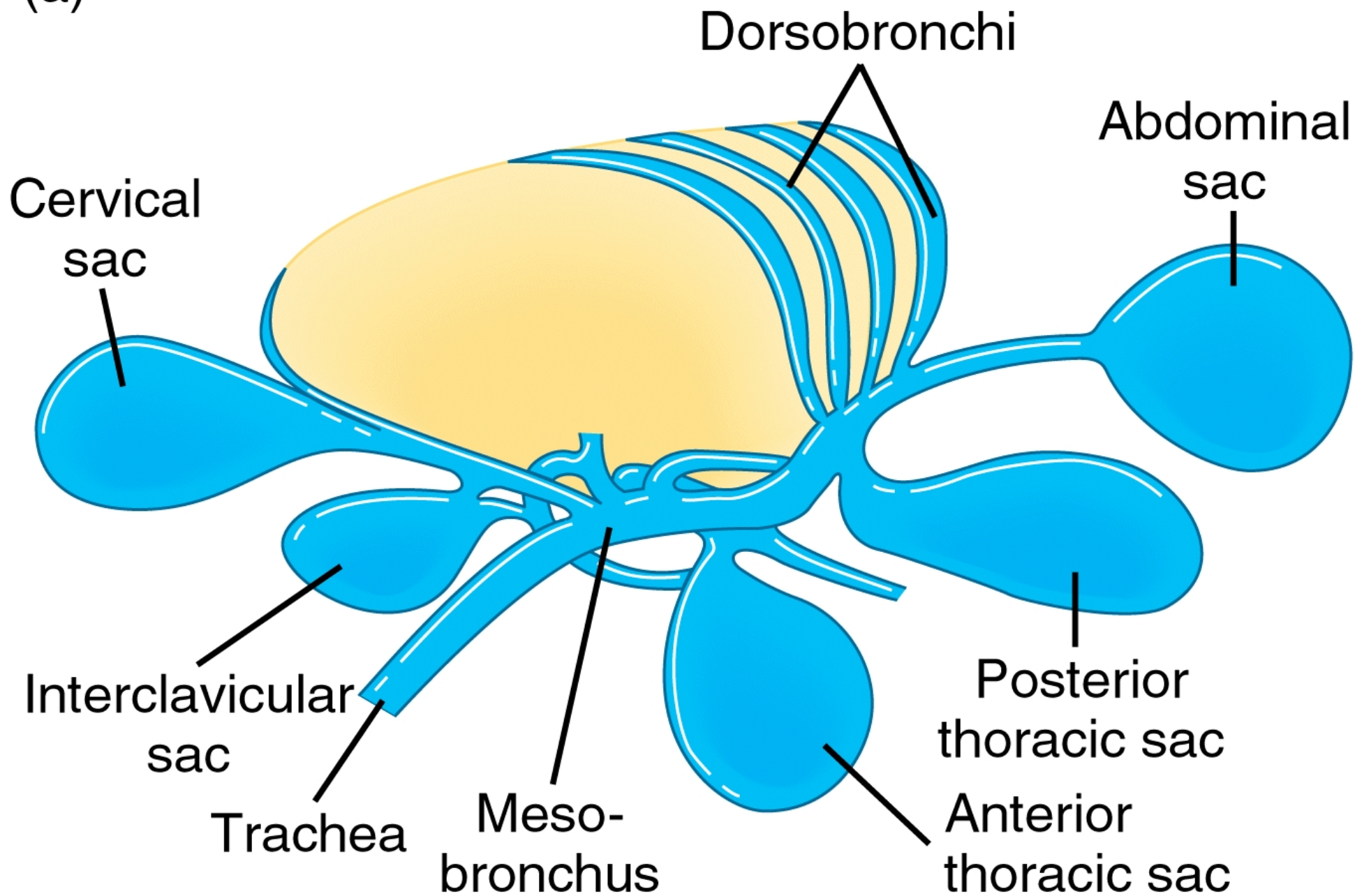
D. Expiration 2

(a)

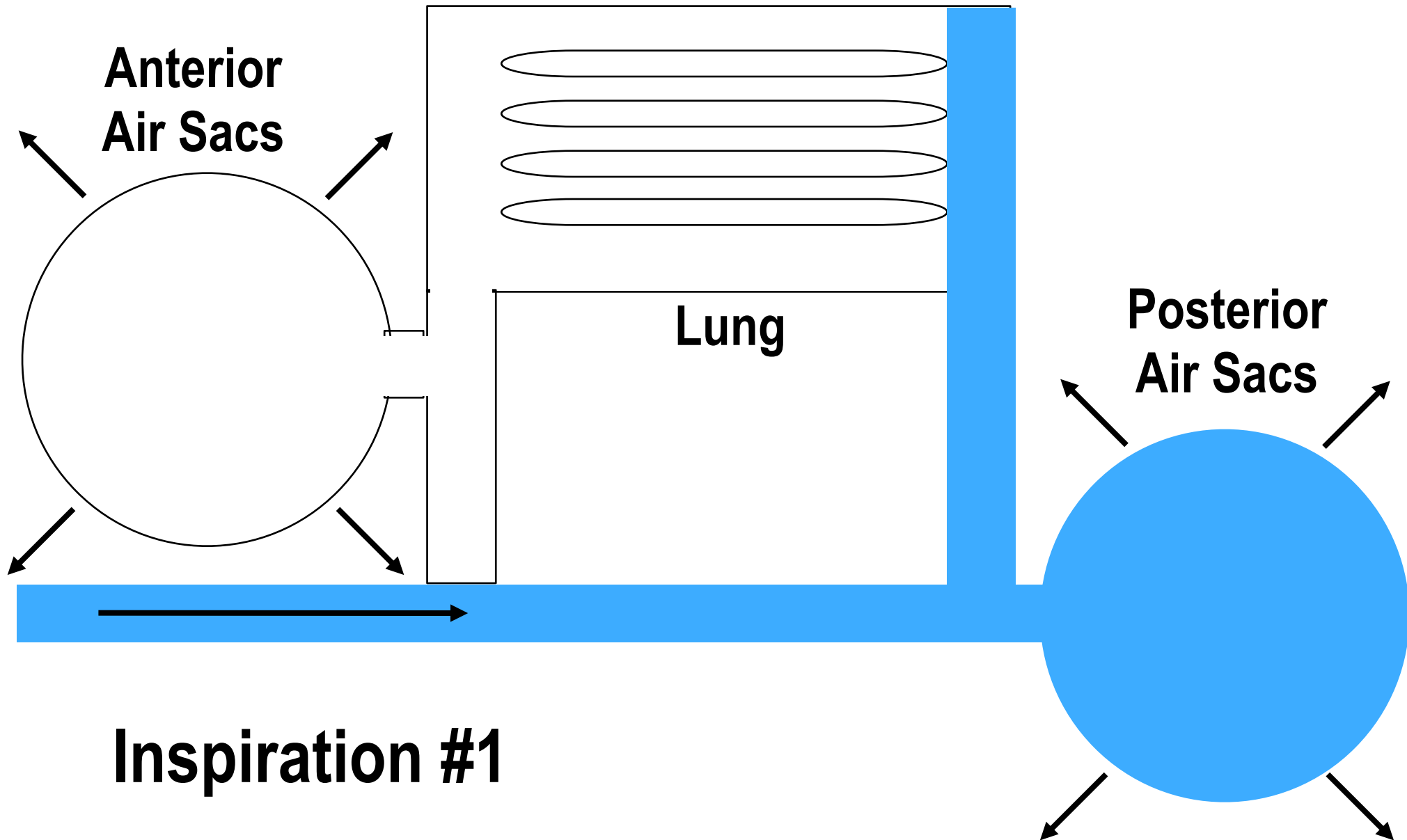




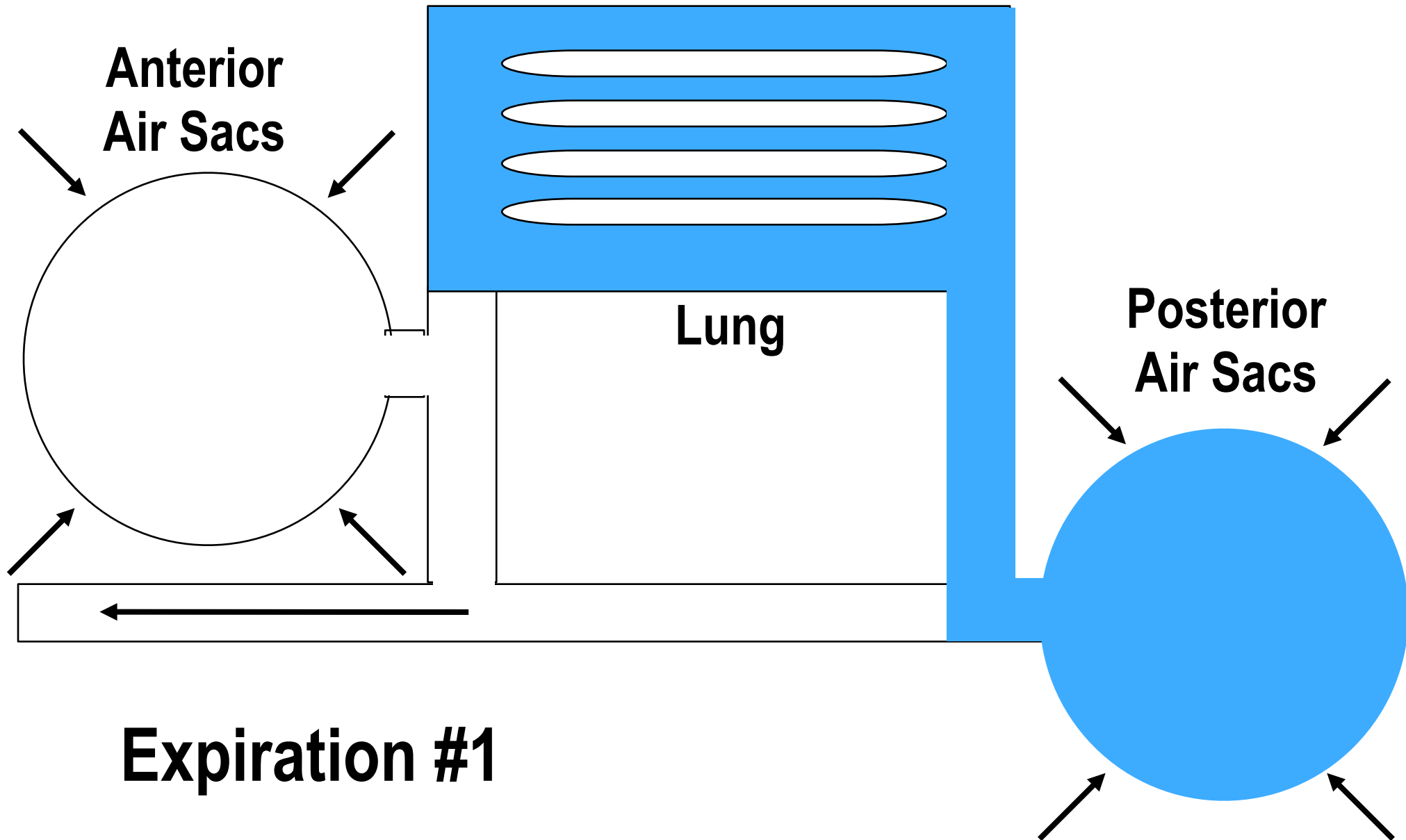
(a)



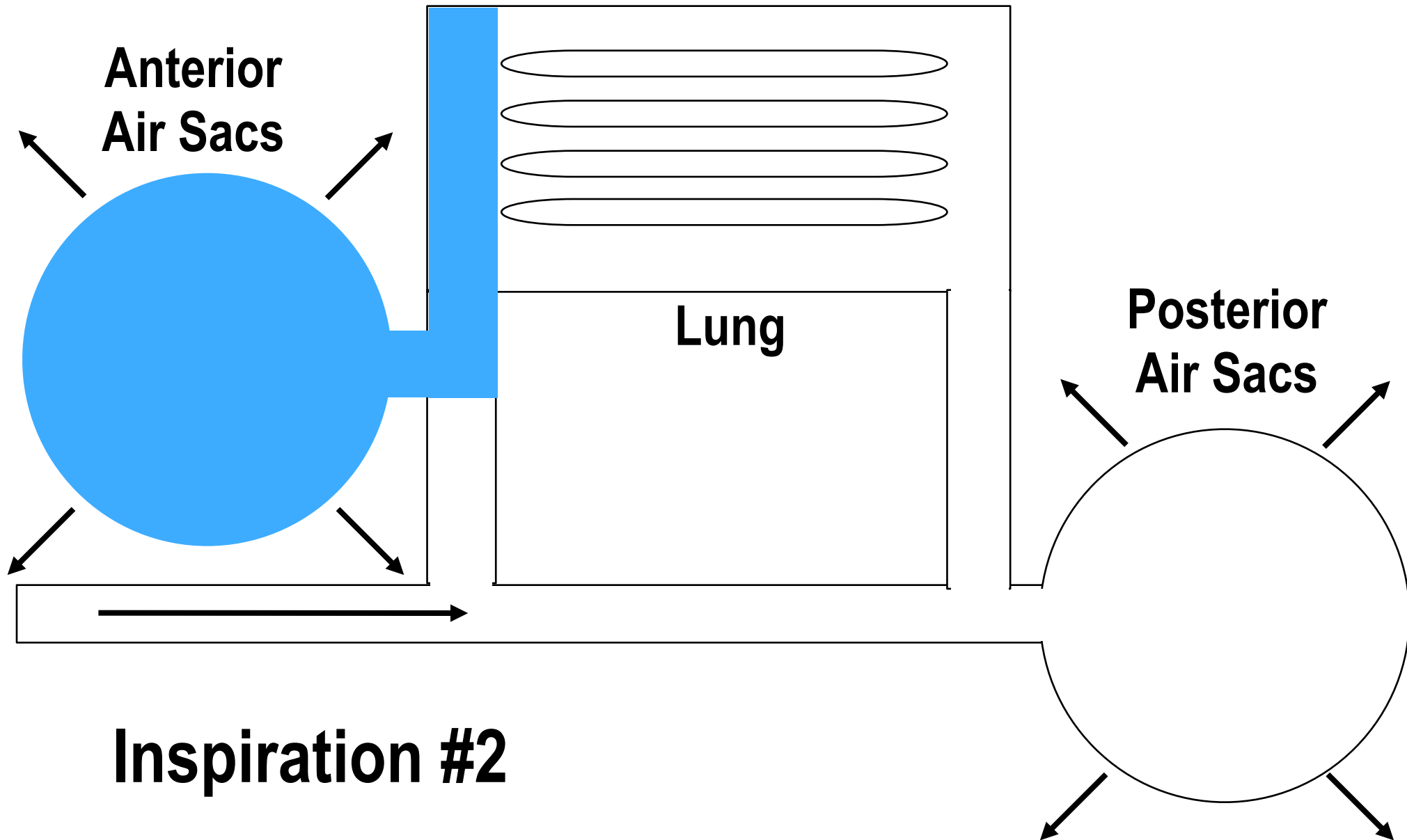
Ventilation Pattern



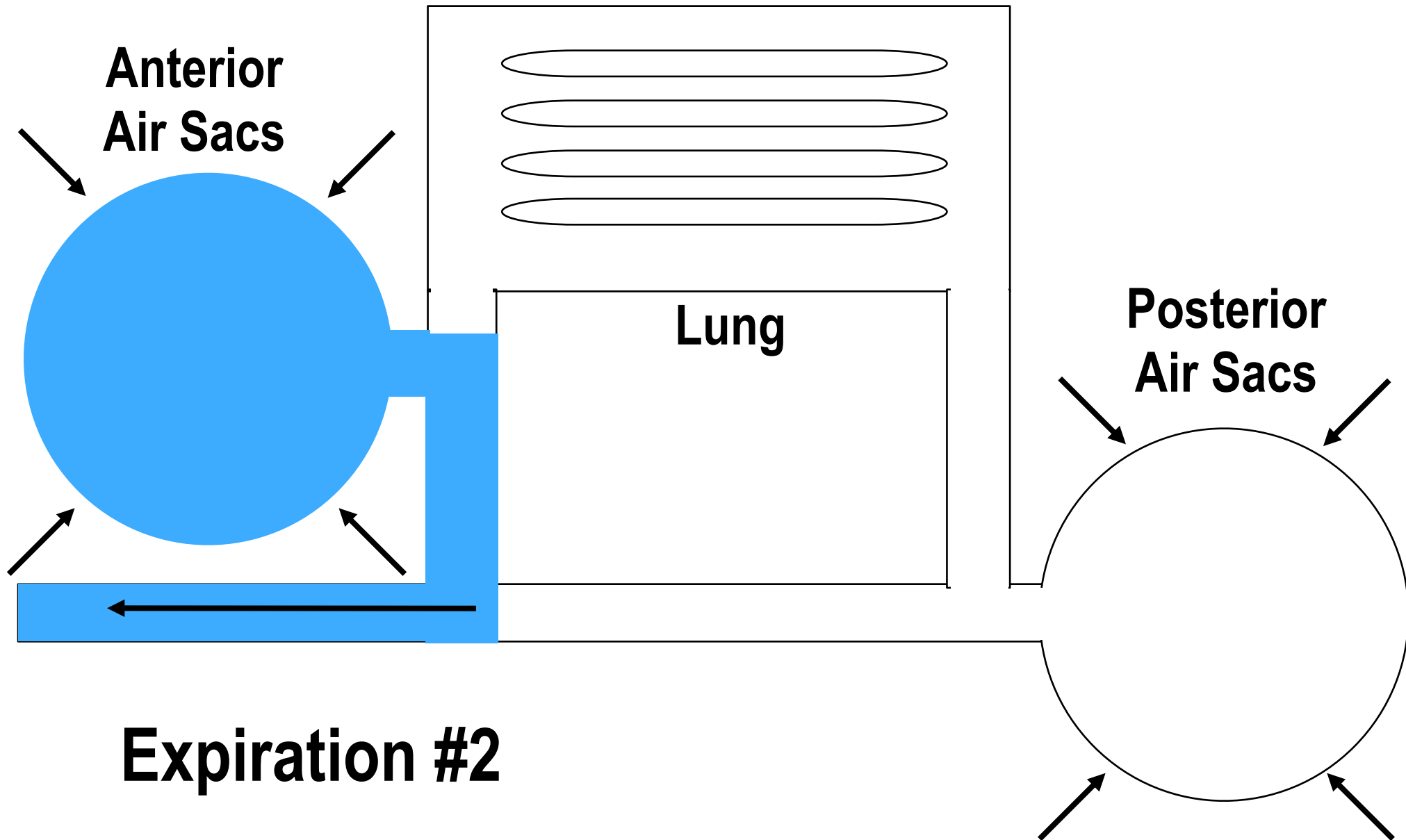
Ventilation Pattern



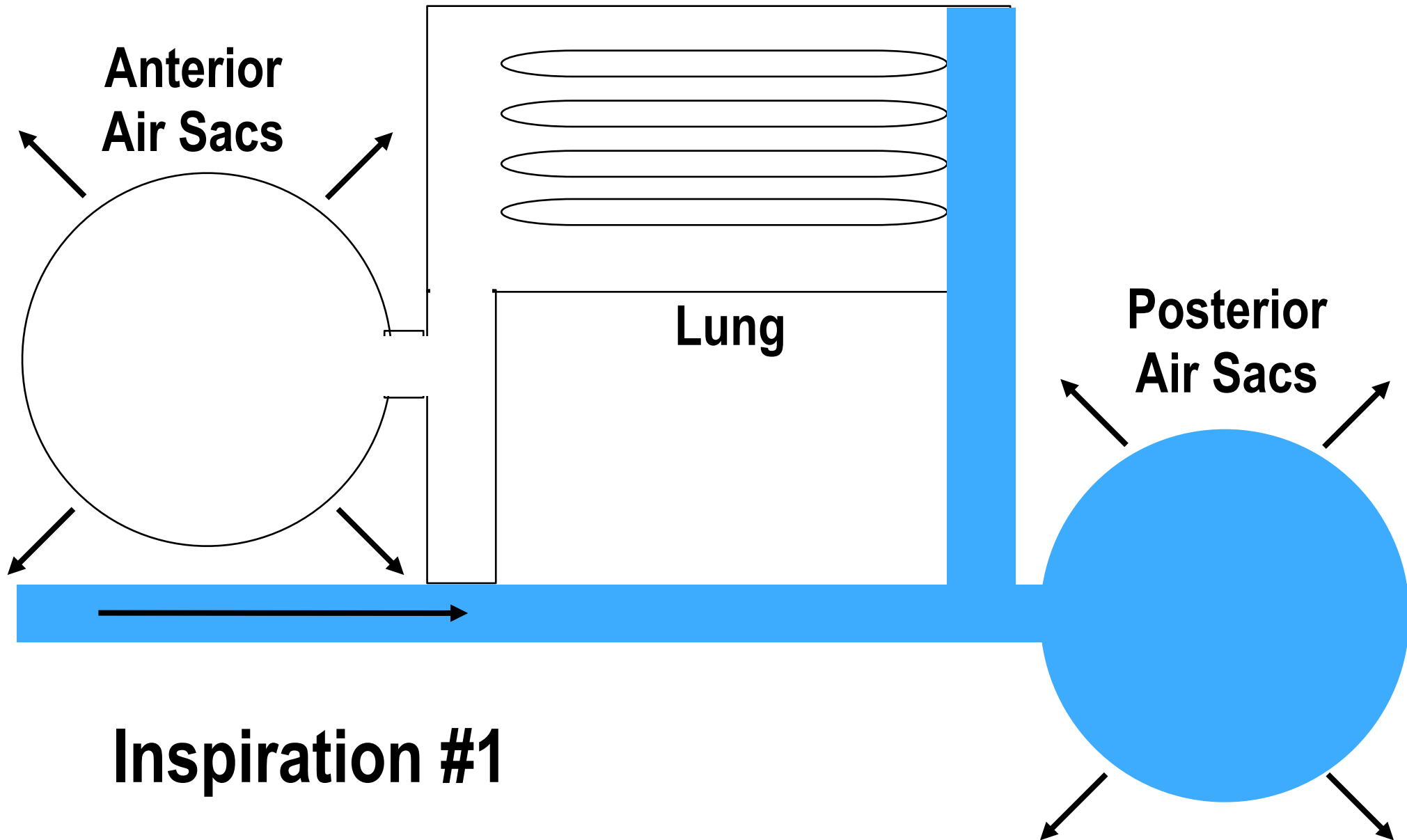
Ventilation Pattern



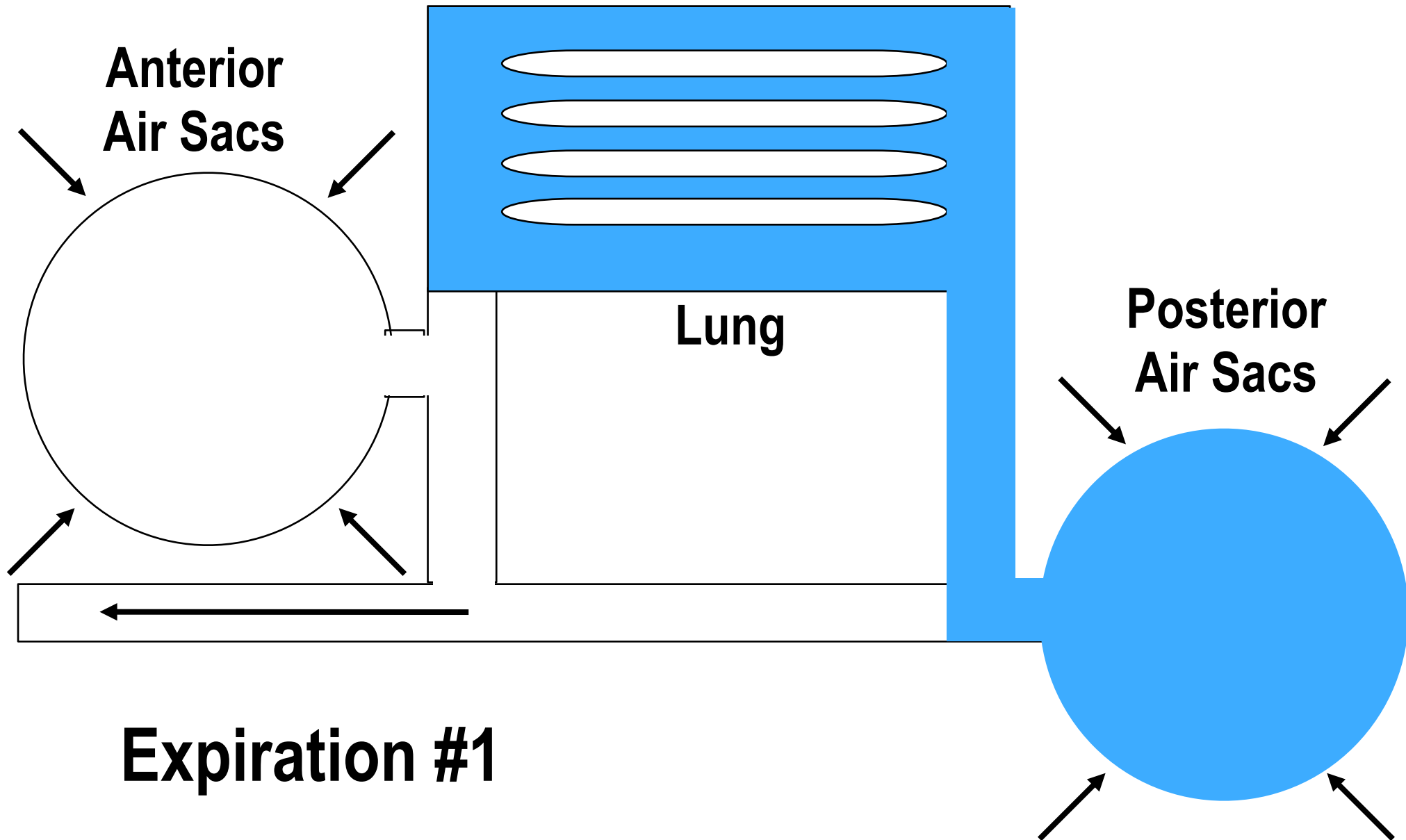
Ventilation Pattern



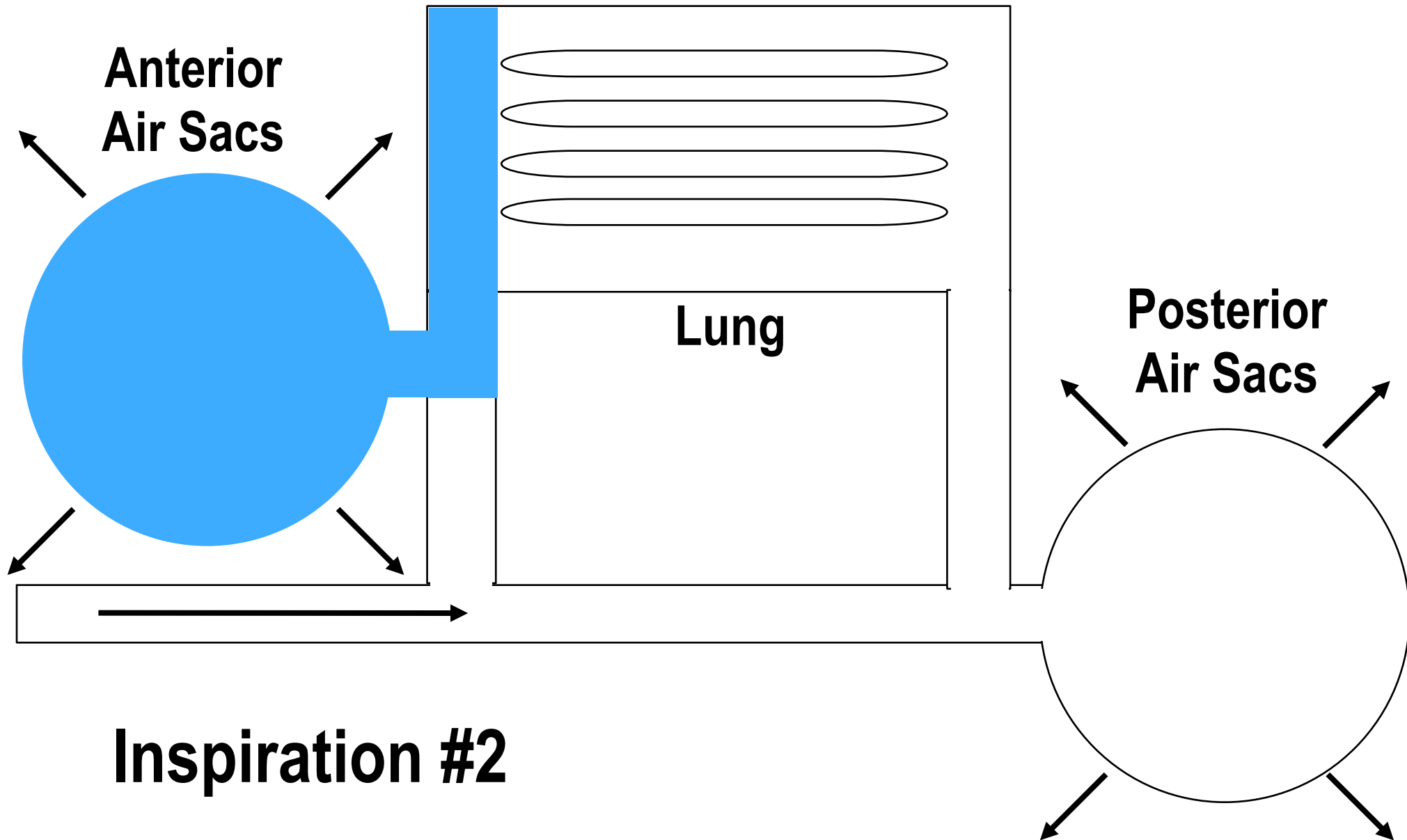
Ventilation Pattern



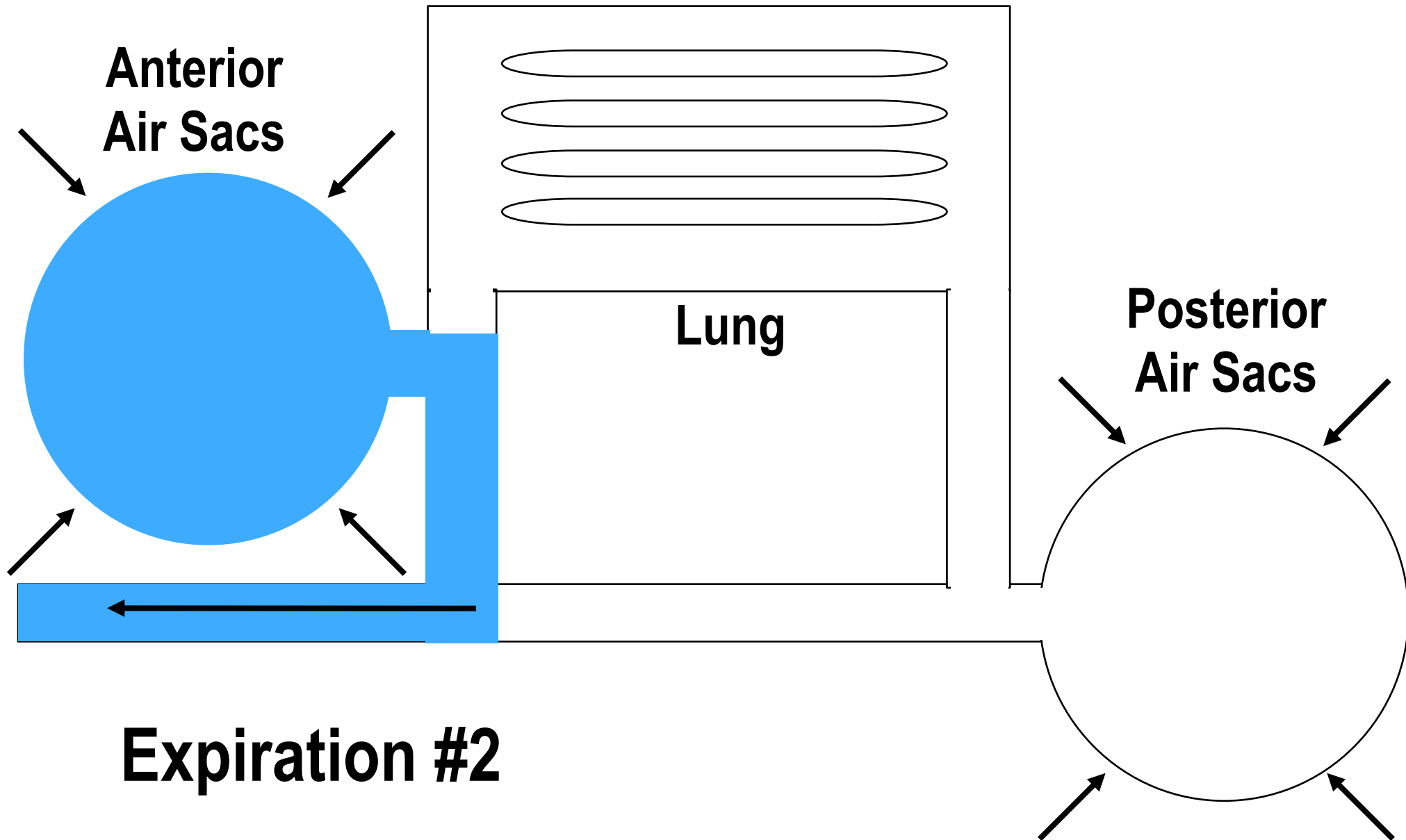
Ventilation Pattern



Ventilation Pattern



Ventilation Pattern



Flow Patterns

O2 extraction efficiency

$$E = 100(p_{\text{inO}_2} - p_{\text{exO}_2})/p_{\text{inO}_2}$$

p_{inO_2} = incurrent partial pressure of O₂

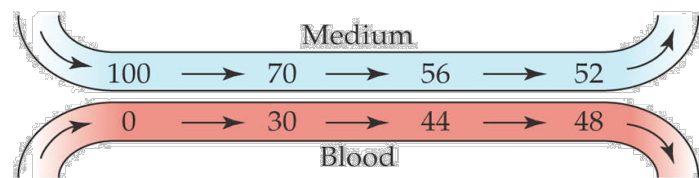
p_{exO_2} = excurrent partial pressure of O₂

O₂ Extraction Efficiency:
fish 20-60%
terrestrial tidal lungs 20-25%
birds 40-50%

$$E = 100(100 - 52)/100 = 52\%$$

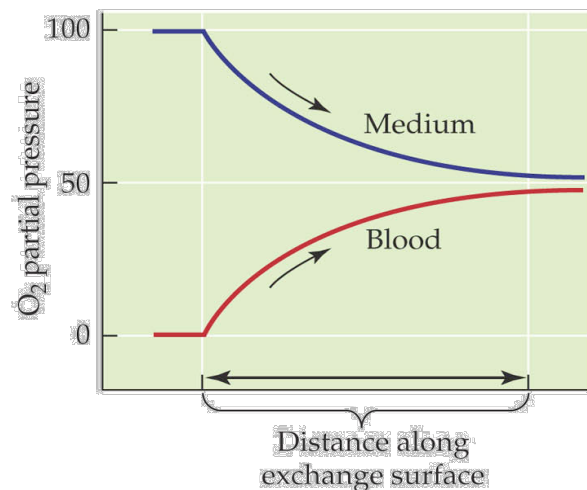
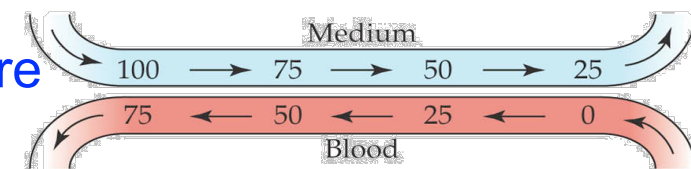
$$E = 100(100 - 25)/100 = 75\%$$

(a) Concurrent gas exchange



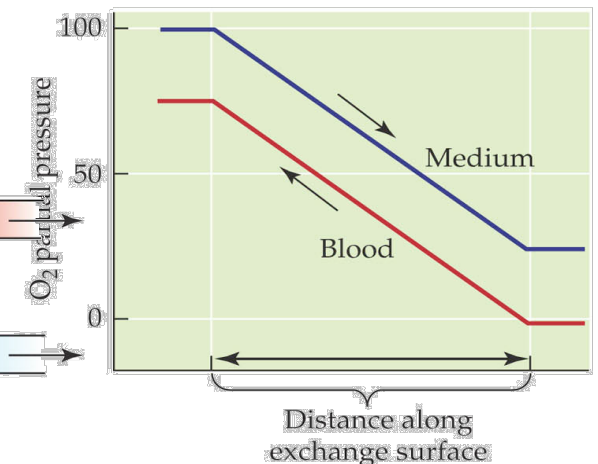
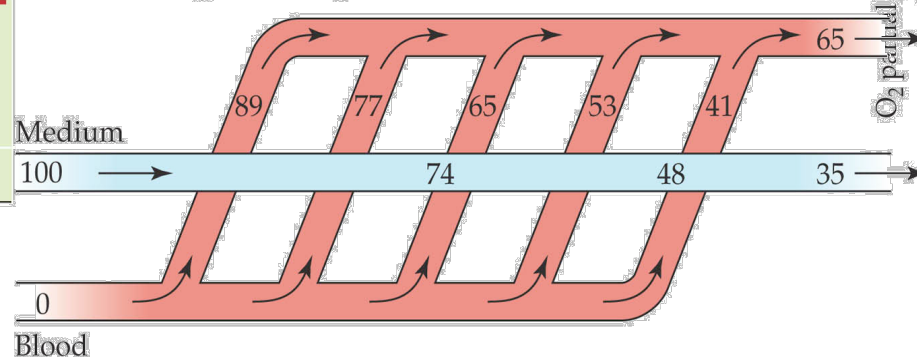
(note: numbers in equations are fake; just for illustration of the calculations)

(b) Countercurrent gas exchange



$$E = 100(100 - 35)/100 = 65\%$$

Cross-current gas exchange



Simplified Flow patterns

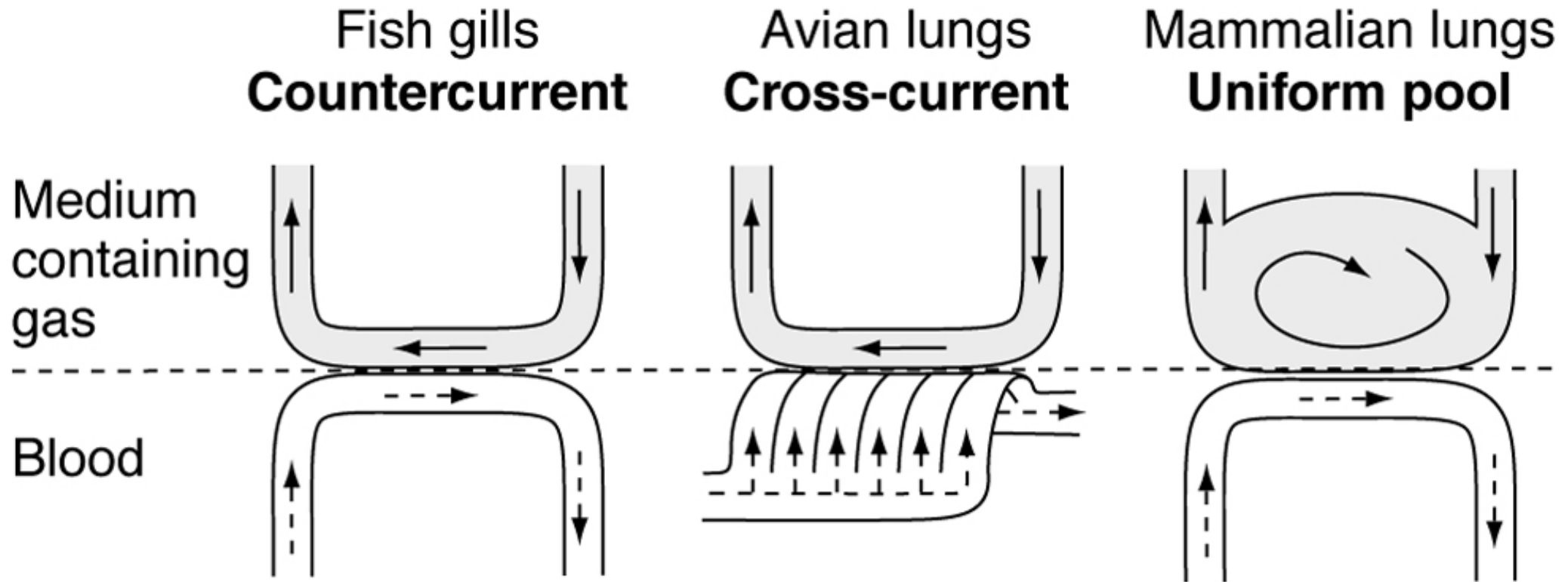
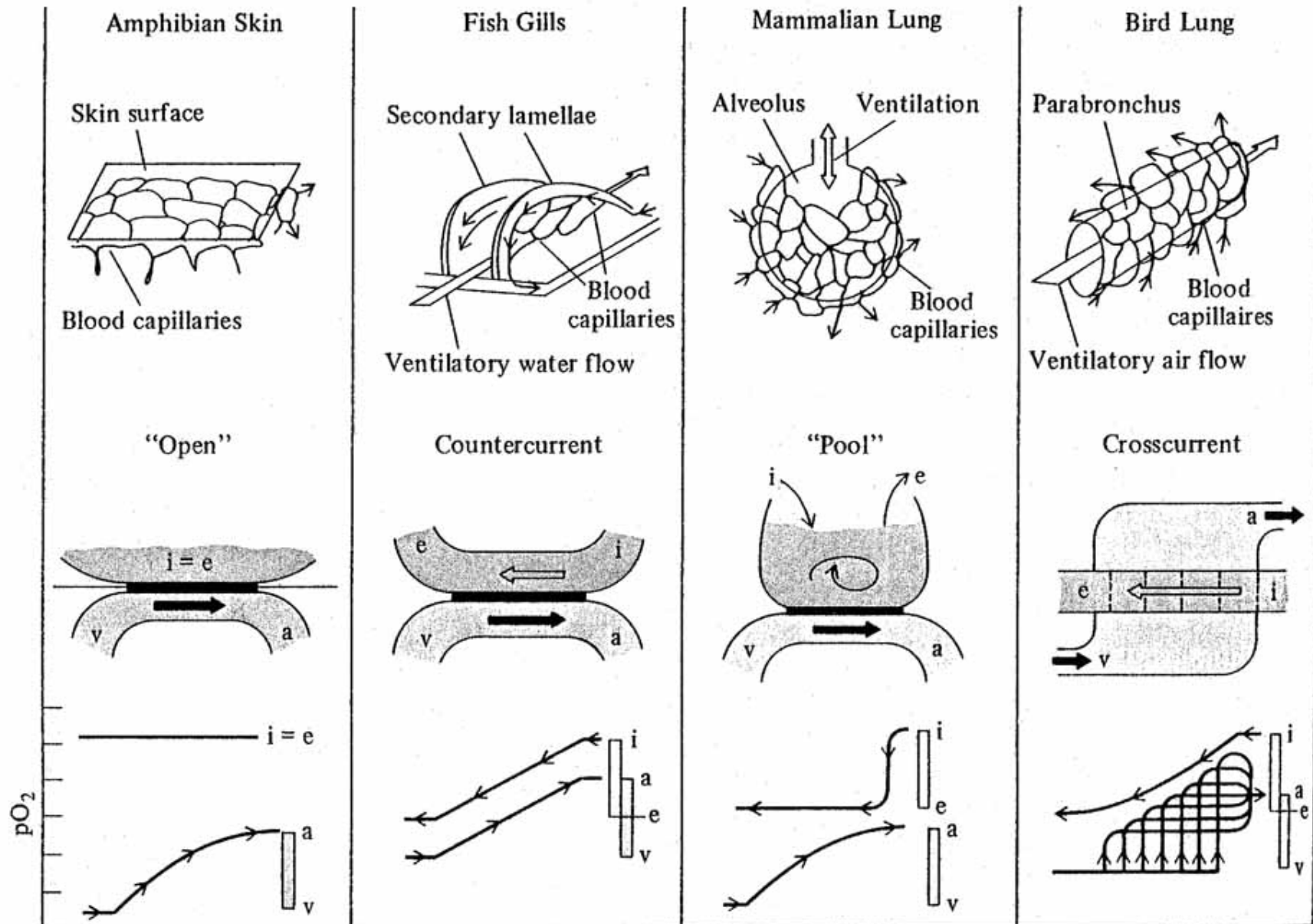


Fig. 18.19

Gas Exchange Model Variations



Vital Volumes and Breathing

Eupnea:

normal, quiet breathing at rest

Hyperventilation/hypoventilation:

increased or decreased breathing uncoupled to blood P_{CO_2} levels

Hyperapnea:

increased lung ventilation coupled to elevated blood P_{CO_2}

Apnea:

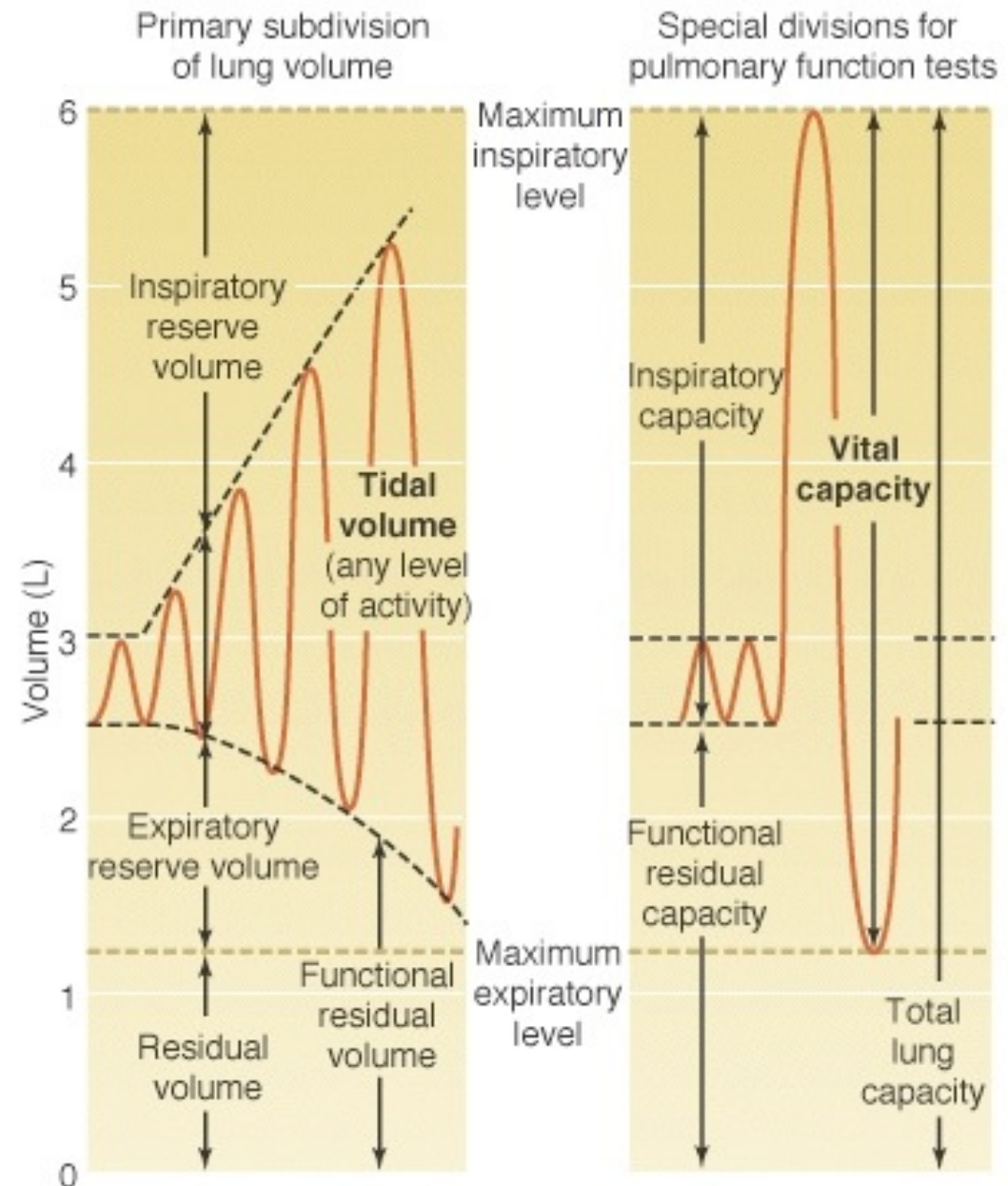
Absence of breathing

Dyspnea:

Labored breathing with sensation of breathlessness

Polypnea:

breathing rate increases, but volume does not



Breathing Control: Both volume and frequency important

Respiratory Minute Volume: overall amount of breathing per minute.

$$= \text{volume/breath} \times \text{breaths/min}$$

Alveolar Minute Volume: overall amount of air that moves across gas exchange surfaces (alveoli) per minute.

$$= (\text{Tidal Volume} - \text{Dead Volume}) \times \text{breaths/min}$$