Swimming adaptation

- **Life in Fluids**:
  Dynamic Fluids
  - Water and air are fluids
  - Air is certainly thinner and less viscous than water, but it is a fluid nonetheless.
  - The physical phenomena that act on fishes in water generally apply to birds in air.
  - Air and water differ in viscosity, but they place similar physical demands on animal designs.
  - When a body moves through a fluid, the fluid exerts a resisting force in the opposite direction to the body's motion. This resisting force, termed drag, may arise from various physical phenomena, but forces caused by friction drag (or skin friction) and by pressure drag are usually the most important.
  - As an animal moves through a fluid, the fluid flows along the sides of its body. As fluid and body surface move past each other, the fluid exerts a resisting force (drag) on the surface of the animal where they make contact. This force creates friction drag
  - friction drag depends, among other things, on the viscosity of the fluid, the area of the surface, the surface texture, and the relative speed of fluid and surface.
  - Individual particles in a fluid traveling in a flow describe individual paths. If the average direction of these particles is plotted and points connected along the line of overall flow, nonoverlapping streamlines that represent the general layered pattern of fluid flow can be produced. The derived streamlines therefore express the statistical summary of layered flows slipping smoothly across one another within a moving fluid.
  - Special and often complex events occur within the boundary layer, the thin, fluid layer closest to the surface of the body.
  - Generally, it is a thin gradient slowing from the velocity of the general flow down to zero on the surface of the object across which the fluid flows. In a Boeing 747, the boundary layer is about 1 in. thick at the trailing edge of the wing.
  - Natural instabilities in the boundary layer may cause the fluid to become chaotic and the flow is spoken of as turbulent. This increase drags dramatically.
  - Where the flow is nonchaotic, it is described as laminar.
  - If the particles in the boundary layer passing around an object are unable to make the sharp turn smoothly behind the object, then the layers within the flow tend to part; this is termed flow separation.
  - The fluid behind the object moves faster and pressure drops leading to pressure drag, which may be seen as a wake of disturbed fluid behind a boat. Physically, the flow separation results from a substantial pressure differential (pressure drag) between the front and the back of the animal.
  - An extended, tapering body fills in the area of potential separation, encourages streamlines to close smoothly behind it, and thereby reduces pressure drag.
  - The result is a streamlined shape common to all bodies that must pass rapidly and efficiently through a fluid.

- An active fish, a fast-flying bird, and a supersonic aircraft are all streamlined for much the same reason—to reduce pressure drag.
- Together, friction and pressure drag contribute to profile drag, which is related to the profile or shape an object presents to the moving fluid. If you place your cupped hand out the window of a fast-moving car, you can feel the difference when presented edge-on or palm-on to the onrushing air. A change in profile changes the drag.
- A thin, broad wing of a bird meeting the air edge-on presents a small profile. But as the wing tips up, changing the angle of attack, the broad profile of the wing meets the air, increasing drag.
- Fish fins or seal flippers, when used to make sharp turns, are moved with the broadest profile to the water, much like the power stroke of a boat oar, taking advantage of profile drag to help generate cornering forces. Engineers examine the physical problems associated with motion through fluids within the disciplines of hydrodynamics (water) or aerodynamics (air).
- Applied to animal designs that move through fluids, these disciplines reveal how size and shape affect the way the physical forces of a fluid act on a moving body.
- In general, four physical characteristics affect how the fluid and body dynamically interact. One of these is the density, or mass per unit volume of the fluid. A second is the size and shape of the body as it meets the fluid. The resistance a rowboat oar experiences when the blade is pulled broadside-on is, of course, quite different than when it is pulled edge-on. The third physical characteristic of a fluid is its velocity. Finally, the viscosity of a fluid refers to its resistance to flow.
- These four characteristics are brought together in a ratio known as the Reynolds number: m where r is the density of the fluid and m is a measure of its viscosity; l is an expression of the body's characteristic shape and size; and U is its velocity through the fluid. The units of all variables of the ratio cancel each other, leaving the Reynolds number without units. It is dimensionless, a further factor obscuring its message; yet, it is one of the most important expressions that summarizes the physical demands placed upon a body in a fluid. The Reynolds number was developed during the nineteenth century to describe the nature of fluid flow, in particular, how different circumstances might result in fluid flows that are dynamically similar. The Reynolds number tells us how properties of an animal affect fluid flow around it. In general, at low Reynolds numbers, skin friction is of great importance; at high Reynolds numbers, pressure drag might predominate. Perhaps most importantly, at least for a biologist, the Reynolds number tells us how changes in size and shape might affect the physical performance of an animal traveling in a fluid. It draws our attention to the features of the fluid (viscosity) and the features of the body (size, shape, velocity) that are most likely to affect performance. For scientists performing experiments, the Reynolds number helps them to build a scale model that is dynamically similar to the original. For example, several biologists wished to examine air ventilation through prairie dog burrows but lacked the convenient space to build a life-sized tunnel system in the laboratory. Instead,

they built a tunnel system ten times smaller but compensated by running winds ten times faster through it. The biologists were confident that the scale model duplicated conditions in the full-sized original because a similar Reynolds number for each tunnel verified that they were dynamically similar even though their sizes differed.

Static Fluids :

- o Fluids, even thin, low-density fluids such as air, exert a pressure on objects within them. The unit of pressure, Pascal (Pa), is equivalent to 1 newton acting over 1 square meter.
- o The expression "as light as air" betrays the common misconception that air has almost no physical presence. In fact, air exerts a pressure in all directions of about 101,000 Pa (14.7 psi, or pounds per square inch) at sea level, which is equivalent to 1 atmosphere (atm) of pressure.
- o The envelope of air surrounding Earth extends up to several hundred kilometers.
- o Although not dense, the column of air above the surface of Earth is quite high, so the additive weight at its base produces a substantial pressure at Earth's surface.
- o We and other terrestrial animals are unaware of this pressure since it comes from all directions and is counterbalanced by an equal outward pressure from our bodies.
- o Thus, all forces on our bodies balance, inside without.
- o Respiratory systems need only produce relatively small changes in pressure to move air in and out of the lungs. If we drive from low elevation to high elevation in a short period of time, we might notice the unbalanced pressure that builds uncomfortably in our ears until a yawn or stretch of our jaw "pops" and equilibrates the inside and outside pressures to relieve the mismatch.
- o Most of us have experienced increasing pressure as we dive deeper in water. At a given depth, the pressure surrounding an animal in water is the same from all sides. The deeper the animal, the greater is the pressure.

- **Buoyancy**
  - o describes the tendency of a submerged object in a fluid to sink or to rise. buoyancy was related to the volume an object displaces compared to its own weight.
  - o If the density of the submerged object is less than that of water, then buoyancy will be a positive upward force; if its density is greater than water, then the buoyancy is negative and it is forced down.
  - o Since density is related to volume, any change in volume will affect the tendency of the object to rise or sink.
  - o Many bony fishes possess a flexible gas bladder (swim bladder) that can be filled with various gases.
  - o As the fish dives deeper, pressure increases, compressing the air, reducing volume, and thereby effectively making the fish denser.

- o The negative buoyancy now pushes the fish down, and it starts to sink. such a fish can add more gas into the gas bladder to increase its volume and return it, overall, to neutral buoyancy.
- **Fluid Environment**
  - o In an aqueous medium, such as fresh water or marine seas, an organism does not depend primarily on the endoskeletal framework for support. Instead, the body takes advantage of its buoyancy in the surrounding water
  - o For an active aquatic organism, two problems are uppermost. The first is drag on the body as it slips through a relatively dense medium, water. The answer is streamlining, contouring of the body to reduce drag forces. It is no accident that the general body shapes of fast-swimming fishes and supersonic aircraft are both streamlined. This shape improves the performance of both fishes and aircraft as they meet common physical demands while traveling through a medium that resists their passage.
  - o The second problem for an active aquatic organism is orientation in three-dimensional space. Any streamlined body has a tendency to tip and deviate from its line of travel, rotating about its center of mass. In fishes, these perturbations are countered by stabilizing fins appropriately positioned along the body.

Origin of Paired Fins:

- o Like any object traveling in three-dimensional space, the body of a fish is susceptible to deflections from its line of travel about its center of mass. It may swing from side to side (yaw), rock about its long axis (roll), or buck forward and back
- o dorsal and lateral fins control the body by resisting perturbations of the body about its center of mass.
- o pectoral fins do not produce significant lift as in a fixed-winged aircraft. Instead, pectoral fins are used for close maneuvering within enclosed vegetation (some teleosts) and during steady, horizontal swimming (sharks) for initiating rising or sinking turns.
- o As early fishes became more active, they would have experienced instability while in motion. Presumably, just such conditions favored any body projection that resisted pitch, roll, or yaw, and led to the evolution of the first paired fins.
- o The associated girdles stabilized the fins, served as sites for muscle attachment, and transmitted propulsive forces to the body.
- o In gnathostome fishes, two fundamental types of fins developed from two different arrangements of the metapterygial stem or axis, a chain of endoskeletal basals.
- o One fin type is the archipterygial fin, in which the metapterygial stem runs down the middle of the fin. From this central stem, endoskeletal radials project outward to support the preaxial (anterior) and postaxial (posterior) sides of the fin evenly. Slender dermal fin rays extend to the edges of the fin to complete this support. Externally, the archipterygial fin looks leaf-shaped and narrowed at its base.
- o The second basic fin type is the metapterygial fin, in which the metapterygial stem of basals is located posteriorly. Most radials project from this posterior axis into the preaxial side of the fin, and dermal fin rays extend from the ends of the radials to the edges of the fin.

- These two fin types have influenced theoretical work on the origin of paired fins.
- To track the phylogenetic source of early fish fins, the gill-arch and the fin-fold theories have been put forth.
- **Gill-Arch Theory:**
  - C. Gegenbaur proposed that paired fins and their girdles arose from gill arches (figure 9.4).
  - Specifically, the endoskeletal girdle arose from the gill arch, and the primitive archipterygial fin arose from the gill rays.
  - Initially, Gegenbaur based his theory on fin anatomy in sharks.
  - However, the discovery (1872) of the Australian lungfish, Neoceratodus, convinced him that the primitive fins were archipterygial fins similar to the paired fins in Neoceratodus—a central stem supporting a series of radials. This central stem articulated with the lungfish's endoskeletal shoulder girdle, the future scapulocoracoid.
  - Nonetheless, the gill-arch theory left much unexplained. Although it accounted for the evolution of the pectoral girdle, it does not explain (1) the appearance of a posterior pelvic girdle distantly placed from the gill arches, nor (2) the presence of dermal bone in the pectoral girdle, nor (3) the different embryologies of pectoral girdle and gill arches.
- **Fin-Fold Theory**
  - At about the same time, the second half of the nineteenth century, morphologists F. M. Balfour and J. K. Thacher independently put forth the fin-fold theory, an alternative view expanded by later scientists.
  - With this view, paired fins arose within a paired but continuous set of ventrolateral folds in the body wall that were stiffened by a transverse series of endoskeletal pterygiophores, proximally the basals and distally the radials (figure 9.5a–c).
  - Additional stability came from the inward extension of basals and their eventual fusion across the midline to produce the supportive girdles. Dermal bone, a contribution of the overlying bony armor, was later added to the pectoral girdle to strengthen the paired fins further.
  - In support of the fin-fold theory, several indirect pieces of evidence are usually cited.
  - The pregnathostomes with the first fin-folds were Myllokunmingia and Haikouichthys (figure 3.7). Both of these early Cambrian agnathans were equipped with fin-folds.
  - Further, many surviving fossils of early fishes carry hints or presumed remnants of these earlier fin-folds.
  - For instance, some primitive ostracoderms possessed lateral continuous folds along the ventral body wall. Acanthodians possessed a paired row of spines to mark where a paired fin-fold presumably resided in their ancestors
  - Furthermore, if pectoral and pelvic fins arose from a fin-fold, then they likely arose at the same time).
  - In this context, it is significant that the paired fins of embryonic sharks develop together from a continuous thickening of ectoderm along the lateral body wall.

- This has been interpreted as an embryonic recapitulation of the phylogenetic transition from fin-folds to paired fins
- More recently, the fin-fold theory has been given greater detail.
- For example, Erik Jarvik has emphasized the segmental contributions to the archipterygial fins in some living fishes. If fins initially were steering keels, contributions from the adjacent segmental myotomes muscularize the finfolds, making them movable. Jarvik further suggested that the endoskeletal basals and radials developed from the mesenchyme within the core of the fold, supporting the projecting fin and offering attachments to muscles.
- Within the fin, the supportive dermal fin rays developed from modified rows of scales, an event that seems to be repeated during the embryonic development of dermal fin rays in many living fishes. Jarvik has also taken exception to the view that dermal bone is added initially to the shoulder girdle because of selection forces favoring fin stability. He notes that the fish shoulder girdle lies at the transition from trunk to head.
- Radials At this point, the axial musculature is interrupted by the pharyngeal slits. Consolidation of small dermal skin bones into a composite dermal girdle may have been initially advantageous because it offered an anterior site for attachment of the interrupted axial musculature at this point of transition.
- This dermal girdle would also form the posterior wall of the buccal cavity, protect the heart, and be the attachment site of some sets of jaw and gill-arch muscles.
- For one or all of these reasons, an anteriorly placed dermal girdle may have arisen and only secondarily joined with endoskeletal elements in support of the fin. Of course, no similar selection forces would be acting posteriorly, where the axial musculature runs uninterrupted from the trunk to the tip of the tail. This would help account for the presence of dermal contributions to the pectoral girdle and their absence from the pelvic girdles.
- Experimental analysis of limb development in chick, mouse, and shark embryos provides an additional perspective on the underlying genetic basis for the evolution of fin-folds to fins.
- In tetrapods, the embryonic body is compartmentalized with respect to the dorsoventral axis. The Engrailed-1 gene expression is restricted to the ventral compartment of the embryonic body, helping to establish a dorsoventral patterning. Within this ventral expression zone T-box genes, Tbx5 and Tbx4, determine the identity of each paired appendage, anterior and posterior appendages, respectively. Sharks also have these two T-boxgenes specifying anterior and posterior fins attached along their length parallel with the long body axis.
- The sonic hedgehog (Shh)gene, absent in sharks, but present in tetrapods, promotes outgrowth of the limb away from the tetrapod body, freeing the limb from parallel attachment to the body and establishing a proximalto-distal-limb axis.

- On the other hand, the prevertebrate amphioxus has only one such T-box gene, AmphiTbx4/5. These discoveries suggest the following scenario for evolution of the lateral fin-folds into paired appendages.
- The hypothetical ancestor possessed lateral fin-folds with T-box genes (Tbx) expressed within the Engrailed-1 domain along the ventral compartment of the body.
- The presence of pectoral, but not pelvic, fins as in some ostracoderms could be the result of this single Tbx set of genes.
- Next, and before chondrichthyan fishes arose, duplication of the Tbx cluster produced two sets of genes, one anterior (Tbx5) and one posterior (Tbx4), expressing pectoral and pelvic fins, respectively (figure 9.7b).
- The subsequent acquisition of Shh expression established a proximal-distal axis and promoted outgrowth of the fins from the body wall, as for example occurs in sarcopterygian fishes and in later tetrapod

- **Caudal Skeleton and Fins:**
  o In most fishes, the axial skeleton continues into the tail, where it can take several forms.
  o In many fishes, the tail is asymmetrical, with a long dorsal and a small ventral lobe separated by a notch.
  o If the posterior end of the vertebral column turns upward and into this dorsal lobe, forming its central axis, a heterocercal tail forms.
  o In the diphycercal tail, the vertebral column extends straight back, with the fin itself developed symmetrically above and below it. Living lungfishes and bichirs are examples.
  o The homocercal tail, characteristic of teleosts, has equal lobes and appears to be symmetrical, but the narrowed vertebral column that runs to its base slants upward to form the support for the dorsal edge of the fin.
  o The hemal arches below expand into supportive struts, known as hypurals, to which the rest of the fin attaches .
  o Among the earliest vertebrates, the tail was not commonly symmetrical. Rather, most ostracoderms show the heterocercal condition, or even a "reversed" heterocercal condition, termed a hypocercal tail, in which the vertebral axis enters the tail and turns down into an extended ventral lobe.
  o The symmetrical diphycercal and homocercal tails are usually derived from ancestors with asymmetrical heterocercal tails. They are common among fishes with lungs or air bladders that give their dense bodies neutral buoyancy. In sharks, which lack lungs or air bladders, lift to the posterior body is apparently provided by the extended dorsal lobe of the heterocercal tail. When the heterocercal tails of sharks are removed and tested separately in experimental tanks, they have a tendency to push downward against the water, resulting in an upward reaction force on the tail, which produces lift .
  o In fact, removal of the dorsal or the ventral lobe alone reveals that within the tail, lift produced by the two lobes differs in magnitude and direction
  o In general, as the tail sweeps back and forth, the small ventral lobe deflects water upward, causing a small downward component of force, whereas the large dorsal lobe deflects water downward, resulting in an opposite large upward force

- o The overall effect is for the tail to produce a resultant force directed forward and upward. Although at first it might seem strange that the ventral lobe produces forces contrary to the overall upward lift generated by the tail, this action of the ventral lobe might represent a method for fine-tuning the lift.
- o In sharks that have just eaten a large meal or in gravid females, the center of body mass might shift unfavorably, tilting or angling the body out of its line of travel.
- o The ventral lobe might help level the shark in a more direct body orientation.
- o In nautical terminology applied to submarines, adjustment for vertical tilt is called "trimming." Small radial muscles reside in the ventral lobe of the shark's tail.
- o Their contraction might alter stiffness, change the forces produced in the tail, help trim the body, and adjust the shark about its center of gravity. This lift imparted to the posterior body would tend to rotate the shark tail-up and nose-down. It was once thought that the large pectoral fins counteracted this, generating equal lift, like hydrofoils, in the anterior body. However, it now seems that the entire streamlined head end of the shark, not its pectoral fins, produces anterior lift. In a swimming shark, this cranial lift, together with caudal-produced lift, compensates overall for the sinking density of the shark.
- o If this interpretation of the function of a heterocercal tail is correct, then the reversed heterocercal tail, the hypocercal tail of ostracoderms, would have produced forces that tilted the body tail-up, head-down. Without compensation anteriorly, the mouth would be driven into the substrate. This would aid the animal in feeding on foods buried in soft sediments.

- **Basic Components:**
  - o The appendicular skeleton includes the paired fins or limbs and the girdles, the braces within the body that support them.
  - o The anterior girdle is the shoulder or pectoral girdle, to which dermal and endochondral skeletal elements contribute, and that supports a pectoral fin or limb.
  - o The posterior girdle is the hip or pelvic girdle, consisting of endochondral skeletal elements that support the pelvic fin or limb.
  - o Fins Particularly in primitive fishes, the body is apt to carry projecting spines, lobes, or processes.
  - o Unlike these projections, fins are membranous or webbed processes internally strengthened by radiating and thin fin rays.
  - o They form initially at the interface between dermis and epidermis, like scales, but then sink into the dermis, and so are sometimes called dermal fin rays.
  - o In elasmobranchs, these dermal fin rays, termed ceratotrichia, are slender keratinized rods
  - o Fin rays, or lepidotrichia, in bony fishes are usually an ossified or chondrified series of tiny elements that strengthen this web
  - o In some bony fishes, the tip of the fin may be further stiffened by additional keratinized rods, the actinotrichia.
  - o The proximal part of the fin close to the body is supported by pterygiophores of two general types: the enlarged basals within the proximal part of the fin, and the slender radials that extend support from the basals into the middle region of the fin
  - o Fins occur singly, except for a pair near the head and a second pair posterior to this, the pectoral and pelvic fins, respectively.

- o The basal pterygiophores of these projecting paired fins articulate with and are braced by girdles inside the body wall.
- o These paired fins will receive our greatest attention because they are the phylogenetic source of the tetrapod limbs.

Swimming

- the body of an active fish coursing through a viscous medium such as water experiences drag, which slows the fish's forward progress.
- Streamlining prevents flow separation, reduces drag, and improves performance.
- Lateral undulations passing along the body move the fish through the aqueous medium, producing backthrust against the water and providing forward force.
- The basic primitive tetrapod locomotion evolved from this characteristic lateral undulation that fishes use to swim.
- This same mode of progress still serves most modern amphibians and reptiles quite well, giving them access to a great variety of habitats.
- In tetrapods that secondarily become aquatic, as in cetaceans, for example, the limbs again may become secondary to the tail and lose their prominence in aquatic locomotion
- However, not all secondarily aquatic vertebrates have reduced limbs. For example, pinnipeds clasp their hindlimbs together, forming a kind of "tail" that aids in swimming.
- The wings of aquatic birds often take on greater roles in swimming. Their forelimb bones become stouter and more robust, reflecting the increased strength required to provide the bird with flippers to propel them while swimming after food in the water.
- In penguins, the wings are flightless and used exclusively like flippers to enable the animal to swim underwater
- The hindlimbs of swimming birds may become partially or completely webbed feet to increase pressure against the water when these birds paddle

Respiratory Organs

- o **Gills:**
  - Vertebrate gills are designed for water breathing.
  - Specifically, they are dense capillary beds in the branchial region that serve external respiration.
  - They are supported by skeletal elements, the branchial arches.
  - The mechanism of gill ventilation depends on whether the gills are located internally or externally.
  - Internal gills are associated with pharyngeal slits and pouches.
  - Often they are covered and protected laterally by soft skinfolds, such as the interbranchial septum in chondrichthyan fishes, or by a firm operculum, as in many osteichthyan fishes .
  - Ventilation usually involves the muscular pump of the buccal cavity actively driving water across the internal gills.
  - External gills arise in the branchial region as filamentous capillary beds that protrude into the surrounding water .

- They are found in the larvae of many vertebrates, including lungfishes, some actinopterygians, and amphibians.
- Water currents flow across their projecting surfaces, or in still water specialized muscles sweep external gills back and forth to ventilate them.

- **Gas Bladders**
  o Many actinopterygian fishes possess a gas bladder, an elongated sac filled with gas, usually air that enters via a pneumatic ductconnected to the digestive tract or with gas secreted directly into the bladder from the blood.
  o Gas bladders participate in buoyancy control (swim bladders) and sometimes in respiration (lungs).

- **Lungs**
  o Vertebrate lungs are designed for air breathing. Lungs are elastic bags that lie within the body.
  o Their volume expands when air is inhaled and decreases when air is exhaled. Embryologically, lungs arise as endodermal outpocketings from the pharynx.
  o In primitive fishes and most tetrapods, the lungs of adults are usually paired.
  o They lie ventral to the digestive tract and, in amniotes, are connected to the outside environment through the trachea.
  o Entrance into the trachea is gained through the glottis, which is guarded by tiny sets of muscles that open and close it.
  o Usually the trachea branches into two bronchi, one to each lung. In some species, each bronchus branches into successively smaller bronchioles that eventually supply air to the respiratory surfaces within the lung.
  o In tetrapods with slender bodies, one lung may be reduced in size; and in some amphisbaenids and most advanced snakes, only a single lung is present.
  o The trachea, bronchi, and bronchioles can hold a significant volume of air. Although exhalation forces most of the spent air from the lungs, some remains in these passageways.
  o Upon inhalation, this "spent" air is drawn back into the lungs before fresh air from outside reaches the lungs to mix with the used air.
  o This volume of used air within the respiratory passageways is called the dead space.
  o The total volume inhaled in a single breath is referred to as the tidal volume. In a chicken, the dead space may represent up to 34% of the total tidal volume.
  o Normal tidal volume of a human at rest is about 500 ml. Because the dead space is about 150 ml (30%), 350 ml (500 ml–150 ml) of fresh air actually reaches the lungs.

- **Swim Bladders**
  o If the gas bladder is used to control the buoyancy of the fish in the vertical water column, it is referred to as a swim bladder.
  o Occasionally gas bladders may be heavily vascularized as well to participate in supplementary respiration and are called respiratory gas bladder or just lungs.
  o The internal vascular walls of lungs are subdivided into many partitions that increase the surface area available for external respiratory exchange.
  o Swim bladders differ from lungs in three ways.

- First, swim bladders are usually situated dorsal to the digestive tract, whereas lungs are ventral.
- Second, swim bladders are single, whereas lungs are usually paired. Neoceratodus, the Australian lungfish, is an exception, because as an adult it has a single lung dorsal to the digestive tract; however, its trachea originates ventrally from the digestive tract. Its embryonic lung arises initially as a paired primordium, suggesting that the single lung of Neoceratodus is a derived condition.
- Third, in swim bladders, returning blood drains to the general systemic circulation (cardinal veins) before entering the heart.
- In lungs, venous return enters the heart separately from the general systemic circulation.
- Despite their differences, swim bladders and lungs share many basic similarities of development and anatomy.
- Both are outpocketings from the gut or pharynx and have roughly equivalent nerve and muscle supplies.
- Some morphologists take these similarities as evidence that lungs and swim bladders are homologous.
- Even if they are homologous, it is not clear which function came first, gas transfer or buoyancy control.
- The two functions are not mutually exclusive.
- A filled swim bladder that aids gas transfer also makes the fish more buoyant, and a swim bladder used for buoyancy can also be tapped as a temporary source of oxygen.
- Among fishes, evolutionary reversals between respiratory and buoyancy functions have occurred repeatedly.
- Lungs have evolved into nonrespiratory swim bladders that in subsequent evolutionary processes have reverted to lungs.
- Phylogenetically, neither lungs nor swim bladders are present in agnathans, elasmobranchs, or placoderms
- Lungs, ventral in position, likely arose in the immediate common ancestor to actinopterygians and sarcopterygians.
- Swim bladders of actinopterygians, if homologous, would be later derivatives of lungs.
- The behavioral habit of gulping air may have been in place even before lungs.
- Tipping up to gulp surface air occurs in fishes without specialized air-breathing organs, even in some sharks.
- Thus, the habit of gulping air bubbles pressed into gill chambers may have preceded specialized anatomical devices designed to efficiently extract oxygen from air and exploit such behaviors.
- Although double ventral lungs are the primitive condition in bony fishes case of lungfishes may be argued differently, with a single dorsal lung being the primitive condition.
- The Australian lungfish has such a single dorsal lung and may be plesiomorphic compared to the more derived African and South American lungfishes.

- o The Australian lungfish has large, fleshy fins, a large operculum, a hefty fish body, well-developed gills, and until recent overfishing, ventured into salt water as well as fresh water like early bony fishes. Other lungfishes are more derived with diminutive fins, small opercula, elongated eel-like bodies, obligate airbreathers, and strictly freshwater in habitat.
  - o By this view, the double, ventral lung of the African and South American lungfishes would represent a derived state.
- **Cutaneous Respiratory Organs**
  - o Although lungs and gills are the primary respiratory organs, the skin can supplement breathing.
  - o Respiration through the skin, referred to as cutaneous respiration, can take place in air, in water, or in both. In the European eel and plaice, oxygen uptake through the skin may account for up to 30% of total gas exchange (figure 11.6).
  - o Amphibians rely heavily on cutaneous respiration, often developing accessory skin structures to increase the surface area available for gas exchange.
  - o In fact, in salamanders of the family Plethodontidae, adults lack lungs and gills and depend entirely on cutaneous respiration to meet their metabolic needs. Like most mammals, humans respire very little cutaneously, although our skin is permeable to some chemicals applied topically (spread on the surface).
  - o In fact, many medicinal ointments are absorbed through the skin. Bats take advantage of cutaneous respiration across their well vascularized wing membranes to eliminate as much as 12% of their total carbon dioxide waste, but they take up only 1% or 2% of their total oxygen requirement through this cutaneous route (figure 11.6).
  - o Feathers and poorly vascularized skin of birds preclude cutaneous respiration. Similarly, in reptiles, the surface covering of scales limits cutaneous respiration.
  - o However, in areas between scales (at the hinges of scales) and in areas with reduced scales (e.g., around the cloaca), the skin is heavily vascularized to allow some cutaneous respiration.
  - o Sea snakes can supplement up to 30% of their oxygen intake via cutaneous respiration across the skin on their sides and back. Many turtles pass the cold winter in hibernation safely at the unfrozen bottom of ponds where the limited respiration around their cloaca is sufficient to meet their reduced metabolic needs.
  - o The newly hatched larva of the teleost fish *Monopterus albus*, an inhabitant of southeast Asia, uses predominantly cutaneous respiration during its early life.
  - o At hatching, the large and heavily vascularized pectoral fins beat in such a fashion as to drive a stream of water backward across the surface of the larva and its yolk sac.
  - o Blood in superficial skin vessels courses forward. This establishes a countercurrent exchange between water and blood to increase the efficiency of cutaneous respiration in this larva
  - o Such a respiratory organ allows the larva to inhabit the thin layer of surface water into which nearby oxygen from the air has dissolved.
  - o Similarly, in many amphibians, increased surface area allows for increased cutaneous gas exchange

- **Accessory Air-breathing Organs**
  - Lungs and skin are not the only organs that tap sources of oxygen in the air.
  - Many fishes have specialized regions that take up oxygen from the air.
  - Hoplosternum,a tropical catfish ows it into its digestive tract
  - Oxygen in the gulped air diffuses across the wall of the digestive tract into the bloodstream.
  - The digestive tract is richly supplied with blood vessels that supplement gill respiration.
  - The electric eel Electrophorus gulps and holds air in its mouth to expose capillary networks of the mouth to oxygen (figure 11.8d). Gills ordinarily are unsuitable organs for air breathing.
  - The moist, leaflike exchange surfaces stick together in air and collapse without the buoyant support of water.
  - However, in some fishes, gills are used in air breathing
  - The rockskipper Mnierpes, an inhabitant of wave-swept rocky shores of the tropical Pacific coast of Central and South America, occasionally makes brief sojourns onto land to scrounge for food, to evade aquatic predators, and to avoid periods of intense wave action. During these sojourns, it holds gulped air against its gills to extract oxygen. Its gills are reinforced to prevent their collapse during these bouts of air breathing.
- **Water Ventilation:**
  - Dual Pump In water-breathing fishes, the most common pump is a dual pump
  - This gnathostome system, as the name suggests, is two pumps in tandem, buccal and opercular, that work in a synchronous pattern to drive water in a nearly continuous, unidirectional flow across the gill curtain between two-stroke pump.
  - The first stroke, or suction phase, begins with compressed buccal and opercular cavities and closed oral and opercular valves.
  - As the buccal cavity expands, creating a low intraoral pressure, the oral valves open and outside water rushes in following the pressure gradient.
  - The simultaneous expansion of the more posterior opercular cavity with its closed valve also creates a pressure that is even lower than in the adjoining buccal cavity.
  - Consequently, water that first enters the buccal cavity is encouraged by the pressure differential to continue on across the gill curtain and into the opercular cavity.
  - During the second stroke, or force phase, the oral valves close and the opercular valves open.
  - Simultaneous muscle compression of the buccal and opercular cavities raises pressure in both, but because of the open opercular valve, pressure in the opercular cavity is slightly lower.
  - Consequently, water flows from the buccal cavity across the gill curtain and exits via the open opercular valve.

- o The timing of the suction and force phases, together with the pressure differentials between them, results in a unidirectional, nearly continuous flow of new water across the gills. spheric air, such as lungfishes, are no different from other fishes when they are actively water breathing.
- o They use the same dual pump mechanism to irrigate their gills.
- o However, when the lungfish breathes air, the dual pump is modified into a buccal pump to move air in and out of the lungs.
- o The four-stroke buccal pump can be summarized as an exhalation phase and an inhalation phase.
- o The exhalation phase begins with the transfer (expansion 1) of spent air from the lungs into the buccal cavity.
- o In some fishes, relaxation of a sphincter around the glottis permits this transfer from the lungs to the buccal cavity.
- o Exhalation concludes with expulsion (compression 2) of air from the buccal cavity to the outside either through the mouth or under the operculum. As the fish rises and its snout breaks the surface, its mouth opens to intake (expansion 3) atmospheric air, the first step in the inhalation phase. Inhalation concludes with compression (4), which forces a bubble of fresh air from the buccal cavity into the lungs
- o Theoretically, this bidirectional or tidal exchange of air to and from the lungs of air-breathing fishes could be aided by the hydrostatic pressure of the water column surrounding the fish.
- o Because surrounding hydrostatic pressure increases with depth, a fish rising to the surface with its head tipped upward experiences slightly greater pressure on its deeper body than on the buccal cavity near the surface.
- o During exhalation, this could help force air from the lungs into the buccal cavity and out the mouth.
- o In reverse, after the fish has gulped atmospheric air and turned downward, air in the deeper buccal cavity would be under slightly greater pressure than air in the slightly shallower lung.
- o This could help move the bubble of freshly gulped air into the lung. In practice, some fishes do take advantage of the hydrostatic differential in water pressure on their bodies when transferring or expelling air during exhalation.
- o Usually this is augmented by muscle contractions within the buccal cavity and with striated muscles around the lung.
- o However, inhalation seems to be based primarily on active contractions of the branchial musculature.

Functional (Secondary) Adaptation to an Aquatic Life in Vertebrates:

- One of the great transformations in evolution of vertebrates has been the return to the aquatic environment after the conquest of terrestrial ecosystems.
- With structural and physiological characteristics adapted to function on land, the various non-piscine taxa had to modify these characteristics to perform in water.

- Secondary aquatic vertebrates successfully transformed mechanisms for feeding, locomotion, osmoregulation, and sensory systems to function and thrive in an aqueous environment.
- In the course of vertebrate evolution, there have been a number of great transformations (e.g., acquisition of jaws, amniote egg, limbs, wings, endothermy) that have directed the trajectory of various lineages (Carroll 1997; Dial et al. 2015).
- Among the key transformations are the adaptations to specific environments, and notably the movement of vertebrates from water onto land (Ashley-Ross et al. 2013; Zimmer 2014).
- The changes associated with evolution of fins to legs and the departure from an obligate aquatic existence have been the hallmark of evidence for evolutionary change (Clack 2012).
- This transformation has emphasized the importance of homology.
- Indeed, fossils have been traced through common descent, supporting a singular evolutionary event that led to the diverse assemblage of vertebrate tetrapods.
- However, the converse event of the secondary invasion of the aquatic realm by reptiles, birds, and mammals has emphasized not only homology but homoplasy.
- Indeed, there are strong selective pressures that inflict functional constraints on whole-organism performance.
- These constraints led to the acquisition of numerous convergences that were imposed by the aquatic physical environment (Mazin and de Buffre ´nil 2001; Thewissen and Nummela 2008).
- The aim of this symposium was to focus on vertebrate secondary adaptations to an aquatic life, which is a major theme in vertebrate evolutionary biology.
- The change from terrestrial to aquatic lifestyles required a combination of morphological, physiological, and behavioral adaptations, with modifications in reproduction, sensory organs, locomotor systems, etc.
- This ecological shift occurred in various taxa exhibiting different phylogenetic backgrounds and diverse body plans (Carroll, 1985; Houssaye 2009).
- Beyond convergences, different solutions evolved to common problems associated with an aquatic existence.
- Convergences of highly derived aquatic vertebrates have been the quintessential examples of evolutionary transition, like the similar (thunniform) swimming mode and morphological design exemplified by tuna fishes, ichthyosaurs, and cetaceans (Howell, 1930; Braun and Reif, 1985).
- However, a wide range of adaptations exist that reflect compromises to the degree of adaptation between semi-aquatic and fully aquatic species (e.g., shallow water versus open sea; ambulatory versus swimming locomotion; surface swimming, shallow or deep diving).
- **Feeding and sensory adaptations:**
    - The ecological shift from land to water imposed changes in sensory systems, foraging strategy, and feeding mode.
    - Sensory adaptations include changes in, for example, electroreception for electrolocation and electrocommunication, olfaction (vomeronasal system), balance (spatial orientation, movement perception), vision (cornea curvature,

retinal topography), and hearing (acoustics, ear anatomy) (Thewissen and Nummela 2008).
- o Ketten (2016) discussed the underwater sound reception mechanisms in various aquatic amniotes. She uses computerized tomography (CT) and magnetic resonance imaging (MRI) to map densities of tissues associated with the outer, middle, and inner ears of sea turtles, sea birds, pinnipeds, odontocetes, and mysticetes. Her study reveals the occurrence of similar bundles of fatty tissues contacting the tympanum in all examined taxa suggesting the parallel evolution of similar soft-tissues involved in underwater sound conveyance to the middle and inner ear.
- o Feeding in water is challenging for organisms originally adapted to a terrestrial existence.
- o Associated with different biomechanical systems, there are naturally different types of prey capture (suspension feeding, suction feeding, or jaw prehension), and ingestion (Schwenk and Rubega 2005).
- o Heiss (2016) presented the phenotypic plasticity in feeding mode associated with the multiphasic (aquatic versus terrestrial) lifestyle of salamanders (Amphibia): He highlighted the shift from suction feeding in water to tongue prehension for terrestrial prey capture and how the associated changes prevent suction feeding abilities. Though snakes do not use suction feeding, Segall and collaborators (2016) showed that the aquatic milieu constrained head shape evolution in snakes (Squamata), engendering morphological convergences through the numerous independent reinvasions of water. Their observations validate their predictions based on biomechanical models and show a narrower anterior part of the head and posteriorly located nostrils and eyes in aquatic snakes, as compared to their terrestrial relatives.
- o Domning (2016) illustrated the very diverse feeding modes and associated skull and tooth morphologies observed in Sirenia (Mammalia). Indeed, through their evolutionary history, these aquatic plant feeders resorted to various feeding strategies, such as selective browsing, less selective grazing, rhizivory, algivory, durophagy, and even hard food crushing. Goodall and Purnell (2016) illustrated the dietary transitions accompanying cetacean origin through 3D texture analysis of tooth microwear.
- o Based on correlation between tooth microtextures and diet in modern aquatic mammals, they analyzed the shift from terrestrial omnivory/herbivory to aquatic piscivory/carnivory in archaeocete whales and showed a complex picture of dietary evolution in these taxa , analyzed cetacean feeding evolution with regard to the origin of baleen and filter feeding in mysticetes (Berta et al. 2016).
- o They resorted to morphological, molecular and isotopic data to analyze this transition in diet and environment, and highlighted the ontogenetic changes in skull development, resorption of fetal dentition, and growth of baleen.
- **Osmoregulation**
  - ▪ Brischoux (2016) elucidated the osmoregulation challenge associated with a marine existence by discussing hypernatremia in marine snakes and the evolution of an euryhaline physiology.

- He highlighted a relatively high physiological tolerance to hypernatremia in all snakes, compared to other marine tetrapods, and suggested that high tolerance to hypernatremia constitutes an important step in the evolution of an euryhaline physiology that may have preceded the evolution of salt glands.
- **Locomotion**
  - Locomotion in a dense and viscous medium, such as water, imposes strong hydrodynamic demands on the musculoskeletal system by implying greater forces and specialized locomotor kinematics and muscle activation patterns (Gillis and Blob 2001, Herrel et al. 2012).
  - Thus, drag reduction, increase in propulsive force production and buoyancy control are the main constraints driving adaptive changes required to improve locomotor performance and stability (Fish and Stein 1991; Fish 2000, 2002).
  - Fish discussed the evolution of advanced swimming modes, through enhanced locomotor performance (increased speed, drag reduction, improved thrust output, and increased manoeuvrability) based on biomechanical models.
  - He showed that recently discovered fossils validate much of a previous model built for mammals (Fish 2000). He went on to propose a biomechanical model for birds to describe the evolution of specialized lift-based foot and wing swimming (Fish 2016).
  - Botton-Divet and collaborators analyzed morphological changes in the long bones of semi-aquatic mustelids (otters and minks) as compared to their terrestrial relatives and highlighted the joint effects of size, locomotor mode, and phylogeny on limb shape evolution and the difficulty to separate them (Botton-Divet et al. 2016).
  - Blob and collaborators analyzed differences in the locomotor system between semi-aquatic and marine turtles.
  - They illustrated the transformation of forelimb skeleton and associated musculature from tubular limbs with paddles used for rowing to flippers used for flapping. They also discussed the interactions between performance advantages and locomotor stability in this context (Blob et al. 2016).
  - Lingham-Soliar and collaborators treated the convergences associated to the independent evolution of high-speed thunniform swimming in some ichthyosaurs and the lamnid shark Carcharodon.
  - He presented the various associated adaptive features, including the fusiform body shape, crossed-fiber architecture of the skin, dorsal and caudal fins, caudal peduncle, and the ligamental series providing power transmission from anterior muscles through the peduncle to the caudal fin (Lingham-Soliar 2016).
  - Pabst and collaborators presented the toolkit required to build a deep diver. Based on dissections and the weighing of different parts of the body (e.g., integument, muscles, organs, bones) as a percent of total body mass, they compared the deep-diving mesoplodonts (Cetacea) and elephant seal (Pinnipeda) to shallow-divers.

- They showed that deep-divers display similar integument and bone proportions, as compared to shallow divers, but relatively smaller brains and thoracic and abdominal viscera.
- Conversely they showed significantly larger locomotor muscles with a unique muscle fiber profile that suggests low rates of oxygen use. They suggested that these adaptive changes probably play a major role in reducing metabolic rate in these deep-diving taxa (Pabst et al. 2016).

- **Bone inner structure:**
  - Secondary adaptation to an aquatic life is associated with changes in inner organization of bone (¼bone microanatomy; i.e., the distribution of the osseous tissue in bone) and in bone histology (i.e., collagen fiber orientation, cell distribution, vascularization).
  - Houssaye and collaborators presented a review of the bone microanatomical specializations encountered in semi-aquatic and aquatic amniotes.
  - Based on the analysis of vertebrae, ribs and stylopod long bones of numerous modern and fossil amniotes, they highlighted the important diversity of these patterns, as opposed to the two generally recognized types of osseous specializations (bone mass increase versus spongious organization).
  - They also showed the important intraskeletal variation in the microanatomical features and the wide range of combinations observed. Based on these data, they discussed the link between microanatomical features and functional requirements in bones of secondarily aquatic amniotes (Houssaye et al. 2016).
  - Canoville and de Buffre´nil (2016) focused on microanatomical changes observed in the king penguin. They analyzed the ontogenetic and intraspecific variability in order to estimate limb bone microanatomical variability. They revealed important changes during ontogeny, which are linked to an intense remodeling episode during the juvenile molt.
  - In addition, they observed that the various bones present distinct developmental patterns and that some variability occurs even in same bones of different adult specimens.
  - Cooper and collaborators proposed to combine bone microanatomical and isotopic approaches on a large sample of modern and fossil cetartiodactyls to better reconstruct the origins of semi-aquatic habits in cetaceans. They found consistency between microanatomical and isotopic data and suggest that the common ancestor of anthracotheres, hippopotamids, raoellids, and cetaceans probably spent considerable time in water (Cooper et al. 2016).
  - The last study in this collection focused on bone histological features. Dumont and Houssaye examined marine squamates. They analyzed the vascular network in three dimensions of the vertebrae of stem-ophidiomorphs, marine snakes, and mosasaurs, in comparison to terrestrial modern squamates (Dumont and Houssaye, 2016).
  - They showed clear differences in vascular organization and density (e.g., cortical vascularity, canal size diameter, orientation, degree of anastomoses) in accordance with physiological and locomotory changes in the progressive adaptation to an aquatic lifestyle, with clear differences pending on ecological grades.