Did lungs and the intracardiac shunt evolve to oxygenate the heart in vertebrates?

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Abstract.—Traditional wisdom of the evolution of lungs in fishes is that lungs arose when gill ventilation was hindered by an aquatic habitat that was low in oxygen. This scenario has been buttressed primarily by a proposed correlation between extant air-breathing fishes and hypoxic habitats, as well as by the fact that early vertebrate fossils were found in sediments believed to indicate a semi-arid environment. There are problems with this scenario, yet it retains a dominant influence on how the evolution of aerial respiration is viewed. This paper presents a new hypothesis for lung evolution that is more consistent with the fossil record and physiology of extant animals than the traditional scenario; I propose that lungs evolved to supply the heart with oxygen. The primitive vertebrate heart was spongy in architecture and devoid of coronary support, obtaining oxygen from luminal blood. By supplying oxygen to this tissue, lungs may have been important in ancient fishes for sustaining activity, regardless of environment. Furthermore, this function for lungs may have influenced cardiovascular adaptations of tetrapods because their divided cardiovascular system isolates the right side of the heart from pulmonary oxygen. I propose that three innovations compensate for this isolation: In extant amphibians oxygen-rich blood from cutaneous and buccal respiration enters the right side of the heart; in chelonians and lepidosaurs the intracardiac shunt washes oxygen-rich blood into the right side of the heart; in mammals, birds, and perhaps in crocodilians, support of the heart by coronary vasculature eliminates this problem.

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Introduction

Traditional wisdom for the evolution of lungs in fishes is that gills were inadequate in an oxygen-poor aquatic habitat where there was selection for the ability to breathe air. The following environments have been proposed as cradles for the evolution of lungs because they typically have a low oxygen content: river systems subject to seasonal drought, freshwater swamps where detritus and oxygen-consuming microbes deplete the water of oxygen, and hypersaline estuaries and lagoons where high salt content decreases the solubility of oxygen (Krefft 1870; Gunther 1871a,b; Morris 1892; Matthew 1915; Barrell 1916; Packard 1974). The distribution of extant air-breathing fishes has been suggested to support a paleoecological model of semi-arid river systems or of freshwater swamps. Furthermore, for many years the fossil record appeared to support a freshwater scenario.

Although the idea that lungs are a consequence of a hypoxic habitat is well accepted, there are other explanations that also hold a great deal of appeal, for example, that lungs evolved to enhance buoyancy (Liem 1988). In this paper I propose a new hypothesis for the evolution of lungs in fishes that considers historical constraints of the chordate cardiorespiratory condition.

The evolution of fishes from small animals that exchanged gases by simple diffusion across the skin to larger, more active gill-breathing organisms may have caused a hypoxic stress on the heart that was eased by the evolution of lungs. In the prevertebrate condition, oxygen-rich blood from the skin would have flowed through the "heart" on its way to the gills, which functioned in filter feeding (Mallatt 1985; Gans 1989). When gills became the major site for gas exchange, the lumen of the heart would have then been filled with oxygen-poor blood because it was located afferent (upstream) to the gills (Fig. 1). This may have presented a problem for fishes since the primitive vertebrate heart was composed of a spongy matrix of muscle cells (myocardium) that obtained oxygen from luminal blood rather than through a vascular network of arteries, capillaries, and veins (a coronary circulation). The idea that spongy myocardium
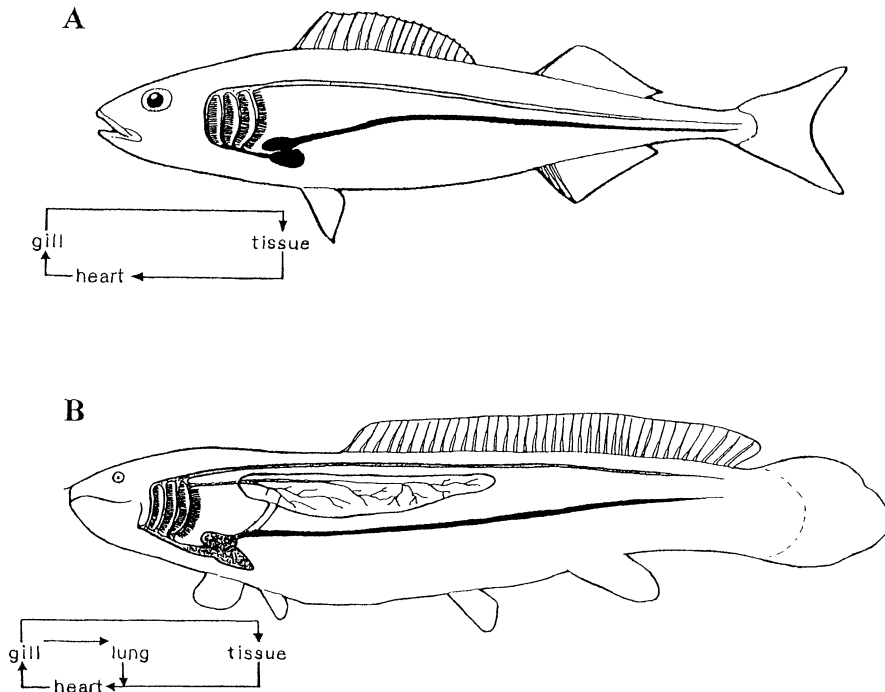
A

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FIGURE 1. Schematic representation of the heart and circulatory system of gill-breathing (A) and air-breathing (B) fishes. A, The heart is in series with the branchial and systemic capillary beds. Blood is pumped to the gills (where it is oxygenated) then to the tissue (where oxygen is unloaded); the blood then returns to the heart. B, Oxygen-rich blood from the lung mixes with oxygen-poor blood from the tissue before returning to the heart (e.g., *Polypterus, Amia, Lepisosteus*). After Nelson (1984) and Reighard (1903).

is primitive for vertebrates is supported by both phylogenetic and ontogenetic evidence. Although numerous vertebrates have a coronary circulation, mapping the incidence of coronary support to the ventricle onto the phylogeny of vertebrates indicates that it is not the primitive condition but that it arose numerous times in parallel, e.g., sharks, birds, mammals (see Table 1). Furthermore, developmental patterns of the heart indicate the ancestral condition was spongy, vascular-free myocardium (reviewed in MacKinnon and Heatwole 1981). The evolution of lungs could have provided oxygen to this spongy myocardium and enhanced cardiac performance. Oxygen-rich blood from the lungs of extant primitive fishes mixes into the systemic blood before entering the heart and therefore is available to this tissue (Fig. 1).

Hence, I propose in this paper that lungs in Osteichthyes served to supply the heart with oxygen and were therefore important for sustaining activity. The need for enhanced cardiac performance would favor fish with lungs,

independent of aquatic oxygen content. Furthermore, if lungs functioned to supply oxygen to spongy myocardium of fishes, then the divided cardiovascular system of tetrapods was a mixed blessing because tetrapods inherited spongy myocardium from their fish ancestors, yet division of the heart isolates the right side from pulmonary oxygen. I propose that cutaneous respiration of extant amphibians and the intracardiac shunt that is found in many amniotes serve to oxygenate the heart. The loss of this shunt mandates the evolution of coronary support to the myocardium.

Problems with the Traditional Scenario

Problem 1: Fossil Record

Past paleoecological models for the evolution of lungs were heavily influenced by the fossil record of the Old Red Sandstone of the Devonian. In 1916 Barrell suggested that these sediments were deposited in fresh water where seasonal drought reduced rivers to stagnant, oxygen-poor environments. Since

lungs were considered to be a feature of both tetrapods and lungfish, the factors that drove the evolution of lungs were linked to the invasion of the terrestrial environment (Barrell 1916). Although this scenario for tetrapod evolution is no longer generally accepted (reviewed in Coates and Clack 1995; Daeschler and Shubin 1995), the idea that selection for lungs occurred in oxygen-poor water remains the dominant scenario (Johansen 1970, 1985; Johansen and Burggren 1980; Randall et al. 1981; Shelton 1985; Graham 1994; Walker and Liem 1994; Coates and Clack 1995).

A great deal of fossil evidence has emerged that poses a significant problem with this model for lung evolution. Although marine environments are less likely to be hypoxic than fresh water (for an alternate view, see Packard 1974), it has become increasingly clear that all pre-Silurian, the majority of Silurian, and many Devonian fishes were marine (Denison 1951, 1968; Thomson 1969a,b, 1980, Vorobjeva 1975; Boucot and Janis 1983; Bray 1985). Furthermore, many of these marine fishes probably had lungs. Since lungs are present in most extant primitive sarcopterygian and actinopterygian fishes (e.g., Dipnoi, Polypteriformes, Lepisosteiformes, Amiiformes), they were probably primitive for bony fishes (Osteichthyes), indicating the evolution of lungs took place at least as early as the Late Silurian (Denison 1956; Liem 1988). Consequently, the preponderance of the phylogenetic and paleontological evidence does not support the idea that lungs initially served to enhance survival in hypoxic freshwater habitats. However, this evidence seems at odds with the ecology of extant air-breathing fishes, which are generally thought to inhabit hypoxic fresh water.

Problem 2: Ecology of Extant Air-breathing Fishes

The distribution of extant air-breathing fishes has been the primary buttress for the traditional scenario for lung evolution (Thomson 1980). Studies of extant animals are important because direct evidence of lungs rarely fossilizes, and there is no hard-part correlate that remains in the fossil record (Bray 1985). Observations of extant animals caused

Barrell (1916: p. 417) to write, "It is especially in fresh-water fishes that accessory respiratory organs are employed and their use is directly related to the varying impurity of the waters in which they live." This assertion, however, is questionable on every count.

When considering only the distribution of primitive Osteichthyes (e.g., Dipnoi, Polypteriformes, Chondrostei, Amiiformes, and Lepisosteiformes), there is not a strong correlation between hypoxic freshwater habitats and the character of air-breathing. For example, early observations of the Australian lungfish, *Neoceratodus*, state that the animals can be found in brackish as well as fresh water in the Mary, Burnette, and Dawson Rivers (Gunther 1871b). Although the presence of lungs in these animals was interpreted as evidence that they inhabited water that was "unfit for gill ventilation" (Gunther 1871b), later studies showed aquatic oxygen was always plentiful, even during periods of drought (Grigg 1965). The distribution of the other lungfish genera have greatly influenced the association of air-breathing with hypoxic water; however, the Australian lungfish in many ways represents the primitive sarcopterygian condition better than the more highly specialized African and South American genera. Other lung-breathing fishes, such as gar, *Lepisosteus*, and bowfin, *Amia*, are found in an extremely wide range of habitats (Becker 1983; Nelson 1984). Both genera are found in fresh water throughout large regions of North America. *Lepisosteus* also inhabit marine environments of the Caribbean (Nelson 1984). Primitive fishes with lungs are not restricted to hypoxic freshwater habitats nor are lungs essential for life in hypoxic water, as is illustrated by the chondrostean *Acipenser* (the sturgeons), which are unusually well suited to survive hypoxic environments (Burggren and Randall 1978) yet are one of the few primitive osteichthyans to have lost the use of lungs for gas exchange.

The putative correlation between hypoxic fresh water and air-breathing among teleosts also is not as strong as is generally assumed. For example, the Amazon River is characterized by extensive warm, shallow water with widespread hypoxia. The river basin supports an extraordinary number of species (at least

1500) including ten families with air-breathing representatives (Roberts 1972; Kramer et al. 1978; Nelson 1984). In a survey of aquatic oxygen content throughout this environment, no correlation between the aquatic oxygen available in a habitat and the number of air-breathing species present was found (Kramer et al. 1978). In even the most hypoxic environments, gill ventilation was the dominant mode of respiration. Furthermore, it is not only freshwater teleosts that breathe air; Graham (1976) lists 40 marine species.

In summary, air-breathing both in primitive, nonteleostean fishes that use a lung for aerial respiration and in teleostean fishes that use a wide variety of air-breathing organs is not restricted to (or even highly correlated with) hypoxic freshwater environments. Consequently, the foundation of the traditional scenario for lung evolution is not as solid as it once appeared.

Problem 3: Physiology of Extant Fishes

A more subtle problem may exist with the traditional hypothesis that involves the view of lung function. In humans and other mammals, lungs function to oxygenate arterial blood and the level of oxygen in our venous blood is of little consequence. Once oxygenated in the lungs, blood is pumped by the heart to capillary beds of the organs and muscles (including the heart muscle through a coronary circulation) where oxygen is unloaded and consumed by those tissues; the venous blood returns to the lungs to be replenished with oxygen.

Probably because lungs function this way in humans, lungs in fishes have been considered as organs that enrich arterial blood with oxygen. From this point of view, the circulatory design of primitive actinopterygians (e.g., *Polypterus*, *Amia*, *Lepisosteus*) is inefficient because blood leaving the lungs flows into the venous circuit without first passing through any capillary beds of the body. Oxygen-rich blood mixes with oxygen-poor blood returning from the systemic circulation (Fig. 1). The combined blood (partially saturated with oxygen) then flows through the gills, where carbon dioxide is unloaded and (if the fish is in hypoxic water) oxygen from the blood can be

lost to the environment. Furthermore, partially saturated blood is returned to the lungs.

Although fishes that altered this blood flow pattern either through the "mammalian-like" partitioning of the circulatory system, which results in separation of pulmonary and systemic venous returns (e.g., the lungfishes), or through the evolution of a gas-exchange organ in parallel with the gills (e.g., *Clarias*, *Saccobranchus*), are generally viewed as having a more "sensible" design, the majority of primitive air-breathing fishes retained a circulatory system that results in mixing of pulmonary and systemic venous returns. Furthermore, a cardiovascular design that results in an admixture of oxygen-rich and oxygen-poor blood in the venous circuit is present in numerous teleosts that use modified gas bladders for aerial gas exchange, e.g., the osteoglossamorphs *Arapaima gigas*, *Gymnarchus niloticus*, *Notopterus chitala*; the primitive elopomorph *Megalops atlantica* (tarpon); and the euteleosts *Pangasius sutchi*, *Hoplerythrinus unitaeniatus*, *Gymnotus carapo* (Brainerd 1994). Hence, from an anthropocentric perspective that lungs function to get oxygen to systemic capillary beds, it is puzzling that so many fishes have settled on this "inefficient" design.

Nonetheless, there are features of the cardiovascular physiology of fishes that may make a mixed design advantageous and therefore explain the persistence of this character. In contrast to the human condition, the level of oxygen in venous blood in the primitive vertebrate condition is exceedingly important because it is venous blood that carries oxygen to the heart. The importance of an adequate supply of oxygen to the hearts of fishes and the impact this may have had on the evolution of tetrapods have been largely ignored. Instead, studies of the cardiorespiratory system of vertebrates have focused primarily on arterial blood qualities.

New Hypothesis: Lungs Enhanced Cardiac Performance

Myocardial Oxygen

Lungs may have evolved in early fishes to support an active lifestyle by supplying oxygen to the heart and enhancing cardiac performance. In extant fishes, levels of sustaina-

ble activity may be determined by the work loads the heart can maintain (Graham and Farrell 1990). These work loads are affected by the availability of oxygen because heart muscle functions primarily through aerobic metabolism, in contrast to skeletal muscle, which can produce tremendous amounts of energy anaerobically (Breisch et al. 1983; Martin et al. 1987; Sidell et al. 1987). Therefore, if myocardium does not receive sufficient oxygen, the ability of the heart to pump blood diminishes (Turner and Driedzic 1980; Farrell et al. 1989; Driedzic and Gesser 1994). Hence, the supply of oxygen to the heart is an important consideration in the design of the vertebrate circulatory system and was probably of importance during exercise in early vertebrates.

In the ancestral vertebrate condition, all oxygen was probably supplied to the heart through luminal blood. This is based on ontogenetic studies (reviewed in MacKinnon and Heatwole 1981) and on the phylogenetic pattern of myocardial oxygenation found in fishes. In the vast majority of fishes studied, the ventricle is not supported with a coronary circulation (Santer and Greer Walker 1980). Instead the muscle cells are arranged in a spongy matrix and are supplied with oxygen through channels that carry luminal blood. Some fishes have mixed ventricular morphology, with a compact, densely arranged layer of muscle that encases the spongy myocardium, and this compact tissue is supplied with oxygen through a coronary circulation.

A plentiful supply of myocardial oxygen was probably available from luminal blood when respiration was cutaneous because oxygen-rich blood from this gas-exchange site entered the heart and was then pumped to the gills, which functioned in filter feeding. The decline of cutaneous respiration and the employment of gills for gas exchange would have caused the heart to contain oxygen-poor blood, as it does in extant gill-breathing fishes (Fig. 1). This circulatory design may have presented a problem, in terms of supply of oxygen to the heart, that would have been exacerbated during exercise for the following two reasons: (1) during exercise the supply of oxygen to the heart drops while the demand for oxygen by the heart increases, and (2) the an-

aerobic metabolism of skeletal muscle during exercise causes acidosis (decrease in blood pH), which inhibits cardiac function, especially when acidosis is combined with hypoxia.

Exercise Stresses the Heart

During exercise the work of the heart increases and consequently the oxygen needs of the heart are elevated (Graham and Farrell 1990), yet exercising skeletal muscles consume more oxygen than resting muscles and so the level of oxygen in the venous blood perfusing the heart decreases (Kiceniuk and Jones 1977; Jones and Randall 1978). If the partial pressure of oxygen drops to a critical threshold, there will not be an adequate gradient to drive diffusion across the thickest parts of the ventricle (Davie and Farrell 1991). Because the supply of oxygen to the heart is depleted at the time it is needed most, i. e., during exercise, an innovation that elevates the level of oxygen in venous blood could improve performance. Blood from the lung drains directly into the venous return and therefore could serve to oxygenate spongy myocardium (Fig. 1).

The addition of oxygen to luminal blood from lung ventilation may be especially important during very intense exercise. This is because intense exercise in ectothermic vertebrates is supported by anaerobic metabolism, which can cause significant acidosis, 0.5 units (Black 1955, 1957a,b,c; Bennett 1978). Myocardial power output can be inhibited by this acidosis and the adverse effects on cardiac function are particularly debilitating when acidosis is combined with hypoxia (Gesser et al. 1982; Gesser and Poupa 1983; Farrell 1984; Gesser 1985). Acidosis can also impair the transport of oxygen by decreasing the affinity of hemoglobin for oxygen (Bohr and Root effects) so that loading of oxygen in the gills is more difficult (Secondat 1950; Black 1958; Black et al. 1962).

Although not completely understood, in gill-breathing fishes these factors appear to result in significant post-exercise mortality associated with disruption of the circulation (Secondat and Diaz 1942; Bates and Vinsonhaler 1957; Black 1957a, 1958; Paulik and DeLacy 1958; Parker and Black 1959; Black et al. 1962;

Beamish 1966; Wood et al. 1983). Air-breathing gar experience a level of acidosis from activity similar to that of gill-breathing fish such as trout, but do not die unless they are kept from air-breathing (Shipman 1989). Hence, lung ventilation may increase the levels of acidosis that are tolerable as well as enhance aerobic performance.

Predictions of the Scenario

Prediction 1: Distribution of Fossil Fishes

Traditional Scenario.—Because lungs evolved in response to the challenges of hypoxic environments, the fossils of early fishes that had lungs should be found in sediments that were deposited in oxygen-poor environments, probably fresh water.

Myocardial Oxygenation Scenario.—Because lungs were important for increasing levels of activity and would be useful in this way in any environment, the fossils should be distributed in both oxygen-rich and -poor environments. Furthermore, early fishes that had lungs should show feeding and locomotor characters that are associated with an active lifestyle.

As previously mentioned, the myocardial oxgyenation scenario is more consistent with the distribution of fossil fishes than the traditional scenario, in that early fishes were primarily marine (Denison 1951, 1968; Thomson 1969a,b, 1980, Vorobjeva 1975; Boucot and Janis 1983; Bray 1985). Furthermore, the locomotor and feeding patterns of these fishes are consistent with a scenario of an active lifestyle (Denison 1956; Thomson 1969a, 1980). In a comprehensive survey of early fossil vertebrates, Denison (1956: p. 430) concludes that "The early Osteichthyes were essentially similar to many modern teleosts in their adaptation, and they must be reckoned among the best swimmers of their time. The crossopterygians had powerful jaws and well-developed, pointed marginal teeth, indicating that they were predaceous."

Prediction 2: The Function of Lungs in Extant Osteichthyes

Traditional Scenario.—The use of lungs will be correlated with low aquatic oxygen.

Myocardial Oxygenation Scenario.—The use of lungs will be related to activity and relatively insensitive to aquatic oxygen. Furthermore, fishes that have retained the use of lungs for myocardial oxygenation will be active, while fishes with spongy ventricles that do not have lungs will be sluggish.

Detailed below are examples of fishes that show a correlation between air-breathing and activity. If observations have been made on air-breathing and aquatic oxygen, they are noted. In these examples the circulatory system is such that the ventricle contains an admixture of oxygen-rich pulmonary blood and oxygen-poor systemic blood. Where possible, information on ventricular morphology is reported in Table 1.

Among the Dipnoi, the Australian lungfish (*Neoceratodus*) retain the following characters thought to be primitive: large scales and dermal bones; big, fleshy, lobed fins; large opercular bone; well-developed gills with all the branchial arteries subdivided into capillaries; pocket valves in the conus with poorly developed spiral valves; poorly developed septa in the atria and ventricle causing significant mixing of pulmonary and systemic venous returns within the heart; and an inability to aestivate (Johansen et al. 1968; Johansen and Hanson 1968; Thomson 1969a; Maisey 1996). In this primitive sarcopterygian fish, lungs are used to support activity. Not only does activity stimulate air-breathing, but measurements of aerobic scope when the animals were swimming in well-oxygenated water and allowed to air-breathe were greater than when prevented from air-breathing (Grigg 1965). If oxygen transport is limited by the heart, then aerobic scope is not expected to increase with elevated gill, or lung, ventilation, unless there is a simultaneous improvement in cardiac performance. As previously mentioned, there is no relationship between aquatic hypoxia and the use of lungs, as the natural habitat is not hypoxic (Grigg 1965).

The polypterids are generally considered extremely primitive actinopterygians. When in oxygen-rich water, *Polypterus senegalis* are capable of meeting their oxygen demands entirely with their gills, yet activity in oxygen-rich water stimulates air-breathing. Further-

TABLE 1. Estimates of ventricular morphology of selected vertebrates.

	Spongy %	Coronary support	Source
CYCLOSTOMES			
hagfish	100	slight	Grant and Regnier 1926
lampreys	100	slight	Grant and Regnier 1926
CHONDRICHTHYES			
Holocephali			
Chimaera mostrosa	95	slight	Santer and Greer Walker 1979
Hydrolargus affinis	92	slight	Santer and Greer Walker 1979
Rajida			
Raja montagui	77	slight	Santer and Greer Walker 1979
Squaloidea			
Scyliorhinus caniculus	78	slight	Santer and Greer Walker 1979
Lamnidae			
Carcharodon carcharias	64	moderate	Emery et al. 1985
Isurus oxyrinchus	60	moderate	Emery et al. 1985
Alopias vulpinus	58–69	moderate	Tota et al. 1983
	64		Emery et al. 1985
OSTEICHTHYES			
Actinopterygians			
Polypterus	100	slight	Santer and Greer Walker 1979
Amia	100	slight	Santer and Greer Walker 1979
Lepisosteus	71	slight	Santer and Greer Walker 1979
Sarcopterygians			
Latimeria	100	slight	Millot et al. 1978
Neoceratodus	100	slight	MacKinnon and Heatwole 1981
Lepidosiren	100	slight	Robertson 1913; Foxon 1950
Protopterus	100	slight	Robertson 1913; Foxon 1950
tetrapods			
amphibians	100	slight	Foxon 1955; MacKinnon and Heatwole 1981
chelonians	90	slight	Brady and Dubkin 1964
lepidosuars	90	slight	MacKinnon and Heatwole 1981; Poupa and Lindstrom 1983
crocodilians	?	extensive	Kohmoto et al. 1997
birds	0	extensive	Sturkie 1986
mammals	0	extensive	Navaratnam 1980

Slight = 0–33%.
Moderate = 34–66%.
Extensive = 67–100%

more, rates of lung-breathing correlate to a greater extant with activity than with aquatic oxygen content (Magid 1966). Resting fish in hypoxic water reduce their rates of air-breathing compared with resting fish in well-oxygenated water (Magid 1966).

Although gar (*Lepisosteus*) are frequently thought to be lethargic, sit-and-wait predators, this is a misconception. Shipman (1989) has shown that gar have aerobic scopes and lactate signatures that classify them as "active" fishes (Turner et al. 1983). Gar engage in strenuous swimming during migration, spawning, and feeding, and it is during these periods of activity that gar have been ob-

served to increase lung ventilation (Saksena 1963; Becker 1983; Shipman 1989). This increase in air-breathing is found even when the fish are exercising in well-oxygenated water (Shipman 1989; personal observation), indicating that air-breathing in gar is relatively unrelated to aquatic oxygen levels. In numerous observations, Rahn et al. (1971) found no correlation between the partial pressure of aquatic oxygen (ranging between 52–198 torr) and air-breathing in *Lepisosteus osseus*.

Bowfin (*Amia*) are also highly active fish (personal observation). Although it has not been scientifically documented, anglers (who know the behavior of these fish well) claim

that bowfin are "one of the hardest fighters that ever took the hook" (Schrenkeisen 1963: p. 22). Air-breathing is important to these fish during activity (Johansen et al. 1970), even when exercising in well-oxygenated water (Farmer and Jackson 1995). Furthermore, the partial pressure of oxygen in water can be as low as 40 torr before resting animals resort to air-breathing (Johansen et al. 1970). Hence, air-breathing in *Amia* is relatively insensitive to aquatic hypoxia.

As in *Amia*, the high activity levels of the pelagic *Tarpon atlanticus* are well known among anglers, making it one of the most sought-after game fish in the Atlantic. This primitive elopomorph teleost also uses a lung for oxygen uptake during activity (Shlaifer and Breder 1940). Anatomical and biochemical evidence indicates that lungs likewise are important in the primitive osteoglossomorph teleost, *Arapaima gigas*, in increasing aerobic capacity of the heart (Hochachka et al. 1978).

Consistent with the myocardial oxygenation theory, fishes that retain a spongy ventricle yet lack lungs do not show an ability to sustain activity, e.g., *Latimeria* (the only extant coelecanth) and *Polyodon* (a chondrostean) (Schrenkeisen 1963: p. 17; Millot et al. 1978; Thomson 1980).

Prediction 3: The Absence of Lungs in Chondrichthyes, Coelacanthini, Chondrostei, and Teleostei

Traditional Scenario.—The absence of lungs will be correlated with a marine habitat (past or present).

Myocardial Oxygenation Scenario.—An explanation for the absence of lungs in these lineages is related to factors other than aquatic oxygen content. Circumstances that could diminish the usefulness of lungs include the following: bottom-feeding or life in deep water, the need for stable buoyancy, aerial predation, an inactive lifestyle, a coronary circulation in the ventricle.

The traditional scenario proposes that Chondrichthyes inhabited oxygen-rich marine environments and therefore did not experience selection for air-breathing. Likewise, Coelacanthini and Teleostei (and presumably Chondrostei) radiated into marine environ-

ments where lungs were not needed. The problem with this scenario is that the presence or absence of lungs in these groups is not highly correlated with environment. As previously discussed, it is clear that early Osteichthyes and Chondrichthyes were both marine. Furthermore, both groups radiated into fresh water in the Devonian, e.g., the Devonian sharks (Xenacanthiformes) that inhabited swamps and bayous. Extant Chondrichthyes inhabit tropical fresh water yet do not have lungs, e.g., Potamotrygonidae of the Amazon River system of South America, the Benoue River of Africa, and the Mekong River in Laos (Nelson 1976).

Although migration from fresh to salt water may explain the conversion of lungs to a swim bladder in the Coelacanthini, Chondrostei, and Teleostei, it is difficult to determine from the fossil record exactly when and in what environments this conversion took place. This scenario also does not account for the presence of marine fishes that air-breathe, e.g., Tarpon (Shlaifer and Breder 1940; Nelson 1983).

The myocardial oxygenation scenario predicts that factors besides aquatic oxygen content influenced whether or not lungs evolved or were retained in these fishes. The fossil scales of Ordovician chondrichthyans provide little insight into the lifestyles of these animals. Whether they were bottom feeders, lived in deep water, or lived a sedentary existence is difficult to determine. The hearts of active extant chondrichthyans (e.g., the great white, the Atlantic shortfin mako, and the common thresher sharks), however, are significantly modified from the ancestral condition in that there is considerable coronary vasculature in the ventricle (Table 1). This supports the idea that there was a problem ancestrally with oxygenation of spongy hearts that needed to sustain an active lifestyle. For whatever reasons, active chondrichthyans appear to have overcome this problem with a coronary circulation rather than lung ventilation.

The loss of lungs in Coelacanthini, Chondrostei, and Teleostei may indicate movement into deeper water or a disadvantage in surfacing to breathe. *Latimeria chalumnae* (the extant coelacanth) have a preferential depth around 200 meters (Fricke et al. 1991). The Chondros-

tei are also largely associated with bottom-feeding as well as with deep-water habitats (Nelson 1976; Becker 1983).

The rise of new types of predators, pterosaurs and birds, may have played a role in the evolution of a swim bladder and the loss of lungs. It is noteworthy that many primitive air-breathing Osteichthyes are extremely wary when approaching the surface for air (Shipman 1989; personal observation). Furthermore, many of these fishes are nocturnal (Gunther 1871b; Reighard 1903; Grigg 1965; Goodyear 1967). This may indicate that there has been intense aerial predation in shallow-water habitats, making a nocturnal lifestyle more successful than a diurnal one if surfacing to breathe is necessary. The origin of teleosts is geologically contemporaneous with the rise of aerial vertebrate predators (e.g., pterosaurs, birds). These ancient predators, like present-day fish-eating birds, may have been diurnal as it is difficult to see into water at night. Hence, conversion of the lung to a swim bladder may have been related to aerial predation rather than to a radiation into a marine environment.

Coronary support and compact myocardium may be hitherto unforeseen key innovations. Like active chondrichthyans, active teleosts rely on coronary support to the ventricle (Santer and Greer Walker 1980). Anatomical and physiological variation has led to the generally accepted idea that the coronary circulation of teleosts and chondrichthyans has evolved independently (Tota et al. 1983; Farrell and Jones 1992). This variation includes the following: the site of origin for coronary blood differs between Chondrichthyes and Osteichthyes (Grant and Regnier 1926); a layer of connective tissue tends to separate compact fibers from spongy ones in teleosts, but these fibers tend to be continuous in chondrichthyans (Sanchez-Quintina and Hurle 1987); and perfusion of coronary vasculature tends to continue throughout the entire cardiac cycle in teleosts but not in chondrichthyans (Tota and Gattuso 1996). Furthermore, holocephalians have only minor coronary support to the ventricle (Table 1), also suggesting that the coronary vasculature of more derived chon-

drichthyans, such as sharks, is not homologous with that of teleosts.

The Tetrapod Heart

Division of the Heart Was a Mixed Blessing

Most sarcopterygian fishes, as well as tetrapods, have a septum in the atrium and various degrees of septation in the ventricle. Although division of the heart has traditionally been considered an innovation that improved the efficiency of gas transport, this division isolates the right side of the heart from pulmonary oxygen. Consequently selection against a divided cardiovascular system would be expected in highly active fishes while septation would be expected to be successful in groups that found a sedentary niche or that compensated for the absence of pulmonary oxygen in the right side of the heart. The idea that there might be advantages to the undivided circulatory system of actinopterygian fishes is contrary to the traditional scenario, which suggests it is an inefficient design, yet it may explain why this character is found in many groups of fishes.

There are several mechanisms found in tetrapods that may compensate for the loss of oxygen due to division of the circulatory system. In extant adult amphibians, oxygen-rich blood from cutaneous respiration enters the right side of the heart and may provide oxygen to this spongy myocardium. In lepidosaurs and chelonians (snakes, lizards, Sphenodon, and turtles), the intracardiac shunt mixes oxygen-rich and oxygen-poor blood within the ventricle. Complete division of the heart and the absence of cutaneous respiration may mandate support of the heart with coronary vasculature (crocodilians, birds, and mammals).

The Dipnoi.—It has traditionally been thought that septation of the heart and vasculature in the Dipnoi evolved in response to a hypoxic habitat. The support for this idea is that lungfish genera relying heavily on lung ventilation also show a greater degree of cardiovascular division than lungfish relying on gill ventilation. In the predominantly air-breathing African lungfish, Protopterus, the capillary network in several gill arches is de-

generate. Furthermore, spiral valves in the conus and well-developed septa in the ventricle and atria enable these fish to send oxygen-rich pulmonary blood entering the left side of the heart into the degenerate gill arches, preventing loss of oxygen to their hypoxic environments. Oxygen-poor systemic blood enters the right atrium and flows through the other gill arches, unloading carbon dioxide (Johansen and Lenfant 1967; Johansen et al. 1967; Lenfant and Johansen 1968). In contrast, the septation of the predominantly water-breathing Australian lungfish is less developed, such that there is considerable mixing of oxygen-rich and oxygen-poor blood. Furthermore, these fish lack other features that are associated with a hypoxic environment (aestivation, degenerate gills, etc.)

The Coelecanth and Amphibians.—Whether the same circumstances (i.e., a hypoxic environment) gave rise to division of the early tetrapod heart is unknown. The coelacanth, *Latimeria*, shows no sign of septation. Most amphibians contain a spiral valve in the conus and a septum in the atrium. A septum is lacking in the ventricle, yet the trabeculae are aligned such that there is functional separation of pulmonary and systemic blood (Johansen and Hanson 1968). The septation of the amphibian circulatory system cannot be ascribed a priori to a hypoxic habitat; it is possible it was a consequence of a heavy reliance on lung ventilation that was mandated by either aquatic hypoxia or a terrestrial existence.

Although the reasons for division of the early tetrapod heart remain obscure, it is clear that it occurred. In adult amphibians, oxygen-rich blood returning from the lung enters the left atrium, remains on the left side of the ventricle, and is ejected into the systemic arches. Consequently the right side of the heart is isolated from pulmonary oxygen, a potential problem for cardiac function. Because cutaneous and buccal respiration enriches with oxygen the blood in the right side of the heart, it could function to compensate for the lack of pulmonary oxygen. Buccal and cutaneous respiration may also obviate the need for coronary vasculature (Foxon 1955). Indeed, extant amphibians have little coronary support to the ventricle (MacKinnon and Heatwole 1981).

Whether early tetrapods used cutaneous and buccal respiration is unknown. Considerations of the body size of early tetrapods and blood acid-base balance of extant groups suggest that the skin was not a major site for gas exchange (Gans 1970; Ultsch 1996), implying that the right side of the heart contained only oxygen-poor systemic blood. Selection against a spongy ventricle that contained only oxygen-poor blood in the right side may have been important in the evolution of the intracardiac shunt.

Chelonians and Lepidosaurs.—The unique ventricular morphology of chelonians and lepidosaurs results in complex blood flow patterns and the mixing of oxygen-rich and oxygen-poor blood within the ventricle. Because of the poorly developed septa, the morphology of these ventricles was originally seen as some sort of evolutionary halfway stage between amphibians and mammals, with "lowly second-rate" reptiles having an inefficient design. Further studies revealed a high degree of control over the mixing within the ventricle, suggesting this morphology was highly functional (see below). Most studies of the functional significance of shunting have emphasized the role it may play in diving, yet very few reptiles are habitual divers.

Unlike the condition in amphibians, a ventricular septum is found in all amniotes. In chelonians and lepidosaurs an incomplete horizontal septum divides the heart into ventral and dorsal chambers, known as the cavum pulmonale and the cavum dorsale, respectively (reviewed in Hicks 1995). The dorsolateral edge of the septum is free; consequently blood can flow between the chambers. The free edge of the septum can abut another septum, completely separating the two chambers. Depending on the species, another smaller septum subdivides the cavum dorsale into the cavum arteriosum and the cavum venosum and is commonly referred to as the vertical septum.

Without an intracardiac shunt, blood flow through this type of heart results in the cavum pulmonale containing only deoxygenated blood, yet the ventricle of chelonians and many lepidosaurs is primarily spongy (Grant and Regnier 1926; Brady and Dubkin 1964; MacKinnon and Heatwole 1981). However,

due to the incomplete septa, communication between the ventricular chambers is possible, giving these tetrapods the ability to uncouple within the heart systemic and pulmonary perfusion. Rather than directing oxygen-rich blood returning from the lung into the systemic circulation, these animals can return it to the lung. This blood flow pattern is known as a left-to-right shunt and results in oxygen-rich blood entering the cavum pulmonale (hemodynamics and anatomy reviewed in Hicks and Wood 1989; Hicks 1993, 1995). Hence the left-to-right shunt could bring oxygen to the spongy myocardium of this region. Oxygen-poor blood can also be directed from the systemic circulation back into the systemic circulation rather than flowing to the lungs, known as a right-to-left shunt.

As in fishes, the need for oxygen by the heart is greatest during exercise. However, there is greater extraction of oxygen from the blood by working skeletal muscles than by resting muscles; consequently the blood returning to the right side of the heart is oxygen-poor. Furthermore, exercise can result in the catabolism of carbohydrates to lactic acid, lowering blood pH and bicarbonate and depressing oxygen transport. As with fish myocardium, acidosis combined with anoxia has a far more debilitating effect on the heart than either alone (Wasser et al. 1992; Jackson et al. 1995). Consequently, it is during exercise that additional oxygen is needed by the heart and therefore the left-to-right shunt ought to occur at this time.

There are indeed observations of an increase in left-to-right shunt in chelonians during activity (Shelton and Burggren 1976; West et al. 1992; Krosniunas and Hicks 1994). Although this blood flow pattern may be functioning to oxygenate the heart, it also improves systemic oxygen transport. Hicks (1994) has demonstrated in anaesthetized, supine turtles that an adrenergically induced left-to-right shunt eliminates the right-to-left shunt and thereby increases the oxygen content of the systemic arterial blood to levels that are equal to pulmonary venous values. This increase in arterial saturation has also been seen in exercising animals (Farmer and Hicks personal observations).

By oxygenating the heart, this shunt may not only increase the aerobic scope of these animals but may extend the tolerable level of acidosis, increasing the scope of their anaerobic metabolism as well. Although fish and ectothermic amniotes have similar levels of acidosis following activity, it frequently leads to death in gill-breathing fishes but is not lethal for tetrapods (Bennett 1978). Just as lung ventilation in gar appears to ward off exercise-induced mortality (see above) the intracardiac shunt may spare ectothermic tetrapods from a similar fate.

Crocodilians, Birds, and Mammals.—Complete division of the ventricle (found in crocodilians, birds, and mammals) enables the lungs to be perfused at a lower pressure than the systemic circulation, preventing excessive stresses in the pulmonary capillaries; however, the division of the heart prevents an intracardiac shunt. Hence, lineages that have lost the ability to shunt blood within the ventricle must have compensated for this loss of oxygen in the right side of the heart by supplying oxygen through a coronary circulation.

Although it is already known that mammals and birds rely extensively on coronary support to the heart, the importance of coronary blood to the crocodilian heart remains to be fully determined. This hypothesis predicts that the crocodilian heart will be well endowed with coronary support, especially to the right side of the heart. Indeed, preliminary work indicates that the crocodilian ventricle is well supplied with coronary vasculature (Kohmoto et al. 1997) and that the right atrium has more coronary vessels than the left (personal observation).

Summary

For well over one hundred years, the scenario that lungs evolved in hypoxic environments has dominated the literature. Since lungs generally do not fossilize, and there is no hard-part correlate that yields information concerning the evolution of this organ, the physiology and ecology of extant fishes have provided information about the origin of lungs. No group of fishes has been more important in this regard than the lungfishes; their remarkable natural history has played a

pivotal role in establishing this scenario. Assumptions about the ecology of these, and other extant air-breathing fishes, have long been considered the most compelling evidence for the traditional scenario.

Further support for this scenario was thought to be found in the fossil record. Large numbers of Devonian fossils were found in sediments believed to indicate a fluviatile, semi-arid environment where periodic droughts made freshwater habitats hypoxic. The evolution of lungs was proposed to have had an advantage for species inhabiting these habitats.

There are several problems with this scenario. Mapping of soft anatomy features onto the vertebrate phylogeny indicates that lungs are primitive for Osteichthyes; yet the fossils of the earliest bony fishes are marine (Denison 1951, 1968; Thomson 1969a,b, 1980, Vorobjeva 1975; Boucot and Janis 1983; Bray 1985). Hence, the phylogenetic and paleontological evidence supports a marine origin for lung evolution, although marine environments are not widely hypoxic. In addition, the ecological foundation for the traditional scenario was based partly on assumption; field data on oxygen content of habitats and the discovery of new species reveal little correlation between hypoxic habitats and air-breathing.

I have proposed a new scenario for the evolution of lungs that may be more consistent with the fossil record as well as with the behavior and ecology of extant animals. This hypothesis maintains that the level of oxygen in the venous blood of fishes is exceedingly important because it is venous blood that carries oxygen to the heart. The fact that venous blood supplies oxygen to the hearts of fishes is a historical constraint of the original vertebrate cardiorespiratory condition. The myocardium that is ancestral for vertebrates is arranged in a spongy matrix. Rather than obtaining oxygen from a coronary circulation, these muscle cells obtained oxygen from luminal venous blood being pumped by the heart.

Because the heart (which has primarily an aerobic metabolism) can be a bottleneck in the oxygen transport system of extant fishes, and because the oxygen-rich blood from lung ven-

tilation in primitive fishes (e.g., *Polypterus, Lepisosteus, Amia*) mixes into the systemic venous return before entering the heart, lungs may serve to supply spongy myocardium with oxygen, increasing the levels of activity attainable by these fishes. Indeed, these animals rely heavily on lung ventilation while exercising in well-oxygenated water. Similarly, lungs could have been useful in this way to early osteichthyan fishes inhabiting well-oxygenated environments.

Probably because venous oxygen content is of little physiological significance in mammals, a traditional view of lung function in fishes has focused on the role of lungs as an organ that enriches arterial blood with oxygen, rather than as an organ that increases venous oxygen content. However, an important tenet of this scenario for lung evolution is that oxygen content of venous blood is important for animals with spongy myocardium. Because tetrapods inherited this tissue from their fish ancestors, I have proposed that oxygenation of luminal blood continued to play an important role in the selection of many of the morphological adaptations found in the cardiovascular systems of tetrapods. Because the remodeling of the chelonian and lepidosaurian ventricles enables oxygenated blood from the lung to traverse the ventricle and enter the right side of the heart (the left-to-right intracardiac shunt), it may function to carry oxygen to spongy tissue of this region (the cavum pulmonale). Furthermore I propose that progressive septation of the heart, which is found in some lepidosaurs and in mammals, birds, and crocodilians, mandates progressive support by coronary vasculature. Mammals and birds have extensive coronary support to the heart. Similarly, the ventricle of crocodilians should also contain an extensive coronary network.

In conclusion, numerous features of the vertebrate cardiovascular system have been reinterpreted from a nontraditional standpoint. Rather than viewing the evolution of lungs in bony fishes as an adaptation that enabled fishes to increase the oxygen in their arterial blood when the gills were rendered inadequate by hypoxic water, I have considered how lungs may have affected venous blood

gases, cardiac performance, and, consequently, activity levels regardless of the oxygen content of the environment. If lungs evolved in response to myocardial hypoxia, then morphological adaptations seen in tetrapods (e.g., the intracardiac shunt, coronary circulation) also may have resulted from the need for myocardial oxygen.

Acknowledgments

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