

# The Coupled Evolution of Breathing and Locomotion as a Game of Leapfrog\*

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## ABSTRACT

Because the increase in metabolic rate related to locomotor activity places demands on the cardiorespiratory apparatus, it is not surprising that the evolution of breathing and of locomotion are coupled. As the respiratory faculty becomes more refined, increasingly aerobic life strategies can be explored, and this activity is in turn expedited by a higher-performance respiratory apparatus. This apparent leapfrogging of respiratory and locomotor faculties begins in noncraniate chordates and continues in water-breathing and air-breathing vertebrates. Because both locomotor and cardiorespiratory activities are coordinated in the brain, neurological as well as biochemical coupling is evident. In spite of very different breathing mechanisms in various vertebrate groups, the basic respiratory control mechanisms appear to have been conserved, and respiratory-locomotor coupling is evident in all classes of vertebrates. Hypaxial body wall muscles that were strictly locomotor in fish have respiratory function in amniotes, but some locomotor function remains in all groups.

Respiration provides energy, and locomotion uses it. Thus, it is not surprising that cardiorespiratory and locomotor systems appear as a single functional unit, or “faculty” sensu Bock and Wahlert (1998). Attempts to characterize this coupling within the framework of the symmorphosis hypothesis, however, have met with only limited success (Weibel et al. 1987; Garland 1998;

Weibel and Hoppeler 2005). The reasons for this lack of general congruence could be the extreme complexity and plasticity of the relationship between structure and function. The following three papers illustrate for fish, amphibians, noncrocodilian and crocodilian reptiles, and birds that this coupling has both ancient, homologous central elements (Taylor et al. 2006; Vasilakos et al. 2006) and group-specific anatomical variants, in which nonhomologous muscular and skeletal elements are recruited to perform analogous functions (Klein and Owerkowicz 2006).

An evolutionary leapfrog game, whereby cardiorespiratory adaptations evolve in conjunction with metabolic demands of the locomotor system, is already evident among noncraniate chordates. Tunicates (larval ascidians and adult appendicularians) are assumed to be the first chordates to use axial muscles in combination with a notochord for locomotion, whereas the branchial basket is ventilated only by cilia (Gans and Northcutt 1983; Goldschmid 1996). This mismatch could have been critical in limiting these animals to relatively small sizes and planktonic or sessile lifestyles.

In Acrania, which are probably the sister group of craniates (García-Fernández and Holland 1994), a tight coupling of circulatory/respiratory faculties with locomotion has arisen but in an aberrant way not seen in craniates (Schmitz et al. 2000). The segmental locomotor musculature is much more extensively developed than in tunicates (Franz 1927). In amphioxus (*Branchiostoma lanceolatum*), however, the morphological diffusing capacity for oxygen in the “gills” is only 1%–2% of the total (Schmitz et al. 2000) and is inadequate for supplying elevated metabolic demand. In addition, a central gill-heart and oxygen-transporting pigment are lacking (Rähr 1981), and gas exchange with ventilatory water takes place mainly over the thin membranous covering of the peribranchial cavity and body wall (Schmitz et al. 2000). Complex and voluminous coelomic spaces comprise a secondary circulatory system for metabolic gases, whereas the primary circulatory system serves in nutrient distribution and excretion. Because coelomlike spaces are also present in the segmental musculature, locomotor and circulatory/respiratory faculties are mechanically coupled: swimming movement deforms the coelomic spaces and thus must result in displacement of body fluids (Schmitz et al. 2000). Ventilation of the coelomic surfaces that cover the peribranchial cavity, however, is still accomplished by cilia of the branchial epithelium, as in tunicates.

The next step in the leapfrog game was taken with the origin of the craniates. The only nonvertebrate craniates, the hagfish,

\* This paper introduces a collection of three papers that were presented at the Seventh International Congress of Vertebrate Morphology, Boca Raton, Florida, 2004, in the symposium “Respiration and Locomotion: Coupled Systems in Vertebrate Evolution,” organized by S. F. Perry and D. R. Carrier.

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lack ciliated gills, and a muscle-driven pharyngeal velum is the primary ventilatory structure (Mallatt and Paulsen 1986). Vertebrates take the game one step further. Larval lampreys also use a velum for unidirectional branchial ventilation (Rovainen 1996). Although the gills of these filter feeders possess ciliated epithelium, it is used for transport of the alimentary mucus sheet and not for water propulsion. Adult lampreys, however, rely on branchial constrictor muscles for gill ventilation, and the velum serves only as a valve to prevent regurgitation of respiratory water (Gans and Northcutt 1983; Rovainen 1996). The branchial cavity is filled passively by backflow through the gill openings, propelled by recoil of the cartilaginous branchial basket. Finally, in jawed vertebrates, five-part jointed gill arches (Mallatt 2005), with sophisticated branchial musculature that is directly innervated by cranial nerves, arise and represent the next stage in the sequential evolution of the branchial ventilatory faculty. The size range and aerobic diversity among jawed fish is, accordingly, enormous.

Thus, the anatomical features involved in cardiorespiratory/locomotor coupling in noncraniate chordates and basal vertebrates appear to have evolved separately in various groups. The study of central nervous integration of this faculty in vertebrates, however, reveals different principles. The nature of the coupling between the branchial and cardiac activity (regulation of ventilation/perfusion relationship) is the subject of the first contribution (Taylor et al. 2006) in this series. The second paper (Vasilakos et al. 2006), on the other hand, focuses on the possible homology of the central nervous control of air breathing in vertebrates from fish to mammals.

In tetrapods, two mechanisms of air breathing emerge (Brainerd et al. 1993). Buccal pump breathing, present in Lissamphibia and some lizards (Deban et al. 1994; Owerkowicz et al. 2001; Klein et al. 2002), involves derivatives of the same branchial and hypobranchial muscles used for gill ventilation in fish (Perry et al. 2005). Aspiration breathing, on the other hand, uses trunk muscles that were originally part of the locomotor apparatus of fishes (Carrier 1990, 1993; Brainerd et al. 1993; Brainerd and Simons 2000; O'Reilly et al. 2000; Bennett et al. 2001; Deban and Carrier 2002; Landberg et al. 2003).

The significance of the dual role of the hypaxial muscles in locomotion and ventilation is illustrated by the constraint on simultaneous running and costal breathing in lizards (Carrier 1987, 1991; Owerkowicz et al. 1999), the integration of ventilation and locomotion in birds (Boggs 1997, 2002) and mammals (Bramble and Carrier 1983; Bramble and Jenkins 1993), and the tuning of the natural frequencies of oscillation of the locomotion and ventilation in birds (Nassar et al. 2001) and mammals (Young et al. 1992). Nevertheless, the degree to which locomotor motions of the musculoskeletal system and viscera actually contribute to tidal volume appears not to exceed 20% (Lee and Banzett 1997). The locomotor activity of the trunk muscles also negatively impacts the capacity of the circulatory system in lizards (Farmer and Hicks 2000; Munns et al. 2004).

The degree to which these hypaxial muscles are still locomotor is dealt with in the last contribution. Klein and Owerkowicz (2006) review specializations in extant "reptiles" and focus on the role of special internal coelomic septation in allowing these animals to effectively walk and breathe at the same time. In birds, special costal projections—uncinate processes—and the associated appendicocostal muscles aid inspiration, while the main expiratory muscle, the external oblique, inserts at the base of the uncinate (Codd et al. 2005). The presence of uncinata processes in some theropod dinosaurs suggests that they, too, may have been highly aerobic.

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