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ABSTRACT

Lung ventilation in Dipnoi and probably all other primitive fishes
is effected by muscular action of the buccopharyngeal region (in-
halation) and the muscular and elastic lung wall (exhalation).
Differential hydrostatic pressure plays no major part in ventilation.
Lung volume is under precise control.

The three genera of surviving lungfish (Osteichthyes: Dipnoi) are of unusual interest to zoologists because of the close relationship that is thought to exist between the Dipnoi and the crossopterygian ancestors of the Amphibia. Although the evolutionary transition between fishes and tetrapods must have occurred at some time in the Devonian or earlier, the bradytelic evolution of the Dipnoi since this time suggests that the structure and behavior of the living lungfish reflect quite closely the ancestral conditions. Since the faculty of airbreathing is an important factor in the evolution of land forms, and is a common denominator between Dipnoi and Amphibia, this system has been the subject of close attention. The purpose of the present contribution is to comment on a current discussion concerning the manner of lung ventilation in primitive fishes in general and lungfish in particular.

According to Schmalhausen (1968), lung ventilation in primitive aquatic vertebrates was based upon the following mechanism. From a resting position on the bottom, with a lung full of gas in which oxygen is becoming depleted, the fish swims vertically to the surface and opens its mouth. At this point, the pressure at the mouth cavity is atmospheric, while the trunk, below, is subject to an external hydrostatic pressure according to the depth below the surface of the water. The differential in pressure, according to Schmalhausen, drives air from the lung out through the mouth. After release of this air, the mouth is closed around a bubble of fresh air and the fish reverses its position, swimming almost vertically downwards. The differential hydrostatic pressure between the head (deeper in the water) and the trunk (nearer the surface) is presumed to drive the bubble of air into the lung. The cycle is then complete.

This ingenious theory was used by Schmalhausen to suggest that true pulmonary respiration is an advanced character and, in the first Amphibia, played a lesser role than cutaneous respiration. The model given seems incorrect, but unfortunately it has been frequently repeated and has gained a wide currency in specialized and general zoological studies (for recent discussions, see Szarski, 1962; Carter, 1967; Cox, 1967). It seems useful, therefore, to make a formal note of some evidence concerning the behavior of lungfish that renders the theory untenable.

1) The suggested mechanism would not work if the fish were to swim to the surface and then simply sink back to the bottom with the head upwards at all times. This is the behavior of all specimens held in a laboratory aquarium where the depth of the water is no greater than the length of the fish (personal observation). This is also the behavior observed in shallow natural waters, and when the fish is emerging from aestivation but still remains within its burrow (Johnels and Svensson, 1954).

2) The mechanism could not operate if the fish were out of water or aestivating in a dry cocoon. In both situations, lungfish have been observed to ventilate normally (Smith, 1931; Johnels and Svensson, 1954).

3) Even in the largest lungfish (*Neoceratodus* and *Protopterus* may reach a length of more than seven feet), the difference in hydrostatic pressure between the lung and the head at the surface (average of 3½ feet of water or approximately 78 mm Hg) would not be enough to ventilate the large lung and maintain an excess internal pressure, or to produce the loud grunting noises made by disturbed lungfish.

In fact, there is evidence that lungfish and other lung-breathing fishes maintain an excess internal pressure in the lung at all times through the agency of smooth muscles and elastic tissue in the lung wall, and that exhalation occurs through the agency of these muscles but is controlled so that only some 20% of the total lung volume is normally exchanged at a single breath (personal observation, and from Johansen, Lenfant and Grigg, 1967). Inhalation is effected through powerful movements of the buccopharyngeal floor by which air is pumped forcefully into the lung (see, for example, Grigg, 1965; Bishop and Foxon, 1968).

The following simple experiment was designed to demonstrate the control that lungfish normally exert over the volume and ventilation of the lung. By use of pressure apparatus similar to that of Alexander (1959), the volume of the lung in an intact, unanaesthetised fish may be measured. In the experiments, the fish is held in a closed water-filled chamber to which different pressures can be applied. The only air in the system is that within the lung of the fish. As the ambient pressure is artificially increased,
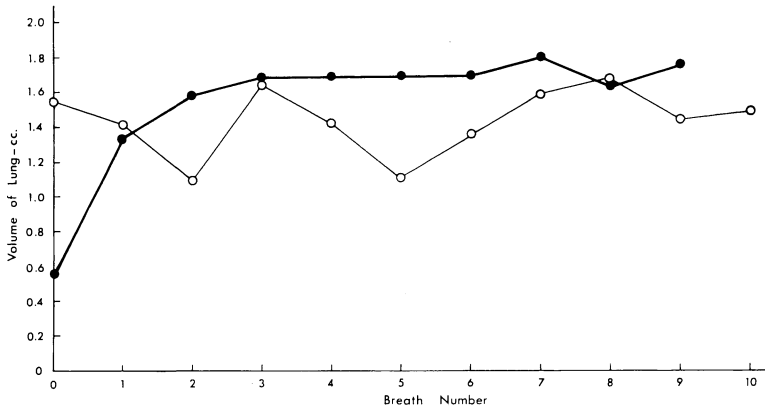
FIG. 1. Graph showing changes in lung volume during active ventilation in
a specimen of *Protopterus dolloi*. After artificial emptying of the lung, the
fish quickly restores the original lung volume and holds it constant (closed
circles — breaths taken approximately one per minute); compare with con-
trol series (open circles — breath taken approximately one per twelve
minutes). Weight of fish, 41.0 grams, length about 28 cm.

the volume in the chamber is decreased by compression of the
air in the lung. By use of Boyle's Law, a simple computation of
the relationship between the pressure and volume changes reveals
the initial volume of the lung. Six different specimens of the African
lungfish *Protopterus dolloi,* weighing between 36 and 100 grams,
were used. Each fish was caused to empty the lung by application of
a strong negative pressure (between —0.5 and —1.0 atmospheres).
The fish then took a series of breaths in rapid succession. The
volume of the lung was measured after each breath. As shown in
Figure 1, the fish brought the lung volume back to normal in a
small number of breaths made less than one minute apart (the
rate would have been faster but for the interruption caused by
measurement). In comparison, in the control experiment, when
the lung had not been emptied, the fish breathed at roughly 12
minute intervals and although there was fluctuation, there was no
overall change in lung volume.

DISCUSSION

The results of the observations and experiments indicate that lung
volume in dipnoan fishes is under rather precise control and that

this control is effected through direct muscular action. Particularly, the mechanism of inhalation involves pumping actions of the buccopharyngeal apparatus and associated structures, and the role of differential hydrostatic pressure in ventilation is minimal at best. Two further implications may be noted. Firstly, it seems most probable that all primitive fishes had a similar capacity for ventilation of the lung through active muscular pumping, since the buccal apparatus used forms part of the normal mechanism whereby the branchial water current is maintained. Secondly, efficient operation of the lung seems to require the presence of an elastic and muscular wall, by means of which expiration is effected. This leads to the development of an excess internal pressure in the lung at all times and therefore seems to afford the possibility for precise control of lung volume. Stretch receptors in the lung wall are probably involved in the sensing of internal pressure and volume. The capacity for the control of lung volume apparently offers a potential for the use of the lung in a rudimentary way to effect hydrostatic balance, even in the most primitive fishes.

The mechanism of lung ventilation in Dipnoi (and probably all primitive fishes) is basically similar to that in Amphibia. It seems improbable that deficiency in the ventilation mechanisms of early Amphibia was an immediate factor in the evolution of cutaneous respiration. Airbreathing fishes seem normally to use the lungs for augmenting oxygen uptake in conditions of low oxygen concentration and they use the gills and skin for carbon dioxide elimination whenever possible (see, for example, Lenfant, Johansen and Grigg, 1967). When the fishes left the water permanently the lungs had to assume both functions. It seems likely that if cutaneous respiration evolved at an early stage in the fish-amphibian transition, its value would have been in supplementing the physiological inadequacy of the lung in gas exchange rather than any gross deficiency in the mechanism of ventilation.

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