

POS 6088

HARVARD UNIVERSITY



LIBRARY

OF THE

Museum of Comparative Zoology









LIBRARY.

SEP 6 1968

HARVARD

POSTILLA PEABODY MUSEUM YALE UNIVERSITY

NUMBER 122. 5 AUGUST 1968.

LUNG VENTILATION IN DIPNOAN FISHES

KEITH STEWART THOMSON



Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office Peabody Museum of Natural History New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla*, *Bulletin*, *Discovery*, special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection*. All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

LUNG VENTILATION IN DIPNOAN FISHES

KEITH STEWART THOMSON

Department of Biology and Peabody Museum of Natural History Yale University

ABSTRACT

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

> MUS. COMP. ZOOL LIBRARY

SEP 6 1968

HARVARD UNIVERSITY

POSTILLA 122: 6 p. 5 AUGUST 1968.

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 $3\frac{1}{2}$ 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,

4



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 control 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 fishamphibian 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.

Acknowledgement

Mrs. Barbara Moss provided valuable assistance in the laboratory work with lungfish. The study was supported by National Science Foundation grant GB-4814.

LITERATURE CITED

- Alexander, R. McN. 1959. The physical properties of the swim bladder in intact Cypriniformes. J. Exp. Biol. **36**: 315-332.
- Bishop, I. R., and C. E. H. Foxon. 1968. The mechanism of breathing in the South American lungfish, *Lepidosiren paradoxa;* a radiological study. J. Zool. London 154: 263-271.
- Carter, G. S. 1967. Structure and habit in vertebrate evolution. Sidgwick and Jackson, London. 536 p.
- Cox, C. B. 1967. Cutaneous respiration and the origin of the modern Amphibia. Proc. Linn. Soc. Lond. **178:** 37-47.
- Grigg, G. C. 1965. Studies of the Queensland lungfish Neoceratodus forsteri (Krefft). 1. Anatomy, histology and functioning of the lung, Austr. J. Zool. 13: 243-253.
- Johansen, K., C. Lenfant, and G. C. Grigg. 1967. Respiratory control in the lungfish *Neoceratodus forsteri* (Krefft). Comp. Biochem. Physiol. 20: 835-854.
- Johnels, A. G., and G. S. O. Svensson. 1954. On the biology of Protopterus aethiopicus (Owen). Arkiv f. Zool. 7: 131-164.
- Lenfant, C., K. Johansen, and G. C. Grigg. 1967. Respiratory properties of the blood and pattern of gas exchange in the lungfish *Neoceratodus forsteri* (Krefft). Resp. Physiol. 2: 1-21.
- Schmalhausen, I. I. 1968. The origin of terrestrial vertebrates. Academic Press, New York. 314 p. (Translated from Russian original of 1964).
- Smith, H. W. 1931. Observation on the African lung-fish, *Protop*terus aethiopicus, and on the evolution from water to land environments. Ecology 12: 164-181.
- Szarski, H. 1962. The origin of the Amphibia. Q. Rev. Biol. 37: 189-291.



INFORMATION FOR AUTHORS

- **REVIEW** The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.
 - **STYLE** Authors of biological papers should follow the *Style Manual for Biological Journals*, Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey*, Fifth Edition (U.S. Govt. Printing Office).
 - **FORM** Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11" paper. Double space everything. Do not underline any-thing except genera and species. The editors reserve the right to adjust style and form for conformity.
 - **TITLE** Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.
- **ABSTRACT** The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.
- NOMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.
- **ILLUSTRATIONS** Must be planned for reduction to $4 \times 6\frac{1}{2}$ " (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to $3\frac{3}{4} \times 6\frac{3}{4}$ ". All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.
 - **FOOTNOTES** Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.
 - **TABLES** Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.
 - **REFERENCES** The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.
- JTHOR'S COPIES Each author receives 50 free copies of his *Postilla*. Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.
 - **PROOF** Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.
 - **COPYRIGHT** Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

















