

The Fossils of Ectoplasm in a Nutshell: A Brief History of the Challenges into the Air in the Animal Kingdom

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ABSTRACT: Evolution of flight in the animal kingdom is a series of challenges for survival in severe natural environments, in particular the thin air and the predators. Although flight is an efficient way of transportation, it requires some special organs suited for respiration and locomotion. Considering about the time history of oxygen concentration in the atmosphere, one knows the reason for the timing of challenges into the air: insects appears in the oxygen rich air; diverse evolution of pterosaurs, dinosaurs and birds occurs under the thin air condition with the aid of air-sac systems. Wind-tunnel experiments reveal the fact about the ancient wings that flapping membrane wings is an efficient way of obtaining thrust owing to the phase difference between heaving and feathering brought about by the passive motion of the trailing-edge.

1. INTRODUCTION

Ectoplasm is a pair of condensation trails originating from the both wing-tips. The aim of this talk is from the mechanical point of view to look back upon the essential events in the origin of flight in the animal kingdom with special emphasis upon respiration and aerial locomotion. Each corresponds respectively to internal- and external-biofluidynamics.



Fig. 1 Ectoplasm of *Archaeopteryx*

2. RESPIRATION AND LOCOMOTION

I shall discuss synchronization of locomotion and respiration that leads us to Carrier's constraint. Animals creeping on all four squeeze their right or left lungs in turn during crawling, because their bodies move sideways in a wavy manner. Therefore they always make use of only one of their lungs, and hence this constraint results in deficiency of respiration; they cannot run for a long distance; this is called Carrier's constraint; old type animals like salamanders and lizards are under Carrier's constraint. Possibly hopping and biped-running are only ways to be free from this constraint. Pterosaurs may be hopping, whilst birds and dinosaurs are surely bipedal. Insects don't have lungs, so there is no way for them to be annoyed by Carrier's constraint; bats are under the spell of Carrier's constraint, but they solved this problem by hanging upside down.

Now I shall introduce respiration systems other than well-known lungs: firstly insects' trachea system; secondly avian air-sac system.

Insects breathe with the aid of the trachea system; this is a pneumatic pipe network spanned all over their bodies and penetrated deeply into their cells; delivery of oxygen is totally dependent on passive diffusion; they do not use the blood circulating system for the gas-exchange purpose. Therefore diffusion constrains their body size. Contemporary insects do not exceed 30 cm in length. One of the reasons why they adopted this respiration system is the result of compromise with their acquisition of wings evolved from gills, respiration devices owned by their ancestors in the water.

I shall explain the efficient air-sac system possessed by birds, presumably by pterosaurs and dinosaurs. Air-sacs are not gas-exchanging organs but flow controllers. Figure 2 shows the schema of a modern bird: in inspiration the fresh air once enters into the caudal air-sacs; in expiration the expired air goes out of the cranial air-sacs, whilst the air goes out of the caudal air-sacs through the parabronchi in the lungs; the flow direction in the parabronchi is always one way; in the pulmonary circulation the blood flows against the direction of the air flow in avian lungs; this arrangement of flows affiliates efficient gas exchange, although the counter-flow gas exchange actually occurs between air and blood capillaries in the peripheries of the parabronchi. In the parallel-flow gas exchange the partial pressure of a gas in blood capillaries never exceeds the expire-ended pressure, but the counter-flow is not the case (Fig. 3).

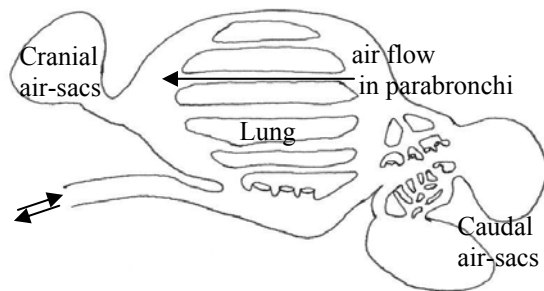


Fig. 2 Air-sac system
Redrawn from Powell^[1]

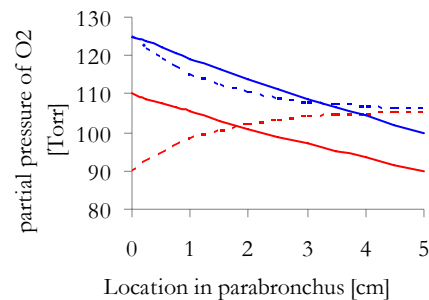


Fig. 3 Gas exchange by counter- and parallel-flow
Solid lines for counter-flow and dashes for parallel-flow; blue for air and red for blood.

3. SPECULAION ON THE ANCIENT ATMOSPHERE ON EARTH

Based on the evidence found in rocks and by use of the simulation, Ward^[2] constructed the charts that show the relative concentrations of oxygen and carbon dioxide for the entire period of the ancient earth. Figure 4(a) is a reconstruction of his charts, whilst Fig. 4(b) shows the air density calculated by me using Ward's charts. Geological time is measured by the Ma unit, *i.e.*, million years. Oxygen is plotted by the percentage; carbon dioxide is plotted by the measure of one unit as the contemporary value, *i.e.*, 400 ppm.

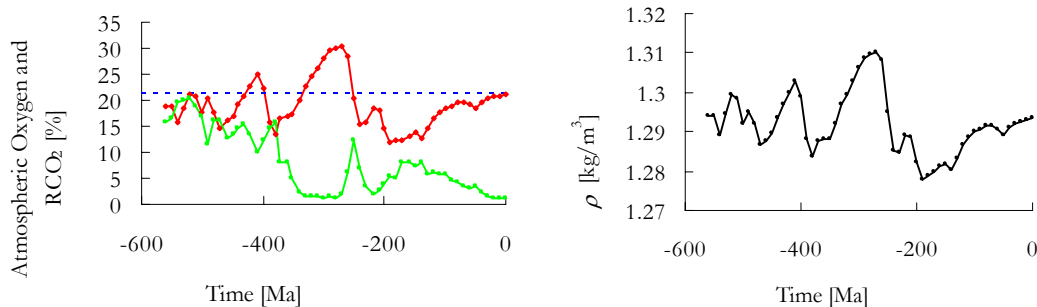


Fig. 4 (a) Time history of the relative concentrations of O₂ and CO₂; (b) Time history of the air density

Blue dash designates the contemporary concentration of oxygen in the atmosphere, *i.e.*, 21%. The first flyer appears 310 million years ago, when oxygen is as rich as 30%; during the Mesozoic era, or the age of dinosaurs from 251 million years ago to 65 million years ago, oxygen is as thin as 10%. The latter atmosphere had driven life on earth to diversity for survival of the fittest. The density of the air is sensitive to the concentration of oxygen. Heavy air can carry heavier animals, and *vice versa*.

4. THE ORIGIN OF FLIGHT

There are two hypotheses for the origin of flight: the *arboreal* one is a glide-down story; the *cursorial* one is a ground-up story. Since the fast runners need downward lift, the arboreal origin seems more plausible to me from the mechanical point of view. In this section I quote my own experimental results^[3]; we designed and built up wings and flapping devices mounted upon the force balance in the wind tunnel.

4.1 INSECTS

The first flyers come from the insect group in the middle Carboniferous period, 310 million years ago. These are gigantic ancient dragonflies with more than one meter wing span. Insect wings derive from gills and have membrane structures. The gigantism and the trachea system were possible, because dense oxygen existed in the Carboniferous atmosphere: oxygen percentage is estimated even up to 30% of the air, whilst the percentage of carbon dioxide was almost the same as the present value.

The challenge into the air would have occurred as a result of escape from amphibians, the predators *recently* coming out of the water to the ground. Insects would have started their flight by gliding down from contemporary high trees with hard trunks, which are now changed into coals.

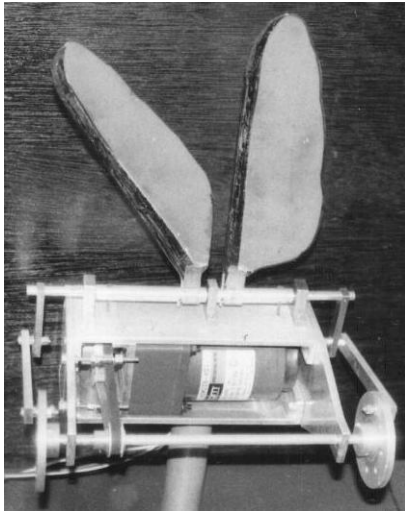


Fig. 5 Model wings of *Meganeura monyi*

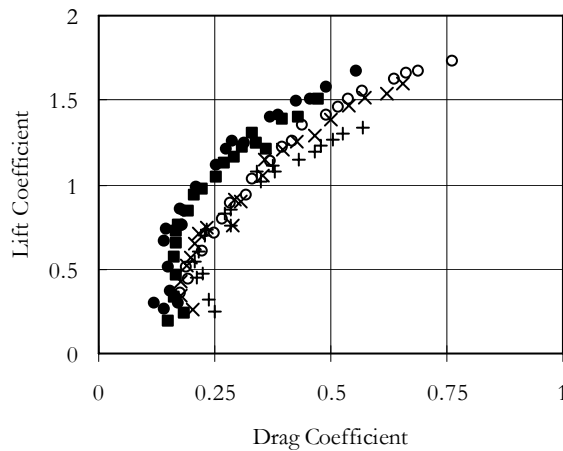


Fig. 6 Polar plot: C_L vs. C_D ○: wings fixed;
●: wings flapped in the same phase;
×: a fore wing 90-degree lead to a hind wing;
+: a fore wing 90-degree lag behind a hind wing;
■: wings flapped out of the phase.

Now I shall show the experimental results for a gigantic ancient dragonfly called *Meganeura monyi*. Figure 5 shows the half-scale (!) model mounted upon a flapping device. Their wing roots are line hinges that allow heaving motion only; the present dragonflies are, however, equipped with spherical hinges, and hence they are adept in acrobatic maneuvers. Devices are designed to flap wings at 30 degree amplitude with its reduced frequency fixed at 0.1 in 6.0 m/s winds. Figure 6 shows the polar plot of lift and drag acting on the fixed or flapping wings in the wind tunnel. Note that thrust corresponds to the difference in drag coefficients to the fixed wings; the results show that flapping in or out of the phase leads to generation of thrust as much as 0.15-0.16 in thrust coefficient.

4.2 PTEROSAURS

The next dominant fliers are pterosaurs. They first appeared in the Triassic sky 220 million year ago. During the Mesozoic era oxygen had been as thin as 12% of the air, while carbon dioxide level had been 8 times higher than the present value. Pterosaurs are thought to have the lung system augmented by air-sacs, which is supported by the fact that fore-limb bones are pneumatic; this configuration makes the gas exchange more efficient than the mammalian lung system. Pterosaurs' gigantism, however, cannot be accounted for, because the density of the air is lighter than the present value.

There are two types of pterosaurs: older *Rhamphorhynchoidea* has toothed beaks and a long tail; newer *Pterodactyloidea* lacks teeth and a tail. Toothed beaks imply the existence of chewing muscle, and hence their head is not so light-weighted. That is why they need tails as counter weight. At the same time tails must serve as tail wings. The style of the new comers imply that they are smarter adepts in flight.

We examined aerodynamic characteristics of *Pterodactylus* wing. Figure 7 shows our model made of stainless steel rods and a natural rubber sheet. The fore-limbs and the elongated forth digits are the main structures that support pterosaurs' membrane wings. Flapping is made possible by use of a stepping motor; the amplitude is 15 degrees with its reduced frequency fixed at 0.1 in 5 or 3 m/s winds. It is noteworthy that even the heaving motion alone generates thrust as much as 0.8 in its coefficient.

Experiments show that heaving such a wing induces lag in the trailing edge motion owing to its deformation and that this passive feathering motion plays an important role in generation of thrust. This motion is schematically shown in Fig. 10. It is theoretically well-known^[4] that thrust-generation by minimum energy is attained by giving quarter a period lag of feathering behind heaving at the reduced frequency around 0.1.

4.3 BIRDS

The first birds *Archaeopteryx* appeared in the Jurassic sky more than 140 million years ago. They are



Fig. 7 *Pterodactylus* model

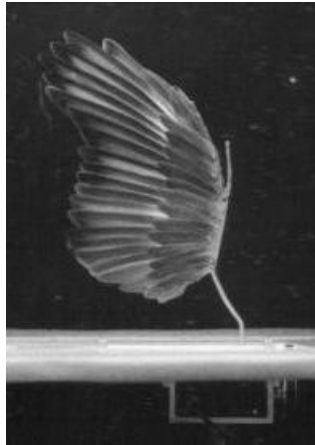


Fig. 8 *Archaeopteryx* model

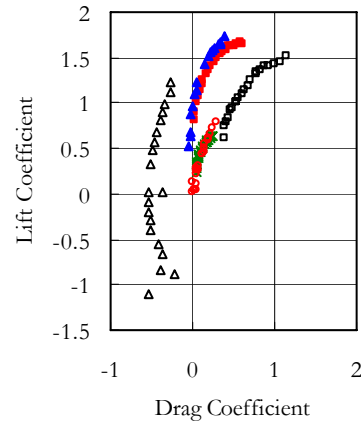


Fig. 9 Polar plot: C_L vs. C_D for *Pterodactylus* and *Archaeopteryx*

- : *Pterodactylus*, wing fixed in 5m/s winds;
- : *Pterodactylus*, wing fixed in 3m/s winds;
- △: *Pterodactylus*, wing flapped in 3m/s winds;
- *: *Archaeopteryx*, wing fixed in 10m/s winds;
- : *Archaeopteryx*, wing fixed in 3m/s winds;
- ▲: *Archaeopteryx*, wing flapped in 3m/s winds.

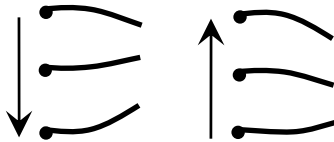


Fig. 10 Deformation of a membrane wing during flapping:
flow from left to right; downstroke (left); upstroke (right).

covered with light-weight and flexible feathers suited for flight and warm-bloodedness. Birds have the lung system augmented by air-sacs. They are also adapted to thin oxygen in the Jurassic atmosphere, and hence they can fly over the Himalayas today.

We examined aerodynamic characteristics of *Archaeopteryx* by use of a model shown in Fig. 8. The results are summarized in Fig. 9, which implies their weight as around 300g. We think they are not mere gliders but active fliers with their wings flapping.

4.4 BATS

Bats appeared as the last active flyers. Their bones are fragile, and hence fossils are not well preserved; the oldest bat record dates back to 55 million years ago; in Tertiary oxygen level has risen up to 20% of the atmosphere. Bats have the mammalian lung system; they don't have air-sacs or pneumatic bones. Their feat of acrobatic flight owes largely to the wing structure; four of five digits span membrane wings; this is not mere fail safe structures. Recent experiments^[5] show the doubly folded vortex wake of bats; digits afford complex camber control during flapping.

5. CONCLUSION

Flying is worth risking lives and energy costs. To know the animal flight it is not sufficient to examine their flight apparatus alone, for respiration is major constraint upon rapid locomotion like flying.

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