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Function shift and the origin of insect flight

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Abstract

It is suggested that the location on the body and close association of gill pads with airways, circulation, and most importantly, muscles and innervation, make these respiratory structures the most likely candidates as incipient insect wings, and provide the most parsimonious example for the evolution and development of arthropod flight. First, surface area expansion of these muscled gill pads was driven by the need for sufficient gaseous exchange in the shallow, warm, oxygen-poor waters of the Devonian. Eventually, these expanded structures began to exchange gases with the air, and possibly served as an epigamic display, helped disperse pheromones, or provided a gliding/flight surface. Thus, gill pads could have had more than one vital function while subject to various selective pressures directing an eventual shifting of their primary function(s) to that of flight. Once true flight began, the increased demand for oxygen by the direct flight muscles would be satisfied by the already existing associated respiratory and circulatory elements with development of larger spiracles. Because this explanation is based on a simple function shift of existing pre-adapted structures, it is not necessary to invoke the emergence of new structures (such as muscles and attendant organs) where they were not originally found, as with other theories of insect wing origins.

Introduction

None of the many theories proposed to explain the origin of insect wings and flight has been fully satisfactory. Among the most popular are those of Alexander and Brown (1963), who proposed that the wafting of pheromones and epigamic display were important, and Wigglesworth (1963b), who favoured paranotal lobes that eventually became wings. Wigglesworth (1976) eventually shifted from the paranotal theory to the gill theory of Oken (1811), Gegenbaur (1878), and Crampton (1916). For about 15 years Kukulová-Peck (1978, 1983, 1985, 1987, 1991) has propounded the origin of wings from epicoxal exites. The arguments are summarised in Lawrence et al. (1991). Rasnitsyn (1981) argued for a paranotal wing origin, and that the paranotum originated from a complex of tergal and pleural elements, and Williams et al (1994) proposed, for higher insects at least, that the dorsal disc patterning fields are derived from ancestral leg patterning fields. However, Williams et al. (1994) cautioned that wings are appendages very distinct from legs, the major differences being the presence of a well-defined edge (margin) and no obvious distal tip. Marden and Kramer (1994) have evidence of surface-skimming stoneflies as an intermediate stage in insect flight evolution. It should be remembered that insect flight may have arisen more than once (Pettigrew 1988), perhaps explaining the conflict surrounding discussions of the evolution of flying insects.

Wootton (1986), in one of the most complete summaries of insect wing origin and flight theory, presented seven critical questions, the most important of which were (1) from what preexisting structures did the protowings emerge?, (2) what function(s) did these early structures serve?, and (3) were

they immobile or articulated? These questions address the centre of the discussion, and will be entertained here.

In order to switch from a previous function to flying, the protowings had to be adaptable for a function shift with little or no interference with the previous function(s). The previous function(s) perhaps became emancipated when other structure(s) took over the original job. Thus, for a while, the protowings still served their previous function(s) as they were undergoing evolution to function as wings.

Initially, the strongest selection pressures driving the function shift would favour escape from predators, inter- and intraspecific competition for food, or sexual functions. The new function of flight would aid in dispersal and the exploitation of new food sources and habitats. The function shift could occur easily because the incipient wings provided other important services during the change. The present discussion strives to present the most parsimonious explanation by enlarging upon the idea that one origin of insect wings was from tracheal gills or the pre-adapted and muscled gill pads of aquatic insects (the gill theory). We support this suggestion by indicating that structures required for initial flight or other locomotory movements were already present and well developed (for example, muscles, flight surface, air and blood supplies), and could have served more than one function simultaneously during the time of transition from (primarily) respiration to flight. Our arguments do not require one or more novel structures to arise from nothing where they are not previously found, such as with the paranotal hypothesis (that is, development of new musculature), or to migrate (that is, as with the epicoxal exite).

Pre-adaptation and flight

Darwin (1859) called attention to the dilemma of a satisfactory shift in organ function ('... how could the animal in its transitional state have subsisted?'). Darwin then stated (1859) that 'We should be extremely cautious in con-

cluding that an organ could not have been formed by transitional gradations ...' or '... the same organ performing at the same time wholly distinct functions ...' Cuenot (cited in Mayr 1963, 1982), during the heyday of mutationism in the early part of the twentieth century, coined the term 'pre-adaptation' for the phenomenon of an organ or structure being suited for a new function before that new function arises. Simpson (1949) wrote that '... true pre-adaptation, although probably extremely rare in evolution, provides a mechanism for sudden and erratic changes in adaptive type. The importance of such an event could be great ...' Mayr (1963) stated '... a structure is said to be pre-adapted if it can assume a new function without interference with the original function.' In short, the organ has the innate capacity for the new function, but the organism has to discover that the new function is possible, and then develop it.

Mackerras (1970) commented that '... the insects alone among the arthropods are structurally "pre-adapted", so that the transition from flexing to flapping movements of the planes would also have been a relatively simple one.' Gould (1985) believed that the theory of pre-adaptation has had little following '... not primarily because it is paradoxical and difficult, but because we have so little firm, direct evidence for such functional shifts.' We disagree! There are many of them. Function shifts may happen often but, because we have not been looking for them, and more often have not recognised them, we have not found them. The development of wings from gill pads is an example.

The use of silk by spiders for ballooning is a classic example of pre-adaptation and a subsequent function shift. The original functions of silk were prey trapping, prey wrapping, lair and burrow lining, and egg wrapping (egg sacs). The function shift was to use silk for ballooning as a means of aerial dispersal. Perhaps this is the reason that spiders, the third most successful terrestrial arthropod group (behind the insects and mites), did not develop wings—the silk-balloon method was

just as useful. Spiders have discovered the multiple capabilities of silk, and have derived various functions from a structure and material originally used for other purposes.

The large pectoral fins of the marine 'flying' fish (two-winged *Exocoetus* species and the four-winged *Cypsilurus* species) are also examples of a function shift. The extended pectoral fins support the body in the air while the elongated lower tail fin provide propulsion. Escape from predation is thought to be the reason for the evolution of aerial gliding or 'flying' by marine fish (Norberg 1985).

Aside from flight, insect wings today may function in gas exchange, sound production, epigamic display, pheromone dispersal, protection, holding an air bubble, flight and thermoregulation. These are eight compatible yet independent functions assumed by an organ we believe was originally used for exchange of gases—perhaps the most immediately vital physiological function. Is it not possible that by behavioural and minor physiological and anatomical changes, the gill pads could gather oxygen from the air instead of from water, enabling a shift of those animals to different environments and so new expressions of genotypes?

One problem blocking the search for organs having made a function shift is that the fossil record contains numerous, sequential, intermediate stages of possible wings (that is, intermediate between an incipient bud and a fully functional wing) (Sharov 1966; Kukalová-Peck 1978, 1983, 1985, 1987). We feel that an intermediate-stage 'wing' is still non-functional as a wing. A protowing in a small or intermediate size will not lift the insect off the ground. Even the most drastic structural changes proceed gradually, particularly when populations, including founder populations, enter new habitats (Mayr 1982). There is no reason that lateral buds should expand to functional-wing size, as selective functions favouring them when they were small would act against them when they

became larger and cumbersome while still non-functional as a flight surface. Further, there is no reason for an epicoxal exite migrate up to the pleura to the edge of the notum unless there were selective advantages during the migration.

Thus, it is likely that small protowings will not be found among fossils of apparent intermediate stages of wings. They will be found as functional, full-sized wings. Perhaps one reason protowings have not been recognised is that we cannot distinguish in fossil specimens the difference between these first wings and gills. In short, we have not been able to recognise wings as an evolutionary novelty.

Lateral notal lobes, pleural lobes, or coxal exites?

Many extant cockroaches have a large pronotal shield that tends to protect the head and other anterior parts of the body. Those Carboniferous insects with larger lateral notal lobes on the meso- and metathoraces probably used them for protection of the legs as well as the head and body. These structures would also change the silhouette of the animal to confuse predators. The slightly rearward angling of the lateral lobes would have allowed some 'wedging' movement into tight places or between spaced, vertical barriers such as plants, in order to escape predators. These lobes, if they were stiff and strong, could have prevented predators from swallowing or crushing their owners as easily as those without the lobes. Wootton (1976) expressed doubt as to the function of paranotal lobes. As for exites migrating up the pleura from the coxal area, there are simply no intermediate examples, and gills are already found either at the coxal area or at the notal/pleural junction area.

None of the lateral, notal lobes in either fossil or extant insects is provided with muscles. Notal lobes offer a poor structural base for the evolution of a wing because there are

no preexisting structures necessary to make the transition to flight. Therefore, any theory based on modification of these lobes would require the new formation of extensive accessory support structures necessary for flight (muscles, circulation and airways).

Neural/thermoregulatory theories, and paranotal protrusions

Edwards (1985), and Edwards and Reddy (1986) suggested that insect flight started as a predator-evasion behaviour in a terrestrial environment by introducing neurological evidence involving cerci and one nerve cell that goes from the cerci to the brain, observing that the same set of motor neurons is now involved in legs (walking and running) and wings (flight). This might support Kukalová-Peck's (1987) contention that wings originated from exite appendages on legs, but does support our proposal that musculature and innervation were in position to support the function shift of gills to wings.

Kingsolver and Koehl (1985) attempted to demonstrate experimentally that thermal regulation may have been the first major function of protowings. However, they concluded that, at any body size, there is a relative wing length at which there is no additional thermal effect, and below which there is no significant aerodynamic effect. In short, the thermoregulatory function of an organ drops in effectiveness before its function as a wing comes into play.

Furthermore, Gould (1985) commented that if incipient, ancestral wings had been used in thermoregulation only, natural selection would not have favoured larger wings and the transition to aerodynamic effectiveness. In addition, if the body size of an insect increased, it might acquire aerial effects based simply on that larger size, without any change of body shape or relative wing size. In contrast, Wigglesworth (1963a) suggested that perhaps the smallest of insects were the progenitors of flight.

Wigglesworth (1963b) subsequently sug-

gested that wings had their origin in '... fixed outgrowths of the thorax which were later to evolve into movable wings ...', but did not speculate on where or how the muscles were derived to operate these lobes. Hinton (1963), Johnson (1963) and Leston (1963) also embraced this idea. However, Wigglesworth (1976) eventually returned to the gill theory of Oken (1811).

Hennig (1981) dismissed all but one theory for the origin of insect wings with this statement: 'Only one hypothesis can be seriously considered, that the direct ancestors of the Pterygota must have been using their paranota for gliding, irrespective of how early they actually acquired them.' Apparently, Hennig did not consider a function shift!

The paranotal theory has had many supporters, and still continues to be a favourite. The necessity to have the protowings, especially the paranota, large enough to promote flight has been the crux of many proposals. That is, a protowing cannot become a functional wing unless it has attained a certain minimum size relative to body size. Also, in the world of predator versus prey, a species or group of species cannot waste a lot of individuals experimenting with bigger and bigger protowings that have no selective value, and which may have possible detrimental consequences.

During the Carboniferous Period, terrestrial predators of insects would have been other invertebrates, amphibians and perhaps reptiles. Aquatic predators would have been invertebrates, fish and amphibians. Birds and bats, which are highly effective terrestrial and aerial predators, were not yet on the scene. The absence of swift, effective terrestrial and aerial predators allowed initial flying abilities of insects to be simple—just good enough to escape terrestrial predators, arrive at new habitats, and access food and mates. Therefore, the protowings must have been of a reasonable size for gliding and fluttering at the time they assumed the function of wings. Moreover, and more importantly, the protowings must have had muscle power with the associated respiratory and circulatory sup-

port at all stages of development.

Wootton (1988) mentioned the appearance of several theories that postulate, on the basis of fossil and recent forms, an aquatic or amphibiotic stage in the ancestry of all insects, or at least the Pterygota. Wootton (1988) suggested that these theories have profound implications on the evolving roles of insects in fresh water. We concur.

Proposal: origin of insect wings and flight by function shift

We propose here several possible mechanisms for the development of insect flight and the identification of the organ from which wings arose. We invoke the Principle of Simplicity (Occam's Razor), as we believe it was an uncomplicated change from pre-wing to protowing to functional wing. We postulate the acquisition of a new function by an existing organ which previously had one or more other functions (that is, a function shift). The idea that gill pads, similar to those of mayflies, were the source of insect wings is not new. It was expanded upon and covered in detail by Wigglesworth (1976). However, our proposal of a function shift is new, and hopefully, will be a basis for future discussion.

We presume that at least some flying insects evolved directly from aquatic insects, and gill pads of the meso- and metathorax assumed a new function while still providing other vital services to the animal. If precursors to wings were the meso- and metathoracic gill pads, then we suggest that it is not necessary to explain the location, musculature or innervation of wings, for they are in the same location on insects today that use direct flight muscles. We suggest that gill pads did not develop on the prothorax because the insect needed 'working room' at the anterior end of the body (feeding and vision, for example). Also, streamlining a body's shape in the thick aquatic environment would tend to shift the gill pads posteriorly. Extreme posterior development would

have been less streamlined for movement in water and more available to predator action (note that the posterior end of most animals—insects, fish, reptiles, birds—is smaller than the thoracic area).

The reason that primitive wing venation was somewhat uniform (veins of about the same thickness and of rather uniformly branched distribution throughout) is that they had just been gill pads, and had been used for gas exchange. Of course, it is also possible that, for many fossils, what we have been assuming to be wings were still gills. Extensive venation in these gill pads could have come from several sources:

- 1) insects lived in shallow, warm, still water (with low oxygen tension), that usually was in danger of drying up and so developed more gill surface area,
- 2) insects needed to wave their gill pads in warm water to increase flow and expose their surfaces to more oxygen by preventing gradient loss immediately surrounding the gill (hence the origin of a musculature to do the waving, as in some mayfly nymphs today),
- 3) musculature for walking required more oxygen than other musculature, thus the proximity of bigger gills to the legs.

The gill pads in primitive insects were probably held above the body in much the same manner that adult mayflies and damselflies (insects that have direct flight muscles) hold their wings today. As the tergites of mayflies and dragonflies are not strongly developed (as compared to those on dipterans, hymenopterans and lepidopterans—insects that have indirect flight muscles) we suggest that the origin of the gill pads was from the dorsal edges of the pleurites. With the pleurites as the origin of the gill pads, the protowings would tend to develop vertically rather than laterally. There are several advantages in having the gill pads held above the body (as vertical extensions of the pleurites): a) as aquatic plants tend to grow upward, such pads would not get in the way when the insect crawled along on the bottom of the pond or lake, and,

b) there is slightly more oxygen just above the bottom of the pond than there is on the bottom of the pond.

Carrying these enlarged thoracic gill pads vertically above the thorax would be natural and beneficial, for there would be small amounts of gases in the wing veins making them light and slightly buoyant. Also, holding the gill pads upright would permit the tips to stick out and above the water's surface as the insects crawled about in shallow water. This exposure to the air would have induced an oxygen 'flush', and permitted the insects to live and feed in a habitat low in, or even lacking, oxygen. Selection would have favoured larger, or at least longer, gill pads, as their owners could get more oxygen and feed in slightly deeper water. Furthermore, insects that crawled out of the water in response to low oxygen tension or to escape a predator also experienced an instant oxygen 'flush', as the air contained 10% oxygen or more (whereas the dissolved oxygen in the water may have been only 0.1% or less). The flush would last as long as the gill pads stayed moist, and repeatedly returning to the water to moisten the gill pads would enable the insect to exploit two environments, one where the oxygen was in plentiful supply, and the other where it was not. Water beetles and many other extant aquatic insects live and feed in the aquatic environment, but return to the air for oxygen. Oxygen levels in the atmosphere have not always been at the present level of about 20%. Until 475 million years ago (mya), atmospheric oxygen was only 3–10% or less of that presently found (Cloud & Gibor 1970). From 475 mya until 75 mya, oxygen was increasing at a fluctuating rate; the present levels have existed for about 75 million years (Cloud & Gibor 1970). Lower levels of oxygen in the atmosphere would mean correspondingly lower levels of oxygen in water. Thus, the demand for oxygen and stress to aquatic organisms caused by a lack of this vital gas would have been greater when proto-insects were developing gills, and would have been a selective pressure for larger exchange surfaces. There is always the

possibility that when oxygen levels were very low, organisms used more anaerobic and less aerobic respiration, or had large internal sacs for storing several hours worth of oxygen, but there is no evidence of this. Thus, there were three events leading to the development of 'wings':

- 1) muscled gill pads developed a vertical orientation because of habitat physiognomy and oxygen distribution in the water,
- 2) in oxygen-poor slow-moving water, gills became larger, longer, and movable in order to enhance gas exchange, and
- 3) these elongated gills began to protrude out of the water into the air, providing their owners with a new rich source of oxygen, and another habitat where they could exist (as long as the gill surfaces were moist).

The next step would have been to use these former gill pads for gliding or fluttering to another part of the pond, probably initiating flight from emergent vegetation, or plants growing along the shoreline. Partially dried gill pads would have been light and could still have functioned as gills, as in this sort of habitat, most gliding or fluttering insects would have landed in water or on wet shores. Furthermore, atmospheric humidity levels would have been high in these habitats, extending the time that the gills/wings stayed moist and were able to exchange gases. The insects could thus find refuge from low oxygen levels and predation while utilising new food sources.

The transition would have been completed when the gill pads/wings were used to get from one pond to another, and from there to other habitats. At that point, even if some gill function remained, the gill pads would have been fully functional wings. It is our contention that wings evolved relatively quickly (geologically speaking) from existing structures that had previous functions, the main one of which was gas exchange (respiration). The protowings combined this original function with flying (an escape mechanism from predators) for a short time. Eventually, the flying function became dominant and was

subject to directed, selective pressures, and the respiration function was acquired by a system of tracheae and spiracles. These actions may have coincided with the increase in oxygen levels in the primeval atmosphere. Because these larger gill pads would have developed in warm, still or slow-moving water, the loss of a streamlined form would not have impaired movement to the same degree as in fast moving water. Aquatic winged insects having hemimetabolous metamorphosis, for example, Ephemeroptera (mayflies), Plecoptera (stoneflies) provide good examples today of ontogenetic events that illustrate how wings could have evolved from gill pads. They are similar even to the point where the penultimate instar leaves the water, then moults to become aerial.

Again, as suggested above, it might not be possible to distinguish between a wing and a gill in fossil specimens during and after this period. We may have been looking for 'distinct gills' and 'distinct wings', and not for an organ that would resemble and function as both during the transition time. It is possible that amphibians and fish were the primary forces pressuring insects into the development of flight. These vertebrate predators would have been feeding in shallow waters and shoreline areas where they would have put selective pressure on insects to assume flight quickly once flight was possible. Any slow, injured, or disadvantaged insects would have been caught, eaten, and removed from the gene pool.

We may now address Wootton's (1986) questions mentioned earlier:

1. from what were the protowings derived? The meso- and metathoracic gills and the associated support structures and systems (for example, muscles, airways and circulation),
2. what initial functions did the protowings serve? The main function was (probably) gas exchange, but there may have been other functions, such as drifting in water currents, epigamic display, etc.,
3. were they immobile, or articulated and

actively movable? They were muscled and movable.

The last point to consider in the transition from being an aquatic insect to a terrestrial one is the loss of the abdominal and other gills as respiratory organs, and the concurrent development of spiracles. Several authors (for example, Chapman 1969, CSIRO 1970, Keilin 1944, Ross et al. 1982, Whitten 1972) have dealt in detail with the morphology of tracheal systems but not, apparently, with the origin of the spiracles.

Tracheae in insects, and veins in the gills on the outside of insects, are parts of an interconnected air tube system. The junction between the two systems is at the body wall. When an aquatic nymph sheds its skin to become an adult, the gills are shed. Spiracles are left at the sites where the gills were attached. Thus, spiracles, or a port in the body wall connected to the tracheae, would have arisen when the gill pads assumed full-time wing function. This means that the air would enter directly into the tracheae instead of indirectly through a gill. As the direct system offers a more efficient exchange of oxygen and carbon dioxide, there would have been quick selection for it.

In summary, all of the prerequisites for the evolution and development of direct flight (innervation, muscles correctly located, attachment of gills at the notal/pleural junction, position of airways and circulation) as found on the nymphs of some aquatic insects, provide the most parsimonious examples for the explanation of the origins of insect flight.

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