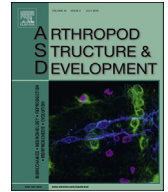




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A century and a half of research on the evolution of insect flight

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ABSTRACT

The gill and paranotal lobe theories of insect wing evolution were both proposed in the 1870s. For most of the 20th century, the paranotal lobe theory was more widely accepted, probably due to the fundamentally terrestrial tracheal respiratory system; in the 1970s, some researchers advocated for an elaborated gill (“pleural appendage”) theory. Lacking transition fossils, neither theory could be definitively rejected.

Winged insects are abundant in the fossil record from the mid-Carboniferous, but insect fossils are vanishingly rare earlier, and all earlier fossils are from primitively wingless insects. The enigmatic, isolated mandibles of *Rhyniognatha* (early Devonian) hint that pterygotes may have been present much earlier, but the question remains open.

In the late 20th century, researchers used models to study the interaction of body and protowing size on solar warming and gliding abilities, and stability and glide effectiveness of many tiny adjustable winglets versus a single, large pair of immobile winglets. Living stoneflies inspired the surface-skimming theory, which provides a mechanism to bridge between aquatic gills and flapping wings. The serendipitously discovered phenomenon of directed aerial descent suggests a likely route to the early origin of insect flight. It provides a biomechanically feasible sequence from guided falls to fully-powered flight.

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1. Earliest theories

Well before Darwin and Wallace proposed the concept of evolution by natural selection, natural historians were attempting to explain the source or origin of insect wings. As reviewed in detail by Crampton (1916), authors throughout the early 1800s suggested that wings were modified from such structures as legs or gills. Not surprisingly, these suggestions were largely proposed on a background of Special Creation. Although at least some were based on sound anatomical work, they were not described in a way we would recognize as fitting a modern, evolutionary framework.

The first scientific description of the origin of insect wings in a modern evolutionary context apparently was published just less than 150 years ago. In his 1870 animal anatomy book, Carl Gegenbaur proposed that insect wings evolved from tracheal gills similar to those present on modern-day aquatic insect larvae (Gegenbaur, 1870). Indeed, Gegenbaur devotes a full page to describing an evolutionary scenario: “The wings must be regarded as homologous with the lamellar tracheal gills ... It is quite clear

that we must suppose that the wings did not arise as such, but were developed from other organs which had another function, such as tracheal gills; ... Every increase of surface area increases the respiratory value of the organ, and so leads toward its future function. ...” (from the English translation: Gegenbaur, 1878, p. 247). This description of an evolutionary change in function, and a possible mechanism to drive such a change, appears remarkably modern, particularly given that the first edition of Darwin's *On the Origin of Species* (Darwin, 1860) was less than a decade old when Gegenbaur was writing. Interestingly, Gegenbaur's hypothesis may have been at least partly inspired by suggestions from many decades earlier that insect wings shared various characteristics with tracheal gills (Oken, 1809–1811).

Soon after Gegenbaur's book was published, Fritz Müller published a series of papers on termites (e.g., Müller, 1873a, b). Müller observed lateral tergal lobes on the thorax of certain termite nymphs. He concluded that these lobes were incipient wings (in the context of the recapitulation theory, widely accepted at the time) and since the lobes did not contain obvious tracheae, he rejected Gegenbaur's contention that wings arose from tracheal gills (Müller, 1875). Whereas Gegenbaur outlined a possible pathway for the evolution of wings, Müller rejected tracheal gills as a source for wings but did not immediately

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propose an alternative evolutionary pathway. (In a footnote, Müller said he planned to publish a more detailed comparison of his views versus Gegenbaur's, but apparently he never did, possibly because other authors made his case for him.) Thus, before 1880, a theory based on tracheal gills and a theory based on lateral tergal lobes were already in print, and variations on these theories would remain the two major insect-wing-origin theories into the 21st century.

At about the time Gegenbaur and Müller were proposing that insect wings arose from tracheal gills or tergal lobes, researchers proposed a number of other possible origins for insect wings. Plateau (1871), for example, suggested that wings arose from hypertrophied spiracles. Jaworowski (1896) built on earlier suggestions that wings arose from legs by suggesting that wings and legs had a common origin, both being variations on dermal outgrowths that he believed were originally respiratory, and that gave rise to all arthropod appendages. None of these theories seemed to gain as much acceptance as those of Gegenbaur and Müller; by 1900, most entomologists seem to have settled on either the gill theory or the tergal lobe theory (Crampton, 1916).

The original form of Gegenbaur's "gill theory" of wing evolution involved gills enlarging for improved gas exchange, then a partial transition to terrestrial life, in which gills might have aided gliding, or steering during leaps, and then with improvements in musculature and articulations, they became wings that could flap for powered flight. Woodworth, in his monograph on insect wing veins (Woodworth, 1906), devotes several pages to greatly elaborating and refining the gill theory. He points out that true tracheal gills – used primarily for gas exchange – would not make effective wing precursors, and some other intermediate stage would have been needed. He suggested that the stiffened covers that form part of (or replace) some gills in immature mayflies would have formed a better source for the evolution of wings. He also points out that the gill theory has the advantage of starting out with an appendage that already possesses a moveable articulation. Such an appendage would thus have no need to evolve an articulation and associated musculature from scratch.

Early in the 20th century, Crampton (1916) reviewed the previous studies addressing insect wing origins. He seems to have coined the term "paranotal lobes" for Müller's tergal expansions, and the theory has been known as the "paranotal lobe theory" ever since. Crampton produced a detailed list of the evidence in favor of both the gill theory and the paranotal lobe theory, as well as listing many authors who had argued in favor of the former (e.g., Lubbock, 1873; Graber, 1877; Lang, 1888; Simroth, 1891; Pratt, 1897; Osborn, 1905) or the latter (e.g., Huxley, 1877; Pancritius, 1884; Korschelt and Heider, 1891; Packard, 1898; Powell, 1904). Although Crampton called the gill theory a "fascinatingly clever one," and said "the logic of its appeal is almost irresistible," (Crampton, 1916), he concluded that the weight of evidence – e.g., wings not being serially homologous with abdominal tracheal gills, and strong evidence for aerial respiration being primitive in insects (even aquatic ones) – was against the gill theory. He also described evidence favoring the paranotal theory – widespread occurrence of leaping ability and of paranota on the prothorax of extant insects – so he argued that the paranotal theory was a better fit to the available evidence. He also pointed out that evolving a new articulation for the wings should not be seen as a major stumbling block, given that tracheal gills would have also had to evolve a new articulation at some point (Crampton even describes the oribatid mites, often touted as examples of arthropods that have evolved a novel articulation for structures very much like paranotal lobes, which have been mentioned in connection with the paranotal lobe theory in books as recently as those by Dudley (2000) and Alexander (2015).)

2. Mid-20th century

For the next five decades or more, the paranotal lobe theory seems to have been generally accepted (Snodgrass, 1931, 1935; Forbes, 1943; Wigglesworth, 1963; Flower, 1964). This acceptance may have been due as much to the general recognition that the insect respiratory system is of fundamentally terrestrial origin, as to Crampton's arguments. In one of the very few papers supporting an aquatic origin for insect flight during this period, Grant (1945) proposed a somewhat naïve model that actually has more in common with the "cursorial" theory for the evolution of flight in birds than with the Gegenbaur-Woodworth tracheal-gill theory.

In the second half of the 20th century, some prominent scientists began arguing in support of a variation on the gill, or more generally, pleural appendage theory. Wigglesworth, who had earlier published a model of insect flight evolution that more or less took the paranotal lobe theory for granted (Wigglesworth, 1963), seems to have changed his mind and become a supporter of the pleural-appendage theory (Wigglesworth, 1973, 1976). He described mayfly larvae that use some of their modified gills for both covers and ventilation, or even as swimming paddles. He suggested that both abdominal gills and wings were modified coxal exites, and proposed that thoracic gill covers might have evolved into paddles. Such paddles then might have been used aerodynamically by semi-aquatic insects stranded by drying ponds and rivers, and blown into the air by winds and updrafts. In this way, those insects which managed to control their flightpath and return to water would have had an advantage, selecting for better aerial control, and eventually flapping.

In an extensive series of papers, Kukulová-Peck (1978, 1983, 1985, 1987, 1997, 2008) used her interpretations of various fossils to theorize on the origin of wings. She developed a scheme to homologize all appendages of all arthropods, which included unrecognized leg segments, including two basal to the coxa that are either lost or fused with the body wall in extant insects. She described both wings and abdominal gills as exites of one of these hypothetical basal leg segments and explicitly stated that they are serially homologous structures (Kukulová-Peck, 2008). She focused much more on pattern than on process, and generally accepted elements of theories describing how thoracic gill covers could evolve into flapping wings proposed by earlier authors (Kukulová-Peck, 1978). Curiously, the arguments of both Wigglesworth and Kukulová-Peck are somewhat reminiscent of the theory of Jaworowski (1896), in that all three authors view legs, wings and gills as all being derived from a common source.

In spite of the arguments of Wigglesworth and Kukulová-Peck, the paranotal lobe theory seems to have been more widely accepted throughout the second half of the 20th century. Most authors seemed to either take the paranotal lobe theory for granted (Wootton, 1976; Bitsch, 1994) or to actively argue in favor of it (Rasnitsyn, 1981; Quartau, 1986; Dudley, 2000).

3. Fossils

Unfortunately, the fossil record has so far offered little help in understanding how insect flight arose. (Although Kukulová-Peck based her arguments heavily on fossils, later workers saw much less detail in the same fossils, e.g. [Rasnitsyn and Novokshonov, 1997; Deuve, 2001; Boxshall, 2004; Béthoux and Briggs, 2008], and few other authors have placed such emphasis on fossil evidence as a basis for theories of wing origins.) Indeed, the lack of any transition fossils between the earliest primitively flightless hexapods and later, fully-volant fossil species has often led paleoentomologists to lament the lack of an "Archaeopteryx" for insects (e.g., Grimaldi and Engel, 2005).

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