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Evolution of flight in insects

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Abstract

Insects were the initial organisms to develop the ability to fly using their own power, more than 400 million years ago. The development of flying in insects has been a crucial advancement that has enabled them to expand into the most diverse collection of organisms on the planet, inhabiting almost every land and freshwater environment. This review article consolidates current understanding of the evolutionary process of insect flight, encompassing subjects such as the fossil record, functional morphology, developmental genetics, and ecological influences that have contributed to the variety of flying insects. We emphasise recent breakthroughs and identify areas requiring additional investigation to achieve a more comprehensive comprehension of this intriguing evolutionary process.

Keywords: Terga, pterygota, halters, neoptera, palaeoptera, hox genes

Introduction

The emergence of flying in insects is a highly consequential occurrence in the chronicles of life on our planet. The presence of flying insects may be traced back to the late Devonian period, approximately 400 million years ago [1]. Since that time, they have spread out and diversified into more than 1 million existing species, making up more than half of all known animal species [2]. Insects have been able to spread over large areas, take advantage of novel ecological environments, and develop intricate behaviours such as migration, courtship, and social interactions due to their capacity to fly [3]. Although flying insects have significant ecological relevance and have been successful in terms of evolution, there are still many aspects of the evolution of insect flight that are not well understood. This article presents a comprehensive analysis of the current understanding of the evolution of insect flight, using information from paleontological, morphological, developmental, and ecological viewpoints. We emphasise significant breakthroughs and adjustments that have influenced the variety of airborne insects, along with domains that want additional investigation.

The most ancient flying insects discovered so far date back to the late Devonian period, some 400 million years ago [4]. These include wingless insects that are primitive, such as *Rhyniognatha*, as well as winged forms like *Delitzschala, Archaeoptera,* and *Engisoptera* [5, 6, 7]. Nevertheless, the available evidence of ancient flying insects is incomplete, and our comprehension of the specific order and timing of evolutionary occurrences that led to the development of wings and active flight is still lacking. An essential inquiry pertains to the origin of the wings of primitive flying insects. There are two primary hypothesis on the evolution of insect wings. One suggests that insect wings originated from movable gill plates of aquatic ancestors, while the other proposes that they evolved from extensions of the thoracic terga of terrestrial ancestors [8]. Developmental genetic evidence supports the gill plate hypothesis, as it reveals similarities in the genetic patterning of crustacean gills and insect wings [9]. The tergal hypothesis is substantiated by comparative morphological and fossil evidence, which indicates that wings initially developed as rigid tergal extensions and then evolved into flexible and movable structures [10, 11].

Results and Discussion

Another significant occurrence throughout the first development of insect flying was the emergence of the capability to retract the wings over the abdomen when they are not being utilised. These adaptations enhanced the aerodynamic efficiency and manoeuvrability of insects, enabling them to navigate through narrow places and effectively avoid predators [12]. Wing folding techniques that include flexion lines and patches rich in resilin are observed in the fossil record from the Carboniferous period [13, 14, 15]. During a later stage of evolution, the Pterygota, which refers to winged insects, split into two main branches. The first branch is called Palaeoptera, which includes dragonflies, damselflies, and mayflies. These insects are unable to fold their wings over their abdomen. The second branch is called Neoptera, which consists of insects with more advanced wing folding ability [16]. The Neoptera saw a significant proliferation during the Permian and Triassic epochs, resulting in the emergence of most of the existing orders of winged insects [17]. Additional advancements in insect anatomy include the development of elytra, which are hardened forewings found in beetles, the presence of halteres, which are modified hindwings used for flight stabilisation in flies, and the existence of hooklike hamuli that connect the fore- and hindwings in bees and wasps [18, 19, 20].

The development of flying in insects required a set of structural and functional changes. These encompass not just the wings, but also specific flight muscles, sensory-motor control systems, and respiratory and circulatory organs that provide the necessary energy for flight [21]. The structure of insect wings consists of a delicate cuticular membrane that is reinforced by a complex network of veins. The veins consist of trachea, nerves, and hemolymph, which serve to supply oxygen, provide sensory feedback, and maintain hydrostatic pressure [22]. The configuration of veins exhibits a standardised pattern that differs throughout insect orders and families, and is frequently employed for taxonomic classification [23]. Insects have developed diverse wing forms and sizes that are specifically suited for various types of flying and ecological functions. Long, narrow wings are linked to swift flight and hunting in the air, whereas broad wings with larger hindwing surfaces are linked to slow, agile flying and the capacity to carry substantial weights [24, 25]. Insects have the ability to actively control the form and surface area of their wings while flying by employing muscles that are connected to the base of the wing [26].

The propulsion of insect flight is facilitated by the presence of robust flying muscles located in the thorax, which generate the vertical oscillation of the wings. Typically, in the majority of insects, these muscles are not directly connected to the wings. Instead, they induce changes in the thorax which then result in wing motions [27]. There are two primary categories of flight muscles: synchronous muscles, where each nerve impulse causes a single contraction, and asynchronous muscles, where contractions are initiated by stretching rather than neural input [28]. Asynchronous muscles, which are present in more advanced insect orders, allow for quicker wingbeat rates. Insect flight control relies on the integration of optical, mechanical, and olfactory inputs [29]. Compound eyes provide visual feedback that is utilised for the purpose of maintaining stability and navigating through intricate surroundings [30, 31]. The detection of rotating accelerations is achieved through the utilisation of mechanical feedback from sensory organs located at the wing bases and gyroscopic halteres [32]. Certain airborne insects, like moths, also rely on olfactory signals to find sources of food and potential partners [33]. Insect flight relies on respiratory and circulatory modifications to meet its energetic requirements. Insects that fly have larger tracheal systems with air sacs that act as bellows to provide ventilation for their flight muscles [34]. In addition, they possess robust circulatory organs, such as the dorsal vessel or "heart," which propels hemolymph throughout the body cavity [35].

Developmental genetics refers to the study of how genes affect the growth and arrangement of insect wings. This process is governed by a consistent genetic regulatory network that includes Hox genes, signalling molecules, and transcription factors [36]. Comparative studies have demonstrated that this network is mostly preserved among winged insect orders, while there are some alterations that correspond to differences in wing form [37, 38]. An important milestone in the development of wings is the formation of the wing imaginal disc in the embryo. This is a group of cells that demonstrates the expression of the wing-patterning genes vestigial, nubbin, and apterous [39]. As the disc expands and undergoes specialisation, it takes on the shape of a flattened sac with distinct top and bottom surfaces, which will eventually develop into the upper and lower surfaces of the mature wing [40]. The arrangement of veins is regulated by the specific expression of signalling molecules such as Decapentaplegic and Hedgehog [41]. Comparative studies have demonstrated that the development of wings can be intentionally disturbed or altered by manipulating the expression of genes responsible for wing patterns. Overexpression of the vestigial gene in the beetle *Tribolium* causes the elytra to change into structures that resemble wings [42]. This implies that the alteration of wing structure over evolution may be linked to modifications in the control of established developmental processes.

Another crucial inquiry is to the origin of the wing imaginal disc. One theory posits that it originated from a group of cells that exhibited similar gene expression patterns as those involved in shaping the leg of an insect. This is corroborated by the fact that certain genes implicated in the formation of wings, such as nubbin and apterous, are also implicated in the formation of legs. Nevertheless, the specific mechanisms by which a gene network responsible for leg patterning could have been utilised to develop a wing are still not fully understood. The emergence of flight in insects has had significant ecological impacts, enabling them to spread across larger areas, inhabit new environments, and develop unique life histories and behaviours. In terrestrial ecosystems, flying insects fulfil crucial functions as pollinators, herbivores, predators, and decomposers. A notable trend in the variety of flying insects is the abundance of species in a few number of dominant orders, specifically Coleoptera (beetles), Diptera (flies), Hymenoptera (bees, wasps, and ants), and Lepidoptera (butterflies and moths). Collectively, these four classifications represent more than 80% of all documented insect species. The observed distribution may be a result of variations in the rates of diversification, ecological opportunities, and important advancements within different lineages [43].

Beetles are the most varied group of insects, with more than 400,000 documented species. Their success can be linked to the development of durable elytra that safeguard the hindwings and enable beetles to take advantage of various habitats, such as beneath bark, in soil, and in freshwater. The development of full metamorphosis and the presence of a larval stage may have facilitated diversification by separating the ecological needs of larvae and adults. Another instance is observed in the eusocial Hymenoptera, such as ants, bees, and wasps, which have developed intricate communities characterised by division of labour and cooperative care of their offspring. The emergence of eusociality has been associated with the emergence of behaviours such as pollen-feeding and nest-building. These behaviours may have been made possible by the ability to transport pollen and building materials while flying. Several airborne insects have developed distinct behaviours and life cycles associated with dispersal and migration. For instance, certain species of butterflies and moths engage in long-distance seasonal migrations in order to take advantage of ephemeral food supplies and evade unfavourable conditions [44]. These migrations frequently need advanced navigational skills, such as the use of solar compasses, detection of polarised light, and magnetic senses. The abundance of airborne arthropods has also been influenced by reciprocal evolutionary relationships with vegetation, predators, and parasites. The diversity of pollinating insects, such as bees, butterflies, and moths, is believed to have been influenced by the emergence of flowering plants during the Cretaceous period. Numerous plants have developed distinct flower structures and incentives to attract particular pollinators, whereas insects have developed sensory and behavioural adjustments to detect and harvest nectar and pollen. Conversely, the development of flight has also subjected insects to novel selective forces from airborne predators like birds and bats. As a result, antipredator defences including as camouflage, mimicry, and aposematic coloration have developed. Certain insects, like tiger moths, have developed the capability to disrupt bat echolocation by emitting ultrasonic clicks through their thoracic tymbals [45].

Conclusion

the development of flying in insects has been a crucial advancement that has influenced the variety and ecological achievements of this group. The fossil record, comparative morphology, and developmental genetics offer an increasing understanding of the sequence of anatomical and physiological changes that led to the emergence of wings and the ability to fly. Nevertheless, numerous inquiries persist regarding the precise selected forces and ecological circumstances that propelled these alterations. The proliferation of aerial arthropods has been influenced by an intricate interplay of evolutionary advancements, ecological prospects, and co-evolutionary engagements with other creatures. To comprehend these elements, one must combine knowledge from palaeontology, phylogenetics, functional morphology, developmental biology, and ecology. In the near future, we are well-positioned to make significant advancements in our understanding of the evolution of insect flying, because to the continuous improvements in imaging technology, genome sequencing, and computer modelling. This finding has significant implications not only for comprehending the history of life on Earth, but also for sectors such as biomimetic engineering, agriculture, and conservation biology. In light of the problems posed by climate change and habitat loss, gaining a comprehensive understanding of the evolutionary adaptations of insects in conquering the airborne domain can aid us in predicting and minimising the impact on global biodiversity and the functioning of ecosystems.

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