

THE ORIGIN AND EVOLUTION OF INSECT WINGS

**A summarized interpretation of the morphological evidence
with explanatory figures showing the homologized system
for the naming of wing veins and axillary sclerites across insect orders
and their key characters for the insectan phylogenetic tree**

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Introduction

This is my personal account and summary of research, discovery and interpretation (to date) of my studies of insect wings: their morphology, evolutionary history and phylogenetic implications in many fossil and modern specimens. My work on the origin of insect wings started around 1954 and has continued to the present (2022). This summary is meant to facilitate and inspire further research. It is not intended to provide a full account of existing knowledge and literature, or to be a regular publication. Instead, it is provided as a helpful contribution for future morphological, phylogenetic and other research projects that require the use of fully interpreted and completely homologized arthropod legs and leg-derived appendages (including mainly insect wings, but also their mouthparts, antennae, abdominal leglets, genitalia, eversible

vesicles, and cerci). A system of nomenclature for the venation and articulation is offered as fully homologized across all pterygote orders (winged insects), and the wing organ is shown to also have serially homologous equivalents on hexapod heads and abdomens. All wing features are derived from a single ancestral Protowing model (*sensu* Hennig, 1981), and their homologues are identified and color-coded in illustrations of over a thousand wing specimens of mostly extant Pterygota. This makes available the wing organ for the broadest possible overview and verification of its phylogenetic key characters and evaluation of pterygote higher taxa. After all, wings are the prime source of pterygote diversification.

On a recommendation from the distinguished Czech-Swiss beetle systematist Dr. Ivan Löbl, and Dr. Nadir Alvarez, the Muséum d'Histoire Naturelle de Genève, Switzerland kindly agreed to make available, through the Internet, this compilation of text and figures of extant and some fossil pterygote wings and wing sclerites, all following Hennig (1981) in being derived from a single *protowing groundplan*, fully homologized in all insect orders, *and with their wing key characters (documenting relationships between the pterygote higher clades above the order-level) identified, documented and analyzed*. The hope is that use of this set of properly identified key wing characters will facilitate, inspire and promote various future phylogenetic projects, whose *results will be realistic and correct only if they are based upon Hennigian monophyletic evolutionary principles*.

The present contribution provides the first homologization of all articular sclerites in all pterygote orders, plus the complete homologization of veinal systems in all pterygote higher clades, from orders upwards. Relationships between the pterygote higher clades above the order-level are proposed and documented. Relationships between orders themselves remain only partly documented. Important parts of the text are in bold and italic fonts according to the wishes of some fellow entomologists, to provide emphasis. Evolution of the insect higher taxa has been based on very broad and tangled evidence, which has been studied for decades. Errors were unavoidable. My own past publications contain mistakes, which were later recognized and not repeated. The gentle reader is asked to consider valid in my own work *only my interpretations offered here and in my 2008 publication*.

I have pursued a reconstruction of the long needed but never satisfactorily documented Hennigian type phylogenetic tree of pterygotes for 60 years, but this goal remains only partially fulfilled. The reason, likely to be muttered by practically all entomologists while passing their 92nd birthday and still at work, is a classical entomological lament: “So many species, so little time”...

Historical background and operational philosophy

Background and application of the comparative morphology method

As discussed below, the **insect higher taxa** bear only **several very stable wing key characters**, which have Early Paleozoic origins and are present in both fossil and modern higher taxa. As a paleontologist, I was mainly interested in the early evolution of Pterygota and their wings, which reflect

their evolutionary diversification. I suspect that winged insects (pterygotes) originated and diversified into their major lineages probably sometime during the Early Ordovician (500-440 Ma (million) years ago with early land plants), Silurian (440-410 Ma, with first vascular plants) and the Devonian (410-360 Ma, with the first trees), which has delivered the first fossil wingless insects. I suspect that in the Devonian the Pterygota probably already reached full aerial flight in all clades above the orders. There is an absence of insect fossils in the “hexapod gap” of the Early Carboniferous, but by the middle Carboniferous, in the Namurian of Eurasia, pterygote insects had already perfectly evolved aerial flapping wings belonging to superorders, which have persisted to the present.

Late Paleozoic fossil pterygotes represent most of the now existing higher taxa above the level of orders. Hence, the Early Paleozoic phylogenetic tree before the appearance of the Carboniferous-to-Present higher clades (lineages and most superorders) is ***not documented by fossils and must be reconstructed.*** The working method used in invertebrate and vertebrate paleontology is that of ***comparative morphology, which carefully avoids dangerous speculation. Since insect wings are placed between the tergum and the leg, and are mobilized by the leg muscles, the reconstruction of the missing evolutionary data is done by inspecting, in all Hexapoda, the lateral margins of their terga and the leg segments at the top of their legs.*** However, the *arthropod leg had not yet been hypothesized as a Hennigian single groundplan model.* Hence, that part of the work had to be done first. The next step was studying the ***plesiomorphic states of all leg-derived appendages,*** scattered throughout all orders of fossil and modern Pterygota and other Hexapoda (see the many introductory figures with their explanatory text). The goal was to identify the Protowing leg model (groundplan) from which the wing blade and sclerites evolved, find changes in veins and articular sclerites which characterize all of the higher taxa, and to use these key characters and their relationships to build up the pterygote phylogenetic tree according to Hennigian phylogenetic procedures. ***Very importantly, the key characters of the highest taxa are immensely old, comparatively few, very little changed between the Carboniferous and Recent, and present in all members of each pterygote higher clade.***

The never changing constraints in the higher-level key characters represent an enormous difference from the abundant, variable and sometimes absent morphological characters in lower taxa. In higher taxa, the character variability is low and the wing differences between the Carboniferous and modern pterygote lineages are mainly in the copious amounts of reductions and loss (even realized by Darwin according to Hennig (1981)). Searching for the old key characters of the higher taxa by the ***same entomological methods used in lower taxa*** can bring completely ***unrealistic results.*** Such frequent errors are easily avoidable by understanding the differences. I was repeatedly criticized for not using modern entomology methods (dealing with variability), which I found completely useless. Hopefully, this contribution provides convincing evidence that ***none of the methods*** working for insect lower taxa is ***appropriate for research on insect higher taxa*** (JKP, 2008).

Why the solution of the insect wing problem must start with the groundplan of the leg and leg-derived appendages

Insecta, the largest clade of Hexapoda (six legged arthropods), are arguably the most diversified and most numerous terrestrial animals. A fundamental basal premise of my following analysis is that early Arthropoda had a segmented body, with each segment bearing a pair of leg appendages, which were *serially repeating, and homonomously* (similarly constructed) *and homologously segmented*. I suspect that work on genetic “homeoboxes”, HOX genes supports this, but I do not know of such specific research. Hexapoda evolved from within the Crustacea, from an early ancestor probably similar to the extant saltwater crustacean class Remipedia (Koenemann et al. 2006), and this is phylogenetically recognized as the sister group of Hexapoda-Insecta (Schwentner et al. 2017). The Early Devonian marine “panhexapod” fossils *Devonohexapodus*, *Wingertshellicus* and *Cambronotus* are seemingly morphological links between Remiped crustaceans and terrestrial hexapods (Haas et al. 2003). As is generally accepted (and documented here) **insect hexapods** later spectacularly *prospered and diversified into their entire phylogenetic tree with the development and diversification of their wings*. I contend that this makes insect wings the most important terrestrial animal locomotory organ. Nevertheless, in spite of their eminent importance, the origin of the wing itself has been an enduring mystery. Diverse explanations have been presented for almost 200 years and were based almost completely on “informed speculations” rather than concrete evidence. These origin hypotheses can be placed into three groups, which proposed either 1) a *fully tergal*, or 2) a *combined tergal and appendageal*, or 3) a *solely leg-derived wing origin*. To date, no documentation of any hypothesis has been found to be convincing enough to be generally accepted.

Here, it is proposed that the insect wing is derived solely from the first leg segment: the epicoxa and its exite. This was studied by using the method of *comparative morphology* applied to many examples and specimens of Arthropoda: Crustacea and Hexapoda, both living and fossil. Illustrations to help elucidate and document the following explanatory discussions are in the six introductory sets of attached figures.

The present contribution documents with hard evidence the *Leg/Wing hypothesis* (JKP 1983), that insect wings originated from the *previously unrecognized first segment of the arthropod groundplan leg, called the epicoxa and its mobilized appendage, the epicoxal exite*. The wing articulation originated from a flattening of the epicoxa and the adjacent exite base, both of which fragmented into the wing sclerites around the inserted leg muscles. The wing blade formed from the flattened membranous part of the exite, supported by eight sclerotized, branched hemolymph veins. Arthropod legs are here documented by plesiomorphies to be originally present and serially repeating, homologous and homonymous on all arthropod body tagmata (cranial, thoracic and abdominal in insects) (figures 4-10).

Arthropod exites, which are membranous (then cuticularized externally positioned) evaginations out of the membrane between the upper leg segments, are here shown to be present in Late Paleozoic pterygote fossils (figures 11-13), and are still retained in some modern Insecta (figure 13). The first

arthropod leg segment, the epicoxa, is shown to be visibly present on the heads, thoraxes and abdomens of some Paleozoic fossil and some living Insecta (see many introductory figures).

In 1983, and again more broadly in 2008, I proposed that insect wings evolved entirely from the *epicoxa (the first arthropod leg segment) and its mobilized exite*. I also documented that this *first epicoxal leg segment was not previously recognized as a part of the ancestral arthropod leg model*. Here, plentiful evolutionary-morphological evidence is offered, supporting the presence of this serially homologous and regular *epicoxal leg segment, and is also present on all hexapod heads and abdomens*. The *solely leg-derived origin of the embryological wing anlagen is also* evidenced by the *winglet buds in modern insect juveniles, which develop in the pleural membrane, far from the tergum and close to the upper leg point of origin* (figures 51, 64). Over 1,000 modern wing examples from all pterygote groups of orders are presented as documentation, with homologous wing veins and articular sclerites color-coded for easier comparisons and verifications. The phylogenetically important **key wing characters identifying the pterygote higher clades** are singled out and interpreted. The number of illustrations of fully morphologically interpreted wing organs is deliberately very large, to demonstrate how stable are the *characters of the higher taxa*, and thus *very different* from those at the species and genus level. This circumstance is not generally realized, but is inevitable for understanding the evolution of the characters in the wings of the higher taxa and in constructing the Phylogenetic Tree, important for progress in Evolutionary Biology.

As a leg-derived organ, the valid interpretation of insect wings must be based upon the *full and correct model of the arthropod and hexapod leg, homologized on all body segments*. Hence, all insect and hexapod leg appendages are here derived from a newly reconstructed arthropod leg groundplan, and *documented as originally present and serially homologous on all insect head and body segments*. The most accessible hard evidence is the presence of the *thoracic flattened epicoxal segment in the living and fossil primitively wingless insect order Archaeognatha (“jumping bristletails”)* (figures 38-41).

Why was the origin of insect wings such an enduring problem?

There were *three morphological wing characters, which appeared to be morphologically inexplicable*. 1) *Insect wings* (placed between the tergum and the “first” leg segment (the subcoxa) *had no recognized homologues on the head and abdomen (the cranial genal duplicature (a fold or doubling) and abdominal paranotal lobes were treated as of uncertain origin)*. 2) All other animals bearing flapping wings have lost the pair of legs from which the wings were derived (*but Insecta kept them*). 3) Pterygote insects bore *two pairs of flapping wings, but retained their three pairs of thoracic legs*. (This fact interfered with deriving insect wings from legs).

When I applied (in 1983) the comparative-morphological method to discover the wing origin with the help of the reconstructed *arthropod leg groundplan* (studied for years by E. L. Smith), I immediately saw some positive comparative evidence in the arthropod leg segments bearing exites. Crustacea (ancestral to Insecta) swim around in water by using the (uniquely arthropodan) externally oriented appendages on

their upper leg segments called exites, which are mobilized by leg muscles, and use them for underwater paddling *without losing their walking legs*. Pterygote insects fly in the air by employing the externally oriented and mobilized leg appendages called wings, and use them for aerial flapping flight **also without losing the walking legs**. But the principle of serial homology of the legs dictated that wings, placed between the tergum and subcoxa, must also have equivalent structures on all cranial and abdominal segments. The *only possibility was that the problematic “genal duplicature” on cranial segments, and equally problematic “paranotal lobes” on the abdominal segments are really homologues of the wing articulation and the wing blade*. This solution appeared to be very probable, but only after a brand-new first leg segment (called by me the **epicoxa**), flattened and bearing an exite and located above the subcoxa, **was added to the previously acknowledged arthropod leg groundplan**. I spent *about a decade* making sure that *the first leg segment, bearing an exite, could have possibly escaped being noticed in such a large and well-studied animal group as the Arthropoda*. The discovered evidence confirming the reality of the epicoxa is reviewed in this contribution.

Pterygote phylogenetic tree, and the key characters of the higher taxa

Here, I demonstrate the evolutionary-morphological (“paleontological”) approach to insect morphological evolution, as used by A.G. Sharov, E. L. Smith, and myself and show its application to the phylogeny of Hexapoda and Pterygota, and to the reconstruction of the coveted but not yet fully resolved pterygote phylogenetic tree. This cannot be credibly done without using the *Hennigian phylogenetic method, which requires using the correctly homologized and evaluated wing key characters in all of the pterygote higher-level clades. This obligatory homologization cannot be even started without deriving all leg-derived insect appendage from the fully interpreted arthropod leg groundplan including the basal composition of all of the leg-derived appendages (mouthparts, walking legs and wings, abdominal leglets, genitalia, vesicles and all documented exites and endites, in the modern, as well as fossil insects and hexapods) (figures 5, 8-10).*

The basal phylogenetic tree of Pterygota is composed of the ordinal and higher pterygote clades defined by their key characters, which reveal their position and relationships in the tree. Hence, recognition of the key characters is the most important information any evolutionary biologist has to reconstruct correctly the phylogenetic tree. The key characters originated by the combination of two evolutionary events, as follows.

The wing organ, placed between the tergum and the pleuron of the subcoxal limb segment evolved in the following way. Perhaps as early as the Ordovician, the earliest groups of pterygotes dispersed into diverse habitats and adapted to different conditions, while their thoracic protowings were enlarging and aiding survival, most probably by assisting escape from predators by flight-hopping. In the process, distribution of veins in the wing blades changed variously to support the flapping protowings. When the wings enlarged sufficiently for true aerial flapping flight, they were in need of a set of strengthening adaptations. Aerial flight of insects is performed by moving wings so that their tips are drawing in the air a

horizontal number 8, called a “lemniscate”. To be able to do all these twists and turns, the wing blade needs additional supports (fusions between veinal stems and branches, struts, braces, sclerotizations) in several locations, exposed to increased aerodynamic stresses, mainly along the anterior wing margin, in the center of the wing base, along the long horizontal wing axis, along a bowed strip surrounding distally the wing base, etc. However, these supports are very differently built. While their placements are quite similar (due to shared physical stresses), *different insect groups had in these predictable places more or less differently arranged veinal stems or branches, which were connected or fortified (by a strut, short fusion, long fusion, bridge, etc.) in somewhat different ways. As a result, pterygote higher taxa differ, from before the Carboniferous up to Recent time, by recognizably the same key characters (with only small variants), which enabled the aerial flight and mirrored their relationships. They are all extremely old features and evolved as a combination of adding, in similar places, diverse aerodynamic supports to diversely arranged branched veins.* Under these circumstances, parallelism is quite possible and has to be recognized.

Insect flight therefore *did not originate only once*, as was long believed, *but several times* independently and in parallel from the same Protowing. Hence, pterygote key characters actually have *two origins combined*. This occasionally quite complex situation underlines the need for a broad study of plesiomorphies, which fortunately are quite frequent, in both fossil and modern insects.

While in pterygote venation the character evaluation and comparison are quite advanced, but in the articular sclerites (especially in Neoptera), it has hardly started. There is a need to advance such work. *If correctly selected and evaluated, the key characters of the pterygote higher clade wing articulation may help to mirror the morphological phylogenetic tree* (JKP 1983/2008).

Winglets of pterygote juveniles, and the metamorphosis-based “taxon” Polyneoptera

It is suspected that pterygotes may have originated in the Ordovician or earlier, but are only known as fossils bearing fully evolved “modern” wings since the middle Carboniferous. Most early fossil juveniles bore articulated and movable winglets, completely separate from the tergum (figures 49, 50, 55). However, the *secondary fusions* of the winglets to the tergum, protecting them from damage while the nymph was moving, were so advantageous for survival that the fusion process started in several clades *already in the Early Paleozoic. In the Late Paleozoic*, fusion of wings with the tergum was marked by a dividing suture, which was sometimes later reduced (figures 61, 62). After the Paleozoic, fused winglets quickly prevailed, and *all later nymphs* without exception have their winglets fully fused to the tergum, while the dividing suture remained unreduced only rarely, in some modern orthopteroid and hemipteroid nymphs. The process of *metamorphosis, which shortens a long development time (an enhanced risk to survival), was originally absent and occurred mostly only after the Paleozoic.* It evolved in several lineages, *independently, in parallel, and a long time after the higher clades were already fully established.* Hence, using metamorphosis for classification of the higher taxa can be very misleading.

A most significant example is the long accepted but **completely faulty taxon** “Polyneoptera” including *Orthoneoptera*, *Pleconeoptera* and *Blattoneoptera*, which all bear **in both wing pairs very different aerodynamic key characters in the veins as well as the sclerites**. *Orthoneoptera have the most different veinal key characters of all Pterygota, and a completely plesiomorphic type of veinal fan in the hind wing anal lobe. Pleconeoptera have the veinal fan uniquely derived, and Blattoneoptera have a highly derived anal fan synapomorphic with Hemineoptera and Endoneoptera* (see figures of the wings in various orders). Note that ***the differences in composition of the aerodynamic wing key characters and in the key veinal support of the anal lobe are the most important informative wing characters for establishment of the pterygote phylogenetic tree based on the veins and sclerites.***

After I have published the leg/wing hypothesis proposing that insect wings evolved from the previously overlooked arthropod first leg segment, the *epicoxa and its exite*, no rejecting contra-evidence was given by others. I received very encouraging comments from some of the foremost evolutionary entomologists, including my former mentor Prof. F. M. Carpenter (Museum Comparative Zoology, Harvard University), and was awarded honors by scientific institutions in Canada and the Czech Republic. But nevertheless, for the following 40 years the question of insect wing origins has generally remained tentative. The main reason probably is that most systematic entomology deals mostly with lower taxa, bearing multiple and often quite variable characters, which require the use of ***completely different study methods than the higher taxa***. Hopefully, plentiful examples provided here, all showing how ***few but consistent the key characters of the higher taxa are***, will open the “morphological door” for pursuing an evolutionary higher-level taxonomy and phylogeny, as has been done for some groups such as vertebrates.

Sources of specimens offered as evolutionary evidence and my collaboration with and E. L. Smith

The wing examples figured here are almost all my originals, constructed over years while working out homologizations of the wing veins and wing articular sclerites. They are intentionally copious to demonstrate ***convincingly and verifiably*** the dependable presence of homologous aerodynamic wing key characters in modern higher taxa. Most of the studied insects were accumulated in 60 years of collecting, for about four months every year, in cooperation with the insect biogeographer S. B. Peck. My hunt for leg/wing plesiomorphies and apomorphies also included specimens from some of the world’s best museum collections, in Paris (France); Canberra, Sydney, Brisbane, Darwin, Perth (Australia); Havana (Cuba); San José (Costa Rica); Kellogg Agriculture School, Zamorano (Honduras); Schlitz (Germany); Moscow (Russia); University of Pretoria and University of Pietermaritzburg (Republic of South Africa); Bishop Museum (Honolulu), Field Museum (Chicago), Academy of Natural Sciences (Philadelphia), California Academy of Sciences (San Francisco), and Florida State Collection of Arthropods (Gainesville), (all U.S.A.); Beijing (China); Tokyo (Japan); and CNCI, Agriculture Canada, Ottawa (Canada). Most of our resulting specimens have been deposited in three museums: in Ottawa (CNCI and CMN), Chicago (FMNH) and Gainesville (FSCN).

My study of arthropod/insect leg evolution was significantly broadened and improved by a long collaboration with the highly accomplished arthropod evolutionary morphologist Edward Laidlaw Smith, Chico State University and California Academy of Sciences, San Francisco, U.S.A., who spent 20 years interpreting the detailed morphology, function, homology and diversification of the hexapod leg-derived appendages, segments, exites and endites, in the mouthparts, genitalia, and other organs across all Recent arthropod groups. I contributed to his interpretations of the plesiomorphic characters of legs present in Late Paleozoic (Carboniferous and Permian) fossil insects from Europe, Russia and U.S.A. He prepared for publication an excellent and information-packed manuscript with exceptionally good morphological figures, of book length, which contained many new and improved organ interpretations and beautifully detailed illustrations, but the manuscript was rejected by a single reviewer and subsequently not offered for publication. My hope is that this outstanding contribution to biology will be eventually printed. The manuscript of this book is in my possession and I plan to place it in my archives in Entomology, Canadian Museum of Nature, Ottawa. The combined comparative analysis of the leg-derived organs is *very useful for the recognition of the key characters determining pterygote diversification into the higher clades* and provides the repeatedly confirmed leg base for the systematic wing interpretations presented in this contribution. The morphological studies of E. L. Smith concerned the classical hexapod leg, exites and endites, *starting with the subcoxa*. Hence, our collaboration *did not contain the first actual leg segment (epicoxa)*, and origin of insect wings and all other epicoxal products, for which I am solely responsible.

Another very important hexapod evolutionary morphologist was A. G. Sharov (Paleontological Institute, Russian Academy of Sciences, Moscow), who introduced a pioneering evolutionary study to interpretation of many organs of Hexapoda, and recognized the evolutionary leg appendage problems solved by E. L. Smith and myself. The Sharov's 1964 book was also very harshly criticized by S. M. Manton and other poorly informed entomologists, and by far did not receive the attention it deserved.

Short history of wing structure nomenclature

The standard nomenclature of the pterygote wing veins and sclerites was proposed by Comstock and Needham (1898, 1899), and again by Comstock (1918). Snodgrass's (1933) conceptualization of the Comstock-Needham system then became the prime interpretation of the wing veinal morphology and articular sclerites used in insect flight. While the Snodgrass version of the veinal system and articulation is still used worldwide for insect descriptions and comparisons, it is not applicable for the full and correct identification of the phylogenetic relationship between the pterygote higher taxa. As best documented by Hennig (1981), to be phylogenetically informative, the morphological key characters of all higher clades must be first correctly identified, which means, ***derived from the single shared groundplan model, and fully homologized between all pterygote orders***. Snodgrass's nomenclature of the pterygote wing veins, as presently used, is typological, incomplete, and often inconsistently applied and compared between different insect orders. As a result, many of the veinal wing characters can be neither identified nor homologized throughout all pterygote orders, which makes them thus useless for phylogenetic evaluation.

As an example, *anal wing veins*, very important for higher-level taxonomy (see figures) in contemporary publications are usually not given their correct phylogenetic symbols, and the missing information makes the wings useless for phylogenetic purposes. Pterygote wing **sclerites** were typologically named as being already grouped into derived composite super-sclerites (1Ax, 2A, 3Ax axillary, anterior and posterior plates, etc.), and never individually derived from their groundplan state. The morphological system of winged insects (Pterygota) is comprised of two basal clades called Paleoptera (“old wings”) and Neoptera (“new wings”), **incorrectly** suggesting that the Paleoptera bear plesiomorphic outspread wings, and the Neoptera bear apomorphic foldable wings, as also proposed by the long accepted but faulty “paranotal hypothesis”. Just the opposite is the true situation, but more on this later. Nevertheless, Snodgrass’ nomenclature was significantly progressive for his time, because it made possible systematic work with the insect lower taxa. Yet, it certainly was insufficient to allow phylogenetic work with higher taxa. ***Such a simplified typological nomenclature and understanding of features ruins their phylogenetic message, and superficial homoplasy (see figure as frontispiece) gets the upper hand.*** It is now necessary that the *wing and leg nomenclature should be corrected and expanded* to match the much-progressed evolutionary-morphological understanding of the main pterygote leg-derived organs.

In leg nomenclature as used by E. L. Smith and myself, *all of the familiar typological names of wing veins and sclerites are kept as much as possible, and the new names are proposed only when absolutely necessary. The reason is that we do not need to add avoidable problems to those, which are still ahead.*

Morphological and molecular agreement on the origin of wings

The intriguingly different contact between the wing articulation and the tergum inspired three main hypotheses, suggesting that insect wings originated either **1)** from laterally extended thoracic tergal lobes, functional for gliding down from tall Devonian trees (the *paranotal hypothesis*), or **2)** from the previously unrecognized first epicoxal leg segment and its mobilized exite (the *leg/wing hypothesis*), or **3)** from the tergum and the first leg segment combined (the *tergum/leg/wing hypothesis*). Presently, some researchers appear undecided about which hypothesis is based on researched facts and which on unlikely speculation. The mystery of the wing origin has been hovering above entomology for nearly two centuries and obscuring higher-level phylogenies. Both morphological and molecular phylogenetic research results of the *insect lower taxa* are now coming closer to general agreement. However, in the higher taxa of Animalia, the data are generalized and less robust, and the conclusions are still often indecisive and quite different (see Wipfler et al., 2019). Some recent genomic studies are suggesting that wings have had a dual origin from both lateral (leg) and dorsal (tergal) structures (the *tergum/leg/wing hypothesis*: Almudi et al., 2020; Clark-Hatchel et al. 2021; Linz and Tomoyasu 2018; Prokop et al. 2017), which my comparative-morphological research falsifies with multiple examples of conflicting evidence. A reliable foundation in evolutionary morphology is now much needed for comparison, to help solve some important and unexplained differences (see below). There have been many attempts at resolving the phylogeny of the insect orders and other higher clades (see Kjer et al. 2016; Beutel et al. 2017), and the timing of the origin

of insect orders (Misof et al., 2014). Many molecular phylogenies have been proposed, which recently seem to be approaching a consensus (Wipfler et al. 2019). But I think that there has been, so far, only minimal use of comparisons between molecular and evolutionary-morphological results, in spite of the ***fully evidenced and generally accepted thesis, that morphologically, the Pterygota diversified into all basal clades with their wings. Obviously, there is a need to revise the morphological phylogenetic tree according to Hennigian phylogenetic procedures. Undoubtedly, final results of all approaches are expected to be trusted only when they agree.***

My broad comparative morphological studies over many years (1983, 2008) have found evidence ***solely for the origin of all wing structures from a single first leg segment (an epicoxa bearing an exite), the presence of which in the leg was long unrecognized*** (figures 8-11). **Bruce and Patel (2020), in a detailed study using a knockout of crustacean leg patterning genes, provided material evidence that insect wings and body walls evolved from the ancient leg, and found no evidence of a dorsal (tergal) component** (the *leg/wing hypothesis*). ***These results from different fields of science, and including the broadest possible comparative-morphological evidence, fully agree that insect wings originated from the leg.***

Results and Discussion

Pterygote leg expressions on the head, thorax and abdomen

Hexapods/insects are documented in the Devonian (ca. 410-360 Ma) as a monocondylous, terrestrial, non-winged, hexapod group with 11-segmented limbs bearing upper leg exites, double claws, and 6 thoracic, longer and Z-shaped legs, as an adaptation for terrestrial life (as in the still existing order Archeognatha). But the **oldest Pterygota represented by fossil, are known only since the middle Carboniferous**. By that time, all leg-derived appendages, including the wings, were already morphologically very similar to those in the modern fauna, only much less reduced. Very often, the legs retained on the head (maxillary and labial palps) and on the abdomen (leglets called telopodites and sexual appendages) are still complete, bearing a distinctively delimited patella and two claws (figures 4-10). Fossils demonstrate that ***abdominal telopodites (leg segments PFE – PT) were originally present in all pterygote adults and juveniles. In the Upper Paleozoic, they were already reduced in most adults*** (figure 8), but ***still retained in many juveniles*** (figure 49).

Biramy or polyramy - the arthropod groundplan leg, exites and endites

Interpretation of the leg-derived appendages is complex and not easy to understand because of the many characters and morphological steps involved. A single read-through will probably not be sufficient, especially for a reader not especially familiar with insect wing terminology. The following text can be much better visualized when observing the **98 figures** in the accompanying six folders of introductory figures. It is probably ***best to study these figures before reading the present text.***

Comparative-morphological research of the role of legs in the origin of wings starts with the premise that *ancestral Arthropoda originally had on all body segments (probably before the appearance of a distinct head tagma) a pair of serially homologous and homonomous legs, composed of 11 tubular leg segments, which bore mobile exites (externally oriented) and endites (internally oriented) on the upper parts of legs (the basipodites) (figure 5). Exites are externally positioned, membranous (later cuticularized), annulated, mobilized evaginations between two leg segments, bearing sclerotized bases inserted by leg muscles. The exite is often embayed into the upper leg segment (sometimes completely enclosed), and is often formed to generate an underwater flapping and swimming movement (in Crustacea, figure 5). In contrast, the endite is an inwardly positioned appendage evaginated from the middle inner portion of the upper leg segments (the basipodites), used as a vesicle or as the working part in mouthparts and genitalia (figures 7, 17, 34). Each exite can be considered a ramus (branch) and can occur on one or more basal leg segments (the basipodites). Hence, arthropod legs are polyramous (not just biramous as often characterized in Crustacea, and the group of Manton (1977) is not supported (JKP 1992)), serially homologous, and originally present on all body segments (of the head, thorax and abdomen in insects).*

Note that early Cambrian marine fossil arthropod assemblages, such as the marine Burgess Shale fauna of British Columbia, Canada, seemingly only partially support this leg groundplan. However, the extant as well as fossil evidence offered here shows that *biramy is a secondary and derived condition involving the reduction of all exites except one* (see trilobite in figure 5). **Arthropod legs were originally polyramous (each exite being a “branch” or ramus).** Reductions of some had exites already occurred in the Early Cambrian (e.g., in trilobites). The hexapod groundplan leg bears *11 leg segments (several upper segments bear short, membranous, usually annulated exites), subsegmented eutarsus, and pretarsus with double claws. Importantly, these characters are still retained in some modern insects, as plesiomorphies* (figure 9).

The leg segments in the hexapod groundplan: currently used names and symbols

1, ECX - epicoxa; 2, SCX – subcoxa; 3, CX – coxa; 4, TR – trochanter; 5, PFE – prefemur; 6, FE – femur; 7, PAT – patella; 8, TI – tibia; 9, BT – basitarsus; 10, ET – eutarsus (subdivided); 11, PT – pretarsus, with two claws. *As proposed by E. L. Smith (in his unpublished book), names which are more logical for two of the leg segments would be: subcoxa changed to precoxa (PCX), pretarsus changed to posttarsus (PT).*

Leg-derived appendages start with an epicoxa on the hexapod head, thorax and abdomen

Arthropod groundplan legs are *serially homologous and homonomous on all body segments* (figure 5). Therefore, legs starting with an *epicoxa bearing an exite* (which evolved into thoracic wings) *were present on all groundplan body segments.*

The cranial epicoxae and their exites. The insect cranium bears a reinforced rim anteriorly called the *“anterior strut”* and on the sides of the head the *“genal duplicature”*. These reinforcements are placed *between the cranial terga and the leg-derived mouthparts starting with a subcoxa, exactly as the wings.*

Previously considered to be morphologically unexplained, the cranial rim is formed by the *epicoxal pleura* (=flattened epicoxal segments) folded into narrow lobes, fused to the cranial terga, and providing a reinforcement of the cranium. The narrow epicoxal lobes also serve as an articulation site for the leg-derived mouthparts, starting with a subcoxal segment (figures 17-28). In modern Hexapoda, all cranial epicoxal exites are reduced, but some fossil silverfish bear under their eyes a short “spike” starting from the epicoxal rim, possibly a remnant of the maxillary epicoxal exite (figure 20).

The thoracic epicoxa and exite. On the thorax, the homologue of a narrow epicoxal lobe fused to the cranial terga is the epicoxa flattened into a pleuron, which fragmented around the muscle insertions into two columns of articular sclerites, 8 proxalaria (PR) and 8 axalaria (AX) (figures 65, 67). Pterygotes with protowings (the early exite extensions before they were fully formed wings) bore on all three thoracic segments the walking legs starting with the epicoxal segment flattened into a pleuron, which embayed and surrounded the muscled base of their flattened mobile exite. Dorsally, the epicoxa subdivided along a pre-existing suture, and fragmented around the muscle attachments into articular sclerites (8 proxalaria (PR) and 8 axalaria (AX)), arranged in two columns and aligned in eight rows (with eight wing veins). The muscled exite base also fragmented into articular sclerites (8 fulcalaria (F)), which joined the axalaria as a third column of sclerites. Ventrally under the wing, the flattened epicoxa formed two large sclerites subdivided by a suture, the *basalare and subalare* (figure 68). Note that a similar suture (of uncertain origin) is also present on the subcoxa and coxa. The membranous, muscle-less part of the exite was flattened and changed into a *wing blade*, supported by *8 branched and sclerotized hemolymph veins*.

Hence, the protowing groundplan articulation consists of **24 small independent aligned sclerites, arranged** antero-posteriorly into **three columns** (proxalar (PR), axalar (AX), fulcalar (F)), and proximo-distally into **eight rows of sclerites, articulated with eight wing veinal bases (basivenalia, B)**. In the protowing groundplan, **proxalaria (PR) were articulated to the tergum, axalaria (AX) to proxalaria and fulcalaria, and fulcalaria (F) to the axalaria and eight basivenalia (B)** forming the sclerotized wing base (see many figures). Protowing pterygotes **flapped the wings promoting forward movement, and folded them backward** by *pulling together the sclerites in the middle of the articulation* (see the Paleozoic order †Diaphanopteroidea († is the symbol used to indicate an extinct taxon) that alone shows the protowing folding (figure 71, and sclerite models).

Abdominal epicoxal lobes and epicoxal exites. Abdominal flattened epicoxae are folded into **epicoxal lobes** (=typological “*paranotal lobes*”), fused to the abdominal terga with a dividing suture (sometimes reduced). In the ancestral Pterygota, epicoxal lobes bore articulated **movable epicoxal exites**. By the Late Paleozoic, abdominal exites were already mostly reduced, and in the Present, they are retained **only in juvenile mayflies (Ephemeroptera)**. Apparently, mayfly nymphs became secondarily aquatic very early in their evolution, and used their modified abdominal **epicoxal exites as tracheal gills up to Recent time** (figure 32). In their sister group Odonoptera (the Odonata group of orders), the juveniles became fully aquatic only *after* their epicoxal exites became reduced, and they used instead as gills the **elongated abdominal leglets** (see nymph at bottom of figure 59). Note that the same nymph also bears plesiomorphic

fully movable and uplifted winglets. The ancient **leg-gills are still present in one living odonate clade.** In nymphal Odonata Anisoptera (dragonflies) their rectal respiration is a later adaptation. In nymphal Odonata Zygoptera (damselflies) their respiration through three plate gills at the apex of the abdomen is also a later adaptation, but the two lateral gills are modified cerci (originally leglets) and the median gill is the modified plesiomorphic median caudal filament.

Thoracic winglets became secondarily fused to the tergum in all Post-Paleozoic Paleoptera clades. In contrast, in Neoptera, **Carboniferous juvenile Plecoptera (stoneflies) nymphs also bore abdominal epicoxal exites, as in fossil and modern Ephemeroptera (mayfly) nymphs** (right of figure 55), and some modern plecopteroid nymphs bear long abdominal leglets working as gills, like some of the Carboniferous-to-extant juvenile dragonflies. (Note that when applying the comparative morphological method, information like this is sought when looking for and evaluating the characters of higher taxa).

Abdominal leglets (= telopodites). In extant Pterygota, the abdominal epicoxa is folded into a lobe fused to the tergum with a dividing suture, the epicoxal exites are reduced (except in mayfly nymphs), and the three leg segments, *subcoxa*, *coxa*, *trochanter* (flattened into pleura, exites reduced) are embedded into the pleural membrane to reinforce the abdominal wall (figure 31).

Many Late Paleozoic juveniles (of mayflies, dragonflies, stoneflies, etc.) and even adults (e.g., some †Diaphanopteroidea) bear plesiomorphic short serial **abdominal leglets composed of six leg segments: profemur, femur, patella, once subdivided eutarsus, pretarsus with two claws.** Note that the patella is always fully articulated. On the abdominal segments in fossils bearing genitalia, the coxal and trochanteral leg segments still bear some exites (figure 34). These became later reduced, while endites persisted and compose the adult male and female genital appendages (figure 34).

Evolution of winglet articulation in pterygote nymphs

Association of juvenile winglets and the tergum. Most Late Paleozoic nymphs of Paleoptera and Neoptera bore articulated movable winglets, as in their adults. These winglets often fossilized separated from the nymphal bodies, having broken off at the line of weakness of the dividing suture. Nymphal development was probably of long duration, with many nymphal ecdyses and several subadult instars, while a definitive metamorphic instar was absent (figures 55, 59-62). However, the movable winglets were exposed to being damaged. *Temporary fusions of juvenile winglets to the terga started independently in separate insect groups, and already in the Early Paleozoic. In the Late Carboniferous, nymphs of all blattoids, some hemipteroids, and even of some †Palaeodictyoptera had evolved winglets fused to the tergum with a dividing suture* (figure 53). Very probably, blattoid and some hemipteroid juveniles lived hidden in plant debris, and such narrow spaces would be damaging to articulated winglets. Large †Palaeodictyoptera nymphs imbibed fructifications on trees with their long rostra (figure 30), and were exposed to being snatched away by the giant long-legged predatory dragonflies (lower left of figure 59). For protection, their bodies became very broad, low-profiled, compact and covered by sclerotized bumps and spikes, and they were apparently clinging to surfaces for protection as in some modern juveniles (figure

62). *A fusion of nymphal winglets to the tergum was so beneficial to survival that over time it independently evolved in all pterygote clades.*

Protowing venation and corrugation

Protowing veinal support. The protowing (figure 15), and the later fully functional flight wing, had a membranous wing blade supported by *eight* sclerotized veins, filled with hemolymph delivered by eight hemolymph canals, running under and protected by eight rows of epicoxal wing sclerites. Every vein is composed of *two corrugated veinal sectors*, a convex (raised) anterior sector A+, and a concave (lowered) posterior sector P-, which both start from a *shared sclerotized hemolymph sinus* (basivenale B).

The wing blade is supported by the following veins, named and color-coded as shown in the table below: **precosta PC** (violet); **costa C** (orange); subcosta Sc (yellow); **media M** (red); **radius R** (blue); **cubitus Cu** (green); analis A (yellow); **juga J** (orange). The symbols for the of dorsal wing sclerites, basivenalia, and veinal sectors are: proxalare, **PR**; axalare, **AX**; fulcalare, **F**; basivenale, **B**; and for the eight veins composed of two veinal sectors (A+ and P-); PCA+, PCP-; CA+, CP-; ScA+, ScP-; RA+, RP-; MA+, MP-; CuA+, CuP-; AA+, AP-; JA+, JP-

Color-coding scheme used to identify and homologize wing veins in the figures for this contribution:

Vein Colour Coding

1. Precosta	PC	 Violet or orange
2. Costa	C	 Orange
3. Subcosta	Sc	 Yellow
4. Media	M	 Red
5. Radius	R	 Blue
6. Cubitus	Cu	 Green
7. Analis	A	 Yellow
8. Juga	J	 Orange

Wing vein nomenclature

Wing basivenalia (B). Eight basivenalia (B) compose the base of the wing blade (figure 15, 67). When a veinal sector divides into branches, the first two branches are numbered 1+2 and 3+4, and when it divides again, the resulting four branches are numbered 1, 2, 3, 4. The wing blade and wing base have no muscle attachments. The protowing wing blade is articulated by all basivenalia (B) to articular sclerites fulcalaria (F) (figure 65, 69, 70).

Homology: Fulcalaria evolved from the muscled base of the epicoxal exite. The wing blade originated from the membranous, annulated and muscle-less part of the exite.

Protowing veinal corrugation in Paleoptera and Neoptera. In the Protowing model, all **three** pairs of wings (on all three thoracic segments) bore regularly corrugated pairs of veinal sectors, convex (+) and concave (-). In the Late Paleozoic, this plesiomorphic position was well retained in Paleoptera: †Rostropaleoptera (figure 71). Paleoptera: Hydropaleoptera (mayflies and dragonflies) (Carboniferous to Recent) share a distinctive aerodynamic accommodation of the *basal portion of RP-*, which became *secondarily convex* (synapomorphy, see figures). In all Neoptera the veinal corrugation is much weaker than in Paleoptera and often more or less irregular. Veinal sectors of PCA+, PCP-, CA+, CP-, ScA+, ScP-, CuP- almost always keep the original protowing corrugation, but veinal sectors RP, MA, MP, CuA, AA, AP, JA, JP are very often secondarily leveled, and exceptionally even corrugated in an opposite way (figure 70).

Veinal sectors, branching stems, and fusions (as demonstrated on medial vein). The medial vein is composed of *two veinal sectors* called MA+ (convex media anterior) and MP- (concave media posterior). The first two branches of the veinal sector are numbered MA1+2 and MA3+4, and when they divide again, resulting in four branches numbered MA1, MA2, MA3, MA4. When MA and MP fuse basally into a (derived) single vein, this is called *the stem of M*, or the *medial stem*. At the wing base, and in aerodynamically stressed places, the veinal sectors variously fuse *one to another*.

Protowing evolution before flight

Wing adaptation before aerial flight. A hexapodus morphology evolved in or from Crustacea perhaps as early as in the Cambrian. *Hexapodous and terrestrial proto-pterygota originated perhaps in the Ordovician or earlier (there is no fossil evidence)* and they lived on low vegetation growing near or out of water, and bore on all of their cranial, thoracic and abdominal body segments the leg-derived appendages, which had mobilized upper-leg exites (figures 7 - 13). They probably had many arthropod predators (especially chelicerates) from which they probably escaped mainly by hopping (as do present day terrestrial crustaceans Amphipoda, wingless monocondylous Archaeognatha, and the extinct **most primitive Dicondylia, wingless †Cercopoda** (bearing instead of wings, the epicoxal lobes on thorax as well as abdomen). Still surviving primitively wingless **monocondylous Archaeognatha**, bear upper leg exites on head palps and on the leg coxae (figure 11). The ancestral proto-Pterygota had epicoxal exites on their thoracic segments larger than those on the abdominal segments (figure 56, in mayfly nymphs), and very probably, *they started using them to facilitate escape from predators*. Flapping thoracic exites significantly improved survival, and early proto-pterygotes multiplied and started inhabiting different habitats. With time, flattened epicoxal exites enlarged into winglets motorized by the leg muscles, and their flapping movement became more efficient. They bore eight sclerotized wing hemolymph veins, each of which was composed of two branched and corrugated (+ and -) veinal sectors, distributed to support the wing blade, especially its anterior wing margin and the long wing axis. With time, as proto-pterygotes moved through vegetation and struggled to survive, various lineages that became Pterygota evolved adaptive differences in the veins supporting the wing blades, the wing articulation motorizing the flight, and the mechanism of folding the wing backward along the abdomen. As the nascent wings were adapted for aerial flight, these

veinal differences became “fixed” in place by *adding struts, fusions, and sclerotizations in the aerodynamically stressed areas necessary for aerial flight. These aerodynamic characters, which are different in the higher taxa and show their mutual relationship, are key characters in the insect Phylogenetic tree.*

What type of flight came first: flapping or gliding?

For 100 years or more it was broadly believed that insect wings evolved from laterally extended tergal lobes used for gliding (the “paranotal hypothesis”), based on the speculation that gliding is simpler than flapping and is performed by the laterally placed parts of body like the wings, and therefore must have come first, before flapping. However, concrete observation shows exactly the opposite. Nature has a number of various gliders (e. g., frogs, lizards, snakes, squirrels, phalangers, etc.), which glide by spreading parts of their bodies to gain a greater surface area as an airfoil, and use it to slow the rate of descent. Yet, *none of these gliders ever developed flapping flight.* Opposed to this, all animals bearing flapping wings use the leg muscles to motorize **not only their flapping, but also their gliding.** In Pterygota, all Neoptera can flap, glide and fold their wings through the use of their leg muscles, as in all other winged animals. But in Paleoptera, *only the fossil order † Diaphanopteroidea (figures 53, 54) of the extinct Paleozoic clade Rostropaleoptera shares wing folding with the Neoptera, but it is performed in a much more primitive way. The lineage Hydropaleoptera (mayflies and dragonflies) share seven aerodynamic veinal key characters enabling aerial flight, unique for the lineage and always present (from Carboniferous to Recent times). They are a good example of key characters of the higher taxa uncovered by comparative morphology. The oldest and largest known Carboniferous mayfly *Bojophlebia prokopi*, (figure 93) and the oldest six-winged dragonfly (see title page or figure 87) already shared these “modern” characters, but bore triangular hind wings like most of the other oldest Paleoptera. Because of them, some entomologists have excluded *Bojophlebia* from the lineage Hydropaleoptera, the seven synapomorphic veinal key characters shared with Odonatoptera notwithstanding.*

A systematist working with order-level and higher entomological taxa must absolutely avoid applying in character evaluations the methods which are successfully used in the lower taxa.

Secondary fusions between the wing sclerites and the wing base, which hold the wings of most Paleoptera in a permanent *energy-saving gliding position without muscular pull have a big survival disadvantage. This fusion prevents the wings from being folded backward along the abdomen, and hiding in litter or vegetation from their numerous predators* (figures 53, 54).

Motorization of flapping wing movement in insects requires multiple, diversely adapted and delicately synchronized upper-leg muscles attached to the wing sclerites, which completely surround the wing blade base. In Recent Neoptera, the wings are manipulated by about 15 leg muscle bundles (figure 14) strategically distributed and grouped together in irregular super sclerites, which secure a faster and firmer folding of the wing backward than existed in the ancestral protowing and in the fossil Paleoptera order †Diaphanopteroidea (figure 71 and text below). Such a complex apparatus could have evolved only

gradually, by improving a flapping function while simultaneously enlarging and providing better support and control of the wing blade. Note that *this kind of muscular activity is completely absent when an animal simply extends some part of its body and holds it outstretched for gliding. Flapping requires a complex muscled articulation, which directly manipulates the wing by an adapted leg musculature. These complex changes happen by gradual improvement of muscular action, not by a sudden super-complex mutation, which puts the muscular complex where it never had been before.*

For these reasons, *none of Natures' gliders ever developed flapping flight.* In contrast, **all of the powered flappers (pterodactyls, birds, bats and pterygote insects) can both flap or glide by using the pulling action of the same modified leg muscles.**

In another words, the insect *ability to fold the wings backward is plesiomorphic and was already present in the epicoxal wing exites*, from which the wing blade evolved. Also, thoracic exites/wings (plus fulcral sclerites) are serially homologous with the still foldable abdominal exites (as gills) retained in modern mayfly nymphs (figure 55-58, JKP 2008). Fossil plesiomorphic (†Diaphanopteroidea) had foldable wings as both nymphs and adults (figures 53, 54) like most of the juvenile Paleozoic Neoptera. However, all modern juvenile Neoptera have their wings firmly (albeit secondarily) fused to the terga.

In the Paleozoic Neoptera nymphs, the wings that became secondarily fused to their terga, have the **contact line marked by a dividing suture.** In modern nymphs, these sutures very often disappeared, but not always, especially in the hemipteroids and orthopteroids. Gliding is in Pterygota a secondary consequence of flapping, which in Neoptera and plesiomorphic Paleoptera (†Diaphanopteroidea) always requires a muscular pull. Secondary muscle-less gliding present in all other known orders of †Rostropaleoptera and in all Hydropaleoptera, originated twice, independently and in parallel. The evidence is that it is enabled by sclerites fused into a single (posterior) plate in †Rostropaleoptera, and into two plates (anterior and posterior) in Hydropaleoptera (figures 69,70).

Carboniferous prothoracic winglets confirm the Protowing veinal groundplan

Pterygote **prothoracic** winglets originally resembled what were to become the meso- and metathoracic flying wings, but remained small and did not adapt to generate forward flapping flight. In the Late Carboniferous, almost all of them had already become secondarily fused to the prothoracic tergum and mimicked the “tergal lateral lobes”, with which they are often confused (figure 87). Nevertheless, especially in some †Rostropaleoptera, prothoracic winglets remained plesiomorphic, articulated and supported by branched veins, and they are sometimes found as fossils *detached from the bodies.*

To my surprise, *after many years of a comparative morphological study (JKP 2008, figure 15) it turned out that the veinal support of prothoracic winglets agrees with the pterygote protowing veinal groundplan.* This *exceptional direct evidence of an independently reconstructed groundplan of an ancient organ offers real confirmation that comparative morphology*, used for many years mainly in vertebrate paleontology, *really works.*

Origin of pterygote aerial flight and the wing key characters defining the higher taxa

Powered insect flight is highly complex. It requires a large wing surface, the tips of which follow a movement pattern of a horizontal number eight (lemniscate, see below). This movement causes aerodynamic stress in several wing areas, which require additional mechanical support of the wing veinal system, achieved by adding veinal fusions, sclerotizations, inter-veinal struts, bridges, etc. The main stressed areas requiring support include 1) the anterior wing margin, 2) a long horizontal wing axis, 3) the wing base, with thickened and fused veins, 4) the narrow “belt” of struts and/or fusions, surrounding the wing base at some distance distally, 5) in Neoptera, an arrangement of anal veins supporting the anal area in the hind wing, etc. (see many examples in the figures of the orders).

*While aerodynamic stress of aerial flapping wings using lemniscates occurs in similar wing locations dictated by physical conditions, the pre-flight Pterygota evolving in different habitats had these locations occupied by the more or less differently arranged veins. As a result, the **pterygote higher taxa differ from each other by the “before aerial flight” changes in the wing system (happening during the increasing size and flapping power of wings), which were connected by fusions, struts and sclerotization in aerodynamically functional places to enable aerial flight. These combined veinal differences are the key characters of the higher taxa showing relationship and differences, which mirror the phylogenetic tree.***

Hence, **fully aerial flapping flight is expected to have originated in each higher taxon only after the aerodynamic supporting structures were established between differently conditioned veins.** This process was independent, happening in parallel, and probably also at different adaptive rates. For these reasons, the **origin of flight could not have been a single event.** Undoubtedly, it happened **several times, in parallel, and with different rates of change.** The key characters distinguishing the taxonomic relationships are a combination of the pre-flight veinal system adapted for forward flapping, and aerodynamic supports added in predictable places, but using the locally available veins to enable aerial flight in all higher taxa, at different times, and probably **long ago before the documented existence of Pterygota in the middle Carboniferous.** In another words, pterygote sclerites, veins and the veinal system **are monophyletic, but aerial flight is not.** It originated in different higher lineages separately, and probably at very different times.

Probable origin of aerial flight by using thoracic epicoxal exites as hop-assisted winglets

According to the presently available evidence, there is: **1) no doubt** that before insect wings became sufficiently large and equipped with an articulation adapted for true aerial flight, they were **small, imperfect** in flapping, and thus physically unable to produce aerial lemniscates. **2) It is also certain** that the lemniscates can be produced only by **leg muscles** attached to sclerites, **needing evolutionary time** to be distributed and accommodated for particular patterns of wing movement. **3) During this entire adaptive process, the mobilized epicoxal winglets must never stop to aid survival,** or they would stop evolving.

In the Cambrian, Ordovician and Silurian there were no trees for hexapods or proto-insects to climb on, just low vegetation growing out of or close to water and inhabited by predaceous arthropods

(chelicerates). The proto-ptyergotes bore on their thorax six long, 11- segmented, Z-shaped legs with mobile exites between the upper leg segments, and a flexible tarsus with double claws securing a grip. They lifted the body up for moving over uneven surfaces, and provided nimble climbing on vegetation. Many fossil and extant terrestrial Crustacea, Hexapoda, and Insecta hop away from predators. There are two kinds of hops: a vertical hopping and a forward hopping, which add an unexpected aspect to the origin of insect flight.

In Crustacea and Hexapoda (Monocondylia + Dicondylia): **Monocondylia** = (Diplura + Archaeognatha) and **Dicondylia** = (†Cercopoda + (Zygentoma (silverfish) + Pterygota)), hopping is still rather frequent. The ancestral rope muscles causing by their contractions vertical jumping/swimming to escape predators are present in aquatic and terrestrial Crustacea (Amphipoda, land hoppers), in wingless Archaeognatha, and in the early Dicondylia †Cercopoda (related to Pterygota as below). Protowings very probably initially functioned in concert with vertical jumping and possibly promoted their existence by lengthening jumps, allowing the individual insect to be swept away by wind, and controlling landing. Precisely how it did, and what effect such flapping may have been (if any), must be tested experimentally. If the oldest protowings with the smallest protowing exites had abdominal rope muscles, they would be able to jump above the dense and low- growing vegetation. With the help of growing protowings and perhaps also extended legs, they possibly were eventually able to direct their jumps away from predators, toward open water to skim away, or to take advantage of any wind. Later on, the rope muscles diminished, but jumping activity possibly prepared the muscular apparatus, wing articulation and wings themselves to enhance and improve their activity and move closer to the powered flapping flights (see Marden 1995, 2003). Tests are wanting.

Four clades of fossil and modern wingless insects also escape by jumping. In pterygotes, jumping is most common in Orthoneoptera (see figure of the pterygote Phylogenetic tree), and this clade also differs most from all other Pterygota in its aerodynamic veinal supports. Jumping also occurs in some Hemineoptera and other insect groups. This broad occurrence suggests that jumping in arthropods has deep evolutionary roots.

Extinct wingless insects: the order †Cercopoda (JKP 1985, 1987, 1998, 2008). †Cercopoda is the plesiomorphic order of *dicondylous insects* related to Pterygota, in which all thoracic and abdominal epicoxae lost their exites and folded them into side-lobes. Cercopods fossilize with an arched abdomen, suggesting the presence of rope muscles, which produce vertical jumps, and escape predators by their muscle contraction, as do modern terrestrial amphipod Crustacea and the *monocondylous insects Archaeognatha* (=jumping bristletails, which Cercopoda superficially closely resemble). As a very interesting special feature, *†Cercopoda differ from other Hexapoda in bearing cercopods (the plesiomorphic condition of cerci) - a pair of bowed terminal abdominal leglets bearing two claws, oriented away from the body (unfortunately, they get often separated from the bodies)*. Cercopoda bear the following phylogenetically important key characters: 1, *broad dicondylous mandibles with two articulations*; 2, *rounded eyes*; 3, *all epicoxae folded into narrow side-lobes fused with a dividing suture to all cranial,*

thoracic and abdominal terga; 4, unusually long abdominal leglets; 5, plesiomorphic, bowed and double-clawed cercopods instead of cerci; and 6, a pterygote-like massive ovipositor with a gonangulum (figures 42-46). Hence, †Cercopoda combine the plesiomorphic ability of vertical jumping with the key characters shared with Pterygota.

The combination of key characters in †Cercopoda *suggests that Pterygota probably initially evolved from hexapod ancestors escaping from predators by “cercopodan” vertical hopping, which was assisted by a flapping motion of the enlarged mesothoracic and metathoracic epicoxal exites. Later on, protowings possibly earned their existence by prolonging jumps allowing insects to be carried on the wind and in controlling landing. Experimental tests are needed.*

The order †Cercopoda, which appears to be important for a better understanding of insect wings, is not sufficiently described. Morphological differences of wingless insect cercopods from the primarily wingless insects Archaeognatha and related extinct wingless insects (see many figures), were first noticed by accomplished evolutionary morphologist A.G. Sharov (Russian Academy of Sciences, Moscow). Unfortunately, Sharov died suddenly and the cercopod problem remained unresolved. I started accumulating material and photographs, but have not had time to bring the work to a publishable closure. Fossil †Cercopoda are rather weakly sclerotized, long abdominal legs and especially cercopods are often broken off, and heads, ovipositors and the sutures separating “paranotal lobes” may be quite indistinct. By far the best-preserved specimens are from the Permian of the Ural region of Russia, deposited in the Russian Academy of Sciences, Moscow, Russia. The originals probably have to be studied there, because of their rarity. Fossils from Mazon Creek, Illinois, in the Field Museum, Chicago, U.S.A. are often covered by a thin film, which has to be carefully removed. They are visually very appealing (figures 43, 45), and many Mazon Creek specimens that I studied in private collections have been sold to collectors of fossils in Japan. My material from Obora (Moravia) includes an open head, which clearly shows a *mandible with two articulation condyles, placing them in Dicondylia*. The greatest number of †Cercopoda fossils were found in Carrizo Arroyo, New Mexico, U.S.A., but they are preserved in coarse sediment and details are quite obscured. My photographs and figures will be deposited in the Canadian Museum of Nature, Ottawa, Canada. Hopefully, additional specimens will be found in the future, because the order deserves to be studied with special care. The order †Cercopoda was shortly discussed by JKP (1985, 2008) and a fine specimen (showing plesiomorphic cerci and large, composite female genitalia) (figures 42, 44) is deposited in the Royal Ontario Museum, Toronto.

Veinal key characters of the protowing in Paleoptera and Neoptera

The following are the veinal supports in the plesiomorphic protowing, promoting a flapping motion before fully achieving aerial flight:

1) Pterygote fore wing and hind wing share identical veinal systems of 8 veins composed of two corrugated veinal sectors. *PCA+* & *PCP-* & *CA+* are unbranched and adjacent to support the anterior wing margin. *CP-* is free and branched.

2) All remaining veins start from their basivenale (B) as two separate, corrugated veinal sectors: *ScA+*, *ScP-*; *RA+*, *RP-*; *MA+*, *MP-*; *CuA+*, *CuP-*; *AA+*, *AP-*; *JA+*, *JP-* (see many figures).

3) Wing articular sclerites are arranged in 3 columns and 8 rows, and the wings are able to fold backward along the abdomen.

Paleoptera wings: their main aerodynamic veinal key characters:

Paleoptera is composed of two lineages: †Rostropaleoptera + Hydropaleoptera

1) Fore wings and hind wings share very similar veinal systems (a plesiomorphy).

2) In Hydropaleoptera, *RA+* and *RP-* are either basally separate or adjacent (not fused into a single radial stem) (see many figures) (a plesiomorphy).

3) Stem of R (radial stem, *RA+* & *RP-* fused) was probably present in †Rostropaleoptera (an apomorphy).

4) Stem of M (medial stem) is present (see many figures) (an apomorphy).

5) Stem of Cu (cubital stem) is present (see many figures) (an apomorphy).

(6) Wing articular sclerites are arranged in 3 columns and 8 rows as in the protowing (a plesiomorphy), but wings retained the ability to fold backward only in †Diaphanopteroidea of †Rostropaleoptera (a plesiomorphy).

(7) Linear arrangement of sclerites and veins triggered, **twice independently**, fusions between part of the wing base and some articular sclerites, by which the wings became permanently stretched out and ready to glide without using an energy-wasting muscular pull, yet it prevented the wings from folding backwards. In all “gliding-ready” orders of the lineage †Rostropaleoptera the wing base and sclerites formed a **single posterior articular plate** (figure 69) (an apomorphy). All orders of the lineage **Hydropaleoptera** share **two plates**: four *anterior sclerites form the anterior plate*, and the *wing base plus several posterior sclerites*, the **posterior plate** (figure 69) (an apomorphy).

Neoptera wings: their main aerodynamic veinal key characters:

Lineages: (Orthoneoptera + (Pleconeoptera + (Blattoneoptera + (Hemineoptera + Endoneoptera))))

1) The fore wings have a smaller anal area than the hind wings with *AA1+2* basivenale elongated into a sclerotized **anal bar**, pushing the bases of the veins *AA3+4* and *AP* closely together. The hind wings have a larger anal area with fan-like arranged anal veins (an apomorphy).

2) The hind wings include either unreduced anal venation in Orthoneoptera and Pleconeoptera (plesiomorphy) or the *AA* portion of anal field is reduced in Blattoneoptera & Hemineoptera & Endoneoptera (a synapomorphy).

3) The stem of R is present in Neoptera, but sometimes extremely short (an apomorphy).

4) The stem of M is present in Orthoneoptera and Pleconeoptera (an apomorphy, but probably a parallelism).

- 5) MA is fused basally at length with R in Blattoneoptera & Hemineoptera & Endoneoptera (a synapomorphy).
- 6) The stem of Cu is absent only in Orthoneoptera (a plesiomorphy).
- 7) The stem of Cu is present in Pleconeoptera & Blattoneoptera & Hemineoptera & Endoneoptera (a synapomorphy).
- 8) ScA+ is shortened, weakened, and surrounded by a bulge in Blattoneoptera & Hemineoptera & Endoneoptera (a synapomorphy).

A complete insect Phylogenetic tree based on the key characters demonstrating the aerodynamic veinal supports needs to include all higher-level taxa down to orders. At present, the relationship of some orders is not certain and requires revision. The comparative morphological analysis of **the Neoptera wing articulation** has so far delivered, only the homologies of all sclerites. The relationships between the super sclerites and their function, has not been touched and, undoubtedly, documenting the relationships will present one of the most challenging morphological problems to solve in Insecta. I firmly believe that it is possible, but only with a broad and detailed knowledge of modern anatomy and applying comparative morphology.

PALEOPTERA: †Rostropaleoptera: with two superorders †Rugoptera and †Levitoptera

Lineage †Rostropaleoptera. Members of this lineage bore long, strong, pointed beaks adapted to tearing apart and imbibing hanging fructifications of primitive trees (figure 29). This extinct pterygote lineage inherited from Protowing the original wing articular sclerites, arranged in three regular columns and eight rows aligned with wing veins. In the Early Paleozoic already, the lineage divided into two (not formally established) superorders, Rugoptera and Levitoptera. Superorder Rugoptera included only a single order †*Diaphanopteroidea*, which was capable of folding the wings backward along the abdomen, by retaining articulated protowing sclerites, and pulling them together in the middle of wing articulation (figure 71). Superorder Levitoptera included about seven orders: †*Palaeodictyoptera*, †*Megaseoptera*, etc., which evolved derived fusions between six wing basivenalia (B), six sclerites fulcalaria (F) and six sclerites axalaria (AX) into a large *posterior articular plate*, which put the wings into a *permanently spread-out gliding position*, avoiding an (otherwise necessary) energy-using muscular pull. Nevertheless, the wings lost the ability to fold backwards (an aid in hiding from predators). Hence, extinct †*Diaphanopteroidea* as the only known pterygote order which retained the pterygote groundplan protowing articulation capable of folding the wings backward is very important for understanding the evolution of insect wings.

Lineage †Rostropaleoptera subdivides into two superorders, Rugoptera and Levitoptera:

The newly proposed superorder †Rugoptera from *ruga* (Lat.) = *fold* (for wings folding backwards along the abdomen), includes only one Late Paleozoic order, the †Diaphanopteroidea. This order bears a strong pointed beak composed of long mandibular and maxillary endites connected by short spines, and resting in a foldable labial trough (as in all other Rostropaleoptera) (figures 29, 30). Yet, the wing articulation differs by *having all sclerites articulated, and none fused with the veinal bases (B), or into an articular plate*. Hence, the wings are capable of being folded backward along the abdomen, as in the protowing. †Diaphanopteroidea had a somewhat shortened ScP; stem of R, stem of M and stem of Cu present; MA and CuA unbranched. In plesiomorphic members, veinal systems MA is connected with RP close to its beginning by a strut, CuA with the stem of M is also connected by a strut, and the anal area is large with branched AA and AP. Derived wings have short to long fusions of MA to R and RP, and of CuA and the stem of M (see figures).

†Diaphanopteroidea are the most plesiomorphic pterygote order, the only one bearing the protowing type of wing sclerites articulated in rows, and thus having foldable wings. Note that the order also retained some other interesting plesiomorphies. The nymphs and some adults bear *plesiomorphic abdominal leglets* (= the proof that pterygote legs are *serially present and homologous on all body segments* (figure 53). Their fore and hind wings have similar venation (a plesiomorphy of Paleoptera), but *veinal corrugation and aerodynamic supports for stressed locations are similar to those in Neoptera* (which share the same physical function). They *fold their wings and glide by using the muscular pull as in Neoptera*. Diaphanopteroidea with larger sized bodies, strong beaks and presence of wings folding into a roof-like position over the abdomen, occurred mostly in the Carboniferous. Smaller bodies, presence of shorter and thin beaks, and wings flatly superimposed on the abdomen were largely prevalent in the Permian (figure 29). Apparently, some families became adapted to drier environments, since they are abundant in the fossils of the paleo-graben of Obora, Moravia with a drought-tolerant fossil flora in the uplands. †Diaphanopteroidea may have been the last order of †Rostropaleoptera to go extinct.

The newly proposed superorder †Levitoptera, (from levitas (Lat.) = *lightness in movement* (for wings fixed in a muscle-less gliding position), includes about seven Paleozoic extinct orders (†Palaeodictyoptera, †Megasecoptera, etc.) sharing fusions between 6 veinal bases (B), 6 fulcal sclerites (F), and axalaria (AX) into a *single posterior articular plate* (figure 69-72).

Extinction of the lineage †Rostropaleoptera. This is the only lineage of Pterygota which became extinct, very probably mainly because of their bearing permanently spread-out wings combined with their feeding habits. In Paleozoic skies without *aerial predators*, soaring to locate food and mates without losing any energy was an immense advantage. Gliding Paleoptera thrived and, also due to increased atmospheric oxygen, several of their orders (Palaeodictyoptera, Megasecoptera, Odonoptera, Ephemeroptera) reached gigantic wingspans. However, for future life conditions, the neopteran improvement of wings folding over the abdomen brought a definitely more successful route in evolution. Why did the enormously successful

†Rostropaleoptera, *alone*, succumb to extinction without any living descendants? Probably mainly for two reasons: 1) the permanently spread-out large wings made them vulnerable to the newly evolved aerial and other predators, especially while feeding, and 2) their long strong beaks (rostra) were highly specialized for tearing apart and imbibing fructifications of the primitive Paleozoic plants, which also became extinct.

Nymphs of †Rostropaleoptera. In the Late Carboniferous, †Rostropaleoptera included terrestrial nymphs bearing a long, stiff rostrum (beak) as in adults, and fully mobile winglets articulated to the terga. Abdominal articulated epicoxal exites were lost, but abdominal leglets were sometimes retained, especially in †Diaphanopteroidea. Since †Rostropaleoptera nymphs were seriously exposed to predation during feeding by their long rostra (figure 62) many of them developed protective devices. Some Palaeodictyoptera nymphs looked like arboreal trilobites, as they were very broad, flattened, covered by large sclerotized outgrowths, and thus probably adapted to clinging to surfaces (figure 61) so as not to be snatched away by marauding dragonflies. Slender †Megasecoptera nymphs were camouflaged with dense, spiny, long and branched cuticular projections (figure 61), which also occur in some plesiomorphic, wing-folding †Diaphanopteroidea (figure 62). Professor Carpenter and I had wondered how these projections were reformed during ecdyses. In the huge Lower Permian graben-canyon to become the fossil site of Obora in Moravia, drier on its sides and wetter on its bottom, I found a large quantity of small wing-flexing †Diaphanopteroidea but only one giant dragonfly, and the “tropical” large †Palaeodictyoptera and †Megasecoptera were also very rare.

Lineage Hydropaleoptera: superorders Ephemeroptera and Odonoptera

This clade of Paleoptera evolved, very early, the secondarily aquatic nymphs that needed gills. *In Ephemeroptera (mayflies) these present-day nymphs offer the unique hard evidence that the insect thoracic flattened epicoxa embracing the articulated mobile wing exite are also present, in the same place between the tergum and subcoxa, on the abdomen. The “not so big” evolutionary difference is that over there, the serially homologous flattened epicoxae are folded into the epicoxal side lobes (=“paranotal lobes”) embracing the articulated mobile “gill” exites.*

Juvenile mayflies, figures 55-58) and juvenile dragonflies, both with plesiomorphic abdominal leglets (figure 59, bottom), have quite astonishingly survived little changed from the Lower Paleozoic until Recent times (see many figures). All Hydropaleoptera also evolved very early the derived fusions between fulcalaria (F) and the wing base (B), securing the permanent secondary gliding position of the wings, as in †Rostropaleoptera: superorder Levitoptera). However, *instead of only one plate, Hydropaleoptera acquired two, the anterior plate and the posterior one (see figures).* The energy saving *posterior articular plate included, in Ephemeroptera*, six basivenalia (B) fused with six fulcalaria (F), and *in Odonoptera*, six basivenalia (B) fused with six fulcalaria (F) and six axalaria (AX) (figures 69-72). The *anterior articular plate serving to improve flapping flight* was composed *in mayflies of the precosto-costal axalaria (AX) and fulcalaria (F), and in Odonoptera, of the same AX & F fused into a large anterior plate, which was ventrally joined by the basalare sclerite (placed under the wing).* Two plates of sclerites

allowed not only effortless gliding, but also positioning of the wing at rest above and along the body, which made resting dragonflies less conspicuous to predators.

Ephemeroptera wings. Mayflies have the following **seven wing key characters**: very strong recurrent ScA+, short and slightly bowed in Carboniferous wings, becomes much longer and strongly bowed in modern mayflies; RA+ and RP ± basally close to each other or adjacent (*not fused into a single stem*); stem of M- present; MA+ connected by struts or short fusion with RP-; stem of Cu- present; CuA+ connected by struts or short fusion to M-; AA1+2 + joined to CuP- by a prong (see many figures).

The largest and oldest known Carboniferous mayfly *Bojophlebia prokopi* (figures 93-98) from the Czech Republic **shares all of the seven aerodynamic veinal key characters with modern mayflies** (figures 56-58), but most of the fossil inter-veinal struts are replaced by short inter-veinal fusions. The typical short and very strong ScA+ is best visible in the hind wing.

Odonoptera wings. Modern dragonflies (and all extinct sister orders) share with mayflies the following similar aerodynamic key characters: recurrent ScA+ is present but straight and not particularly thick; RA+ and RP ± veins are basally broadly separate to adjacent, but *not fused into a single stem*; stem of M- present (near CuA base, originally connected or shortly fused only with CuA, but later fused also with Cu stem and with CuA; MA+ connected by struts or a short fusion with RP- (near RP- diversion from RA); CuA+ near its base connected by struts or short fusion to M-; CuP bears a kink connected with AA1+2 by a prong, and with CuA, connected by a strut.

Wings of the lineage Hydropaleoptera (mayflies and dragonflies) **share seven similar aerodynamic veinal key characters enabling aerial flight, documented as always present from Carboniferous to Recent times, and unique for the lineage Hydropaleoptera.** They are an example of **key characters, which define the related higher taxa.** The oldest *Odonoptera* (figures 87-91) **bear the same seven synapomorphic wing vein key characters shared with Ephemeroptera, which are also already present in the oldest Carboniferous mayfly, the gigantic Bojophlebia prokopi** (figures 93-98).

Bojophlebia prokopi (fig. 93), the oldest gigantic mayfly, and the primitive six-winged Geroptera dragonflies (see title page or figure 87) **bore triangular hind wings like most of the other oldest Paleoptera.** *Because of them and damaged recurrent ScA+ in the fore wing (but present, small and typical in the hind wing), some entomologists excluded Bojophlebia from the lineage Hydropaleoptera, all seven related veinal key characters shared with Odonoptera notwithstanding.* **A systematist working with the order-level and higher taxa must absolutely avoid working with the characters and kinds of evaluations, which are appropriately used in the lower taxa.**

Survival of Hydropaleoptera untill Resent time. Late Paleozoic nymphs of mayflies and dragonflies are similar in appearance to their modern descendants, except for the winglets, which became fused to the terga. They were obviously quite well accommodated to survive. But the adult mayflies and dragonflies were a different matter. Ephemeroptera adults are so incapable of any defense that they practice the mass-emersion overwhelming predators, followed by mass copulation and mass laying of eggs, which works very well for millions of years.

While venation of the Paleozoic dragonflies is not at all difficult to derive from the all-apterygote Protowing model (figure 90), the wing venation of extant dragonflies is so changed by various added fusions and reductions that it was fully homologized as late as in 1984 (by E. F. Riek and JKP, figure 90). The reason for these most drastic and impenetrable changes in the veinal system known in the pterygote clades was odonate switching to the acrobatic flight, enabled by fusion of the anterior articular plate (= precostal + costal axalare + fulcalare) with the ventral muscled sclerite basalare, which helped the Hydropaleoptera with life endangering permanently stretched out wings, to survive.

Hydropaleoptera nymphs. In all Paleozoic Paleoptera bearing derived outstretched wings (with 6 fulcalaria (F) and 6 basivenalia (B) fused together), the youngest nymphs bear winglets strongly bowed backwards, which gradually straightened up and extended with each ecdysis, until they reached the fully laterally outstretched adult position. A metamorphic instar was non-existent and was replaced by several subadult instars with long, mildly bent and gradually straightening wings (figures 59-62). In Dr. Carpenter's Permian insect locality at Elmo, Kansas, U.S.A., the limestone was in places literally filled with densely packed winglets of Permian mayfly nymphs, separated from their terga and floated away to accumulate as the massed fossils.

Other occurrences of exites. Late Paleozoic Pterygota sometimes still retained membranous exites on their upper leg segments and genitalia (figures 34, 36, 37), and the fossil and modern wingless insects Archaeognatha still bear the leg exites on their head palps and on the coxae of their thoracic legs (figure 39).

Gigantism in Paleozoic Paleoptera

Geochemical evidence suggests an increase in atmospheric oxygen levels during the Upper Paleozoic. This gave animals an opportunity for increasing their rates of metabolism. In the Carboniferous and Permian, oxygen levels gradually rose to roughly 18 percent of atmospheric composition some 380 million years ago, to 25 percent about 350 million years ago, and to a remarkable 30 to 35 percent some 300 million years ago (Berner, 1999; Hazen, 2012). The enhanced oxygen levels were produced by oxygen-producing photosynthesis in the increasingly abundant and luxuriant terrestrial vegetation, and by carbon dioxide being removed from the atmosphere and trapped in living and buried organic matter. The supposedly denser atmosphere would have given some aerodynamic support and made flying metabolically easier, especially for some of the larger Paleoptera bearing two pairs of massive, long and broad wings. These became adapted for energy-saving soaring flight without using a muscular pull, which was necessary for gliding in Neoptera and in the wing-flexing plesiomorphic Paleoptera order †Diaphanopteroidea. Effortless gliding, together with an atmosphere enriched in oxygen enabled insect gigantism (Dudley, 1998), especially in many †Rostropaleoptera (orders †Palaeodictyoptera, †Megasecoptera, etc.) and in some Hydropaleoptera (Odonoptera and Ephemeroptera). Dragonflies became the first animal aerial predators, and the largest known species reached a full 73 centimeters in wingspan. The largest known Carboniferous mayfly *Bojophlebia* had a wingspan of 45 centimeters.

Fore and hind wing differences in Paleoptera and Neoptera

Paleoptera have the Protowing sclerites arranged in the original three columns and eight rows. Neoptera have them grouped into super-sclerites enabling a faster and firmer folding and unfolding of the wings, which served mainly for better protection and faster escape (figures 69-72).

The two basal clade pterygotes, Paleoptera and Neoptera, bear very important *key differences* not only in the arrangements of the wing sclerites (see above), but also in the construction of their fore- and hind wing veinal systems. *In Paleoptera, both wing pairs bear a similarly branched venation*, and the oldest known hind wings were originally broader and shorter than the descendent ones. But *in Neoptera, the forewings and hind wings bear very dissimilar anal fields, supported by a very differently organized anal venation*, as follows. In forewings, the **basivenale of the vein AAI+2 is posteriorly elongated into a strong anal bar**, which pushes the small basivenale AA3+4 close to the basivenale AP (see various Neoptera wing and axillary figures). Basivenale B-AA3+4 and basivenale B-AP are either close but separate, or touching each another, or fused together (see various Neoptera wings and axillary figures). In neopteran hind wings, the anal field is enlarged and includes two kinds of veinal support: in Orthoneoptera and Pleconeoptera, it contains *two plesiomorphic fully branched veinal sectors*, AA (AA1+2 and AA3+4), and AP (AP1+2 and AP3+4); in Blattoneoptera & Hemineoptera & Endoneoptera, sector AA is partially or completely reduced (AA1+2 and AA3+4 are either very weak or absent) (see figures for these groups). *Shared key characters including the disappearance of the AA field in the hind wings, and shared aerodynamic veinal fusions of the wing base (see below)*, show that the **lineage Blattoneoptera is the sister group of the lineages Hemineoptera + Endoneoptera (see figures for these groups)**. Hence, taxon “Polyneoptera” including Orthoneoptera, Pleconeoptera, Blattoneoptera, sharing similar metamorphosis, which occurred much later, separately, at different times, and in parallel does not exist.

Veinal key characters of Neoptera lineages

Lineage Orthoneoptera (Orthoptera and related orders): CP- of medium length present, branched (plesiomorphy); ScA+ long and with long, rich branched (plesiomorphy, unique); stem of R present (apomorphy); stem of M present (apomorphy); stem of Cu absent (plesiomorphy); CuA+ fused at length with the stem of M and with MP (*autapomorphy, unique for Neoptera*); CuP richly branched (plesiomorphy, *unique for Neoptera*); hind wing with a full ano-jugal lobe (plesiomorphy).

Among Neoptera, the lineage Orthoneoptera has the most different veinal pattern from all other lineages, with a mix of the *most numerous (six) plesiomorphic key characters* (branched CP-, branched ScA+, branched CuP, absence of Cu veinal stem, presence of primitive roof-like wing flexing, and a full (unreduced) hind wing anal lobe), combined with *very unusual and highly derived inter-veinal fusion, CuA fused at length with the stem of M and with MP* (see various Neoptera wings for comparison). Some Orthopteroids use hopping combined with wing flapping to escape predators, as probably did ancestral pterygotes, but they do not use abdominal rope muscles for vertical jumping, as very probably did the early

Dicondylia (Cercopoda). Perhaps, they instead used the combination of the help of flapping protowings, extended legs, and originally also abdominal leglets (before they became reduced). It is possible that they were able to jump like that at length across the dense, low growing vegetation, and direct their jumps away from predators. Morphologically, their very strange mix of veinal key characters identifies them as the sister group of the rest of Neoptera. More research should be used. Until now, Orthoneoptera have been usually considered as a sister group to Blattoneoptera, within the grouping “**Polyneoptera**”, but this relationship is morphologically **quite impossible**. The two groups have *different aerodynamic characters enabling aerial flight, different veinal support of their anal lobes, and completely dissimilar fused veinal sectors supporting the long wing axis. Note also differences in the wing articulation.* In a morphological pterygote phylogeny based on wings, the *clade Polyneoptera does not have any justifiable foundation*.

Lineage Pleconeoptera (Plecoptera and related orders): CP- is fused to the anterior margin (an apomorphy); ScA+ reduced (an apomorphy); three fused veinal stems present: radial (R), medial (M), cubital (Cu) (three apomorphies); RP shortly fused near its base with the stem of M (an apomorphy); hind wing bears the full ano-jugal lobe (a plesiomorphy), but with some differences in anal folds. Wing articulation includes *uniquely positioned cubital and ano-jugal fulcalaria (an autapomorphy)* (see Plecoptera figures).

Presence of the radial stem and the cubital stem in the forewing relegates Pleconeoptera closer to the clade Blattoneoptera & Hemineoptera & Endoneoptera, while the very different (plesiomorphic) *full ano-jugal lobe* makes them their possible sister group. Even when unreduced and thus plesiomorphic, Pleconeoptera lobe is not as regularly arranged as in Orthoneoptera. Plecoptera bear **unusual and strongly autapomorphic cubital and ano-jugal fulcalaria**, which influence the anal fan.

Lineage Blattoneoptera (Blattodea and related orders): CP- is fused to the anterior margin (an apomorphy); ScA+ is transformed into a sclerotized blunt ridge (related to the ScA bulge in Endoneoptera, and to a small ScA bulge in Hemineoptera); stem of R present (an apomorphy); *stem of M absent* (a plesiomorphy); *MA basally fused at length to R* (an apomorphy); MA diverging from RP as its first branch (an apomorphy); stem of Cu present (an apomorphy); mp-cua strut (arculus) *sometimes* present (always present in Hemineoptera & Endoneoptera). Hind wing: AA field diminished and joining remigium (an apomorphy), ano-jugal lobe reduced, **starting at the (second) anal fold** (a synapomorphy), instead of at the first cubital fold, like in the two plesiomorphic ano-jugal lobes in Orthoneoptera and Pleconeoptera) (see Blattodea figures).

Shared presence of the *stem of R (a synapomorphy)*, *MA fused basally at length with the stem of R and sometimes diverging from RP (a synapomorphy)*, *stem of M absent and replaced by MP*, *stem of Cu present (a synapomorphy)*, and in the hind wing, the **anal lobe reduced and starting at the (second) anal fold** (a synapomorphy), are all the important key characters which make *Blattoneoptera the sister group of Hemineoptera & Endoneoptera* (see figures for these groups).

Lineage Hemineoptera (Hemiptera and related orders): CP- long, branched (a plesiomorphy), sometimes greatly elongated; ScA+ reduced to small bulge (an apomorphy); ScP- runs basally adjacent to R or is *submerged under R* (an autapomorphy); stem of R present (an apomorphy); *stem of M absent* and replaced by MP (a plesiomorphy); MA+ *basally fused at length to R* (an apomorphy); MA diverging originally from R and later from RP (an apomorphy); stem of Cu present, short (an apomorphy); mp-cua strut or short fusion (arculus) always present (an apomorphy). The hind wing has a reduced ano-jugal lobe, which is starting at the (second) anal fold (an apomorphy) (see various Hemiptera figures).

The shared presence of the ScA bulge (a synapomorphy), stem of R (a synapomorphy), absence of the stem of M (a symplesiomorphy), MA+ *basally fused at length to R* (a synapomorphy), short stem of Cu present (an apomorphy), *arculus* present (a synapomorphy), and *hind wing anal lobe starting at the (second) anal fold* (a synapomorphy), post-anal fold crossed near base by AP vein (an autapomorphy) indicate the sister group relationship to Endoneoptera and the relationship to Blattoneoptera (see various figures).

Lineage Endoneoptera (the endopterygote orders): CP- recurrent to ScP- as a prominent concave “vena dividens” framing the ScA+ bulge (an autapomorphy); ScA+ expressed as a blunt bulge (a synapomorphy); ScP- ending before reaching the wing tip (an apomorphy); stem of R present (a synapomorphy); stem of M absent (a plesiomorphy) replaced by MP; MA+ *fused basally at length to R* (a synapomorphy); MA+ diverging either from R or from RP as its first branch (a synapomorphy); short stem of Cu present (an apomorphy); mp-cua strut/short fusion (arculus) present (an apomorphy); hind wing with reduced ano-jugal lobe starting at (second) anal fold (a synapomorphy) (see figures for various orders).

Shared presence of the ScA bulge and the stem of R, absence of the stem of M, MA+ *basally fused at length to R*, short stem of Cu and *arculus* present, and *hind wing anal lobe starting at the second anal fold*, all indicate the sister group relationship to Hemineoptera and the relationship to Blattoneoptera. Diversification of Endoneoptera orders has been discussed for many decades and, it seems now near a well-documented solution. Homologization of the wing articulation and anal lobes in fore- and hind wings are bound to bring new characters supporting a trustworthier phylogenetic scheme.

The survival “strategy” of Neoptera

The clade Neoptera followed a completely different and improved survival path from that in the Paleoptera, by evolving a faster and firmer folding of the wings backward along the abdomen, achieving better hiding from predators in narrow spaces. In the protowing the regular rows and columns of articular sclerites were mostly separated and the sclerites were grouped into large, irregular axillary super-sclerites (1Ax, 2Ax, 3Ax), tegula, humeral and medial plate, and the anterior and posterior wing process (figures 67-72). The highly derived wing flexing in today’s Neoptera is produced by the super-sclerite 3Ax, which is rotating and diving into the wing membrane pocket, thus anchoring the wings in a flexed position.

Unfortunately, the fossil neopteran articulation is unknown, because the wings in all fossils are more or less folded and thus obscuring the wing articulation. The recognition of the original individual sclerites presented here is nevertheless *based on hard evidence*, because in many modern super-sclerites, the composing sclerites are clearly delimited by strong sutures. In Neoptera, one super-sclerite, *the humeral plate*, contains fusions of four sclerites: *two precostal and costal fulcalaria* and *two precostal and costal basivenalia* (PC-F & PC-B & C-F & C-B). The fusion of fulcalaria (F) and basivenalia (B) in the humeral plate supporting base of the anterior wing margin, is very interesting and probably serves a special purpose. However, it does not affect the ability of the wings to fold backward along the abdomen. The four sclerites of the humeral plate are either completely separate but close one to another, or fused but separated by dividing sutures, or fused and the sutures are reduced (figures 67-72 and explanations).

When attacked, neopteran insects very often flex their wings closed, fall down and hide among narrowly spaced ground debris (a very efficient vanishing act exercised especially by beetles). Neopteran improvements of wing folding for hiding, running and easy feeding, provided over time a much more efficient pathway to survival than did the Paleopteran endless energy-saving gliding for food and mates.

Final words

For almost two centuries, the existence of insect wings and their aerial flight was explained mostly by “informed” speculations, often based on generally known phenomena. One was that aerial flight was derived from gliding, because gliding was much simpler than flapping, and much more commonly distributed throughout animal groups in Nature. The second was that insect wings evolved from the laterally stretched tergal lobes, since most gliders quite clearly used for gliding an extended lateral part of their bodies. The third was that wings surely follow the now outdated rule “ontogeny recapitulates phylogeny”. All modern nymphs have their winglets very distinctly a part of the terga, hence, insect wings evolved either completely, or at least partially, from the insect terga, etc., etc.

Close to the comparative morphological interpretation of insect wing origin as given here came Sir Vincent Wigglesworth’s proposition that insect wings evolved from the coxal exites of the arthropod leg. Nevertheless, his opponents rightfully argued that exites never move up and through the leg segments to the top of the leg (correct), and that Pterygota do not bear any exites (which was wrong: Paleozoic Pterygota bore up to five upper leg exites, short, annulated, and very thinly membranous. They are very indistinctly preserved in fossils or not preservable, and were for long absolutely overlooked (now they are sometimes recognized after removing mineral film, which covers some of the beautifully preserved Carboniferous Mazon Creek concretions). However, the modern wingless insects Archaeognatha wear the upper leg exites, on their mouthparts and on leg coxae. Even better, modern mayfly nymphs have on their abdomens the previously unidentified “paranotal lobes” bearing embayed, articulated, flapping “plate gills” (previously also unidentified), which are located between the tergum and the subcoxal pleuron, just like the thoracic wings. These two organs are now recognized as serially symmetrical, and derived from the first

arthropod leg segment epicoxa of its exite. Hence, insect wing blade is homologous with the membranous part of the mayfly abdominal plate gill.

In the case of insect wings, comparative morphology uses the broadest possible study of the plesiomorphies present in living and fossil pterygotes, hexapods, and arthropods, combined with the Hennigian phylogenetic approach, to reconstruct the missing evolutionary data. This contribution presents some practical examples of this approach: copious informative plesiomorphies, which bring out both missing and “left out” information, such as the absolutely improbable and non-suspected fact that arthropod legs were missing the first leg segment, an **epicoxa bearing an exite**. Suddenly, many unsolvable questions found possible answers, as follows. The insect wing articulation is derived from the flattened epicoxa and exite base, which fragmented around muscle insertions into articular sclerites, and the wing blade, from the muscle-less, membranous and flattened part of the epicoxal exite, supported by sclerotized and branched hemolymph veins.

What is essentially needed at the present state of phylogenetic progress is the reliable insect morphological phylogenetic tree based on **diversification of the key characters identifying the higher taxa**. We need to understand better the evolutionary process, which is morphological as well as molecular, and one part cannot succeed in having a steady progress without the other.

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