Insect wing

Insect wings are adult outgrowths of the insect exoskeleton that enable insects to fly . They are found on the second and third thoracic segments (the mesothorax and metathorax) , and the two pairs are often referred to as the forewings and hindwings , respectively , though a few insects lack hindwings , even rudiments . The wings are strengthened by a number of longitudinal veins , which often have cross @-@ connections that form closed " cells " in the membrane (extreme examples include Odonata and Neuroptera) . The patterns resulting from the fusion and cross @-@ connection of the wing veins are often diagnostic for different evolutionary lineages and can be used for identification to the family or even genus level in many orders of insects .

The physical dynamics of flight are composed of direct and indirect flight . Those species that employ direct flight have wing muscles directly attached to the wing base , so that a small downward movement of the wing base lifts the wing itself upward . However , insects with indirect flight have muscles that attach to the thorax and deform it ; since the wings are extensions of the thoracic exoskeleton , the deformations of the thorax cause the wings to move as well .

The wings may be present in only one sex (often the male) in some groups such as velvet ants and Strepsiptera , or selectively lost in " workers " of social insects such as ants and termites . Rarely , the female is winged but the male not , as in fig wasps . In some cases , wings are produced only at particular times in the life cycle , such as in the dispersal phase of aphids . Beyond the mere presence / absence of wings , the structure and colouration will often vary with morphs , such as in the aphids , migratory phases of locusts and in polymorphic butterflies .

At rest , the wings may be held flat , or folded a number of times along specific patterns ; most typically , it is the hindwings which are folded , but in a very few groups such as vespid wasps , it is the forewings . How and why insect wings evolved is not well understood . Three main theories on the origins of insect flight are that wings developed from paranotal lobes , extensions of the thoracic terga ; that they are modifications of movable abdominal gills as found on aquatic naiads of mayflies ; and that insect wings arose from the fusion of pre @-@ existing endite and exite structures each with pre @-@ existing articulation and tracheation .

Morphology

Internal

Each of the wings consists of a thin membrane supported by a system of veins . The membrane is formed by two layers of integument closely apposed , while the veins are formed where the two layers remain separate and the lower cuticle may be thicker and more heavily sclerotized . Within each of the major veins there is a nerve and a trachea , and , since the cavities of the veins are connected with the hemocoel , hemolymph can flow into the wings . Also veins are the wing 's lumen , being an extension of the hemocoel , which contains the tracheae , nerves , and hemolymph . As the wing develops , the dorsal and ventral integumental layers become closely apposed over most of their area forming the wing membrane . The remaining areas form channels , the future veins , in which the nerves and tracheae may occur . The cuticle surrounding the veins becomes thickened and more heavily sclerotized to provide strength and rigidity to the wing . Two types of hair may occur on the wings : microtrichia , which are small and irregularly scattered , and macrotrichia , which are larger , socketed , and may be restricted to veins . The scales of Lepidoptera and Trichoptera are highly modified macrotrichia .

Venation

In some very small insects , the venation may be greatly reduced . In Chalcidoidea (Chalcid wasps) , for instance , only the subcosta and part of the radius are present . Conversely , an increase in venation may occur by the branching of existing veins to produce accessory veins or by the development of additional , intercalary veins between the original ones , as in the wings of Orthoptera (grasshoppers and crickets) . Large numbers of cross @-@ veins are present in some insects , and they may form a reticulum as in the wings of Odonata (dragonflies and damselflies) and at the base of the forewings of Tettigonioidea and Acridoidea (katydids and grasshoppers respectively) .

The archedictyon is the name given to a hypothetical scheme of wing venation proposed for the very first winged insect . It is based on a combination of speculation and fossil data . Since all winged insects are believed to have evolved from a common ancestor , the archediction represents the " template " that has been modified (and streamlined) by natural selection for 200 million years . According to current dogma , the archedictyon contained 6 ? 8 longitudinal veins . These veins (and their branches) are named according to a system devised by John Comstock and George Needham ? the Comstock @-@ Needham System :

Costa (C) ? the leading edge of the wing
Subcosta (Sc) ? second longitudinal vein (behind the costa) , typically unbranched
Radius (R) ? third longitudinal vein , one to five branches reach the wing margin
Media (M) ? fourth longitudinal vein , one to four branches reach the wing margin
Cubitus (Cu) ? fifth longitudinal vein , one to three branches reach the wing margin
Anal veins (A1 , A2 , A3) ? unbranched veins behind the cubitus

The costa (C) is the leading marginal vein on most insects , although sometimes there is a small vein above the costa called the precosta , although in almost all extant insects , the precosta is fused with the costa ; The costa rarely ever branches because is at the leading edge , which is associated at its base with the humeral plate . The trachea of the costal vein is perhaps a branch of the subcostal trachea . Located after the costa is the third vein , the subcosta , which branches into two separate veins : the anterior and posterior . The base of the subcosta is associated with the distal end of the neck of the first axillary (see section below) . The fourth vein is the radius (R) , which is branched into five separate veins . The radius is generally the strongest vein of the wing . Toward the middle of the wing , it forks into a first undivided branch (R1) and a second branch , called the radial sector (Ra) , which subdivides dichotomously into four distal branches (R2 , R3 , R4 , R5) . Basally , the radius is flexibly united with the anterior end of the second axillary (2Ax) .

The fifth vein of the wing is the media . In the archetype pattern (A) , the media forks into two main branches : a media anterior (MA) , which divides into two distal branches (MA1 , MA2) , and a median sector , or media posterior (MP) , which has four terminal branches (M1 , M2 , M3 , M4) . In most modern insects the media anterior has been lost , and the usual " media " is the four @-@ branched media posterior with the common basal stem . In the Ephemerida , according to present interpretations of the wing venation , both branches of the media are retained , while in Odonata the persisting media is the primitive anterior branch . The stem of the media is often united with the radius , but when it occurs as a distinct vein its base is associated with the distal median plate (m ') or is continuously sclerotized with the latter . The cubitus , the sixth vein of the wing , is primarily two branched . The primary forking of the takes place near the base of the wing , forming the two principal branches (Cu1 , Cu2) . The anterior branch may break up into a number of secondary branches , but commonly it forks into two distal branches . The second branch of the cubitus (Cu2) in Hymenoptera , Trichoptera , and Lepidoptera was mistaken by Comstock and Needham for the first anal . Proximally the main stem of the cubitus is associated with the distal median plate (m ') of the wing base .

Postcubitus (Pcu) is the first anal of the Comstock and Needham system . The Postcubitus , however , has the status of an independent wing vein and should be recognized as such . In nymphal wings , its trachea arises between the cubital trachea and the group of vannal tracheae . In the mature wings of more generalized insect the Postcubitus is always associated proximally with the cubitus and is never intimately connected with the flexor sclerite (3Ax) of the wing base . In Neuroptera , Mecoptera , and Trichoptera the postcubitus may be more closely associated with the vannal veins , but its base is always free from the latter . The postcubitus is usually unbranched ; it is primitively two branched . The vannal veins (lV to nV) are the anal veins that are immediately associated with the third axillary , and which are directly affected by the movement of this sclerite

that brings about the flexion of the wings . In number the vannal veins vary. from 1 to 12 , according to the expansion of the vannal area of the wing . The vannal tracheae usually arise from a common tracheal stem in nymphal insects , and the veins are regarded as branches of a single anal vein . Distally the vannal veins are either simple or branched . Jugal Veins (J) of the jugal lobe of the wing is often occupied by a network of irregular veins , or it may be entirely membranous ; but sometimes it contains one or two distinct small veins , the first jugal vein , or vena arcuata , and the second jugal vein , or vena cardinalis (2J) .
C @-@ Sc cross @-@ veins ? run between the costa and subcosta
R cross @-@ veins ? run between adjacent branches of the radius
R @-@ M cross @-@ veins ? run between the radius and media
M @-@ Cu cross @-@ veins ? run between the media and cubitus
All the veins of the wing are subject to secondary forking and to union by cross @-@ veins . In some orders of insects the cross @-@ veins are so numerous that the whole venational pattern becomes a close network of branching veins and cross @-@ veins . Ordinarily , however , there is a definite number of cross @-@ veins having specific locations . The more constant cross @-@ veins are the humeral cross @-@ vein (h) between costa and subcosta , the radial cross @-@ vein (r) between R and the first fork of Rs , the sectorial cross @-@ vein (s) between the two forks of R8 , the median cross @-@ vein (m ? m) between M2 and M3 , and the mediocubital cross @-@ vein (m @-@ cu) between media and cubitus .
The veins of insect wings are characterized by a convex @-@ concave placement , such as those seen in mayflies (i.e. , concave is " down " and convex is " up ") which alternate regularly and by its triadic type of branching ; whenever a vein forks there is always an interpolated vein of the opposite position between the two branches . A concave vein will fork into two concave veins (with the interpolated vein being convex) and the regular alteration of the veins is preserved . The veins of the wing appear to fall into an undulating pattern according to whether they have a tendency to fold up or down when the wing is relaxed . The basal shafts of the veins are convex , but each vein forks distally into an anterior convex branch and a posterior concave branch . Thus the costa and subcosta are regarded as convex and concave branches of a primary first vein , Rs is the concave branch of the radius , posterior media the concave branch of the media , Cu1 and Cu2 are respectively convex and concave , while the primitive Postcubitus and the first vannal have each an anterior convex branch and a posterior concave branch . The convex or concave nature of the veins has been used as evidence in determining the identities of the persisting distal branches of the veins of modern insects , but it has not been demonstrated to be consistent for all wings .

= = = Fields = = =

Wing areas are delimited and subdivided by fold @-@ lines along which the wing can fold , and flexion @-@ lines along which the wing can flex during flight . The fundamental distinction between the flexion @-@ lines and the fold @-@ lines is often blurred , as fold @-@ lines may permit some flexibility or vice versa . Two constants that are found in nearly all insect wings are the claval (a flexion @-@ line) and jugal folds (or fold line) ; forming variable and unsatisfactory boundaries . Wing foldings can very complicated , with transverse folding occurs in the hind wings of Dermaptera and Coleoptera , and in some insects the anal area can be folded like a fan . There are about four different fields found on the insect wings :
Remigium
Anal area (vannus)
Jugal area
Axillary area
Alula
Most veins and crossveins occur in the anterior area of the remigium , which is responsible for most of the flight , powered by the thoracic muscles . The posterior portion of the remigium is sometimes called the clavus ; the two other posterior fields are the anal and jugal ares . When the vannal fold has the usual position anterior to the group of anal veins , the remigium contains the costal ,

subcostal , radial , medial , cubital , and postcubital veins . In the flexed wing the remigiumturns posteriorly on the flexible basal connection of the radius with the second axillary , and the base of the mediocubital field is folded medially on the axillary region along the plica basalis (bf) between the median plates (m , m ') of the wing base .

The vannus is bordered by the vannal fold , which typically occurs between the postcubitus and the first vannal vein . In Orthoptera it usually has this position . In the forewing of Blattidae , however , the only fold in this part of the wing lies immediately before the postcubitus . In Plecoptera the vannal fold is posterior to the postcubitus , but proximally it crosses the base of the first vannal vein . In the cicada the vannal fold lies immediately behind the first vannal vein (lV) . These small variations in the actual position of the vannal fold , however , do not affect the unity of action of the vannal veins , controlled by the flexor sclerite (3Ax) , in the flexion of the wing . In the hind wings of most Orthoptera a secondary vena dividens forms a rib in the vannal fold . The vannus is usually triangular in shape , and its veins typically spread out from the third axillary like the ribs of a fan . Some of the vannal veins may be branched , and secondary veins may alternate with the primary veins . The vannal region is usually best developed in the hind wing , in which it may be enlarged to form a sustaining surface , as in Plecoptera and Orthoptera . The great fanlike expansions of the hind wings of Acrididae are clearly the vannal regions , since their veins are all supported on the third axillary sclerites on the wing bases , though Martynov (1925) ascribes most of the fan areas in Acrididae to the jugal regions of the wings . The true jugum of the acridid wing is represented only by the small membrane (Ju) mesad of the last vannal vein . The jugum is more highly developed in some other Orthoptera , as in the Mantidae . In most of the higher insects with narrow wings the vannus becomes reduced , and the vannal fold is lost , but even in such cases the flexed wing may bend along a line between the postcubitus and the first vannal vein .

The Jugal Region , or Neala , is a region of the wing that is usually a small membranous area proximal to the base of the vannus strengthened by a few small , irregular veinlike thickenings ; but when well developed it is a distinct section of the wing and may contain one or two jugal veins . When the jugal area of the forewing is developed as a free lobe , it projects beneath the humeral angle of the hind wing and thus serves to yoke the two wings together . In the Jugatae group of Lepidoptera it bears a long finger @-@ like lobe . The jugal region was termed the neala (" new wing ") because it is evidently a secondary and recently developed part of the wing .

The axillary region is region containing the axillary sclerites has in general the form of a scalene triangle . The base of the triangle (a @-@ b) is the hinge of the wing with the body ; the apex (c) is the distal end of the third axillary sclerite ; the longer side is anterior to the apex . The point d on the anterior side of the triangle marks the articulation of the radial vein with the second axillary sclerite . The line between d and c is the plica basalis (bf) , or fold of the wing at the base of the mediocubital field .

At the posterior angle of the wing base in some Diptera there is a pair of membranous lobes (squamae , or calypteres) known as the alula . The alula is well developed in the house fly . The outer squama (c) arises from the wing base behind the third axillary sclerite (3Ax) and evidently represents the jugal lobe of other insects (A , D) ; the larger inner squama (d) arises from the posterior scutellar margin of the tergum of the wing @-@ bearing segment and forms a protective , hoodlike canopy over the halter . In the flexed wing the outer squama of the alula is turned upside down above the inner squama , the latter not being affected by the movement of the wing . In many Diptera a deep incision of the anal area of the wing membrane behind the single vannal vein sets off a proximal alar lobe distal to the outer squama of the alula .

= = = Joints = = =

The various movements of the wings , especially in insects that flex the wings horizontally over the back when at rest , demand a more complicated articular structure at the wing base than a mere hinge of the wing with the body . Each wing is attached to the body by a membranous basal area , but the articular membrane contains a number of small articular sclerites , collectively known as the pteralia . The pteralia include an anterior humeral plate at the base of the costal vein , a group of axillaries (Ax) associated with the subcostal , radial , and vannal veins , and two less definite median plates (m , m ') at the base of the mediocubital area . The axillaries are specifically developed only in the wing @-@ flexing insects , where they constitute the flexor mechanism of the wing operated by the flexor muscle arising on the pleuron . Characteristic of the wing base is also a small lobe on the anterior margin of the articular area proximal to the humeral plate , which , in the forewing of some insects , is developed into a large , flat , scale @-@ like flap , the tegula , overlapping the base of the wing . Posteriorly the articular membrane often forms an ample lobe between the wing and the body , and its margin is generally thickened and corrugated , giving the appearance of a ligament , the so @-@ called axillary cord , continuous mesally with the posterior marginal scutellar fold of the tergal plate bearing the wing .

The articular sclerites , or pteralia , of the wing base of the wing @-@ flexing insects and their relations to the body and the wing veins , shown diagrammatically , are as follows :

Humeral plates

First Axillary

Second Axillary

Third Axillary

Fourth Axillary

Median plates (m , m ')

The humeral plate is usually a small sclerite on the anterior margin of the wing base , movable and articulated with the base of the costal vein . Odonata have their humeral plate greatly enlarged , with two muscles arising from the episternum inserted into the Humeral plates and two from the edge of the epimeron inserted into the axillary plate .

The first axillary sclerite (lAx) is the anterior hinge plate of the wing base . Its anterior part is supported on the anterior notal wing process of the tergum (ANP) ; its posterior part articulates with the tergal margin . The anterior end of the sclerite is generally produced as a slender arm , the apex of which (e) is always associated with the base of the subcostal vein (Sc) , though it is not united with the latter . The body of the sclerite articulates laterally with the second axillary . The second axillary sclerite (2Ax) is more variable in form than the first axillary , but its mechanical relations are no less definite . It is obliquely hinged to the outer margin of the body of the first axillary , and the radial vein (R) is always flexibly attached to its anterior end (d) . The second axillary presents both a dorsal and a ventral sclerotization in the wing base ; its ventral surface rests upon the fulcral wing process of the pleuron . The second axillary , therefore , is the pivotal sclerite of the wing base , and it specifically manipulates the radial vein .

The third axillary sclerite (3Ax) lies in the posterior part of the articular region of the wing . Its form is highly variable and often irregular , but the third axillary is the sclerite on which is inserted the flexor muscle of the wing (D) . Mesally it articulates anteriorly (f) with the posterior end of the second axillary , and posteriorly (b) with the posterior wing process of the tergum (PNP) , or with a small fourth axillary when the latter is present . Distally the third axillary is prolonged in a process which is always associated with the bases of the group of veins in the anal region of the wing here termed the vannal veins (V) . The third axillary , therefore , is usually the posterior hinge plate of the wing base and is the active sclerite of the flexor mechanism , which directly manipulates the vannal veins . The contraction of the flexor muscle (D) revolves the third axillary on its mesal articulations (b , f) and thereby lifts its distal arm ; this movement produces the flexion of the wing . The Fourth Axillary sclerite is not a constant element of the wing base . When present it is usually a small plate intervening between the third axillary and the posterior notal wing process and is probably a detached piece of the latter .

The median plates (m , m ') are also sclerites that are not so definitely differentiated as specific plates as are the three principal axillaries , but nevertheless they are important elements of the flexor apparatus . They lie in the median area of the wing base distal to the second and third axillaries and are separated from each other by an oblique line (bf) which forms a prominent convex fold during flexion of the wing . The proximal plate (m) is usually attached to the distal arm of the third axillary and perhaps should be regarded as a part of the latter . The distal plate (m ') is less constantly present as a distinct sclerite and may be represented by a general sclerotization of the base of the mediocubital field of the wing . When the veins of this region are distinct at their bases , they are associated with the outer median plate .

= = = Muscles = = =

The muscles that control flight in insects can take up to 10 % to 30 % of the total body mass . The muscles that control flight vary with the two types of flight found in insects : indirect and direct . Insects that use first , indirect , have the muscles attach to the tergum instead of the wings , as the name suggests . As the muscles contract , the thoracic box becomes distorted , transferring the energy to the wing . There are two " bundles " of muscles , those that span parallel to the tergum , the dorsolongitudinals , and those that are attached to the tegum and extend to the sternum , the dorsoventrals . In direct muscle , the connection is directly from the pleuron (thoracic wall) to individual sclerites located at the base of the wing . The subalar and basalar muscles have ligament attachments to the subalar and basalar sclerites . Here resilin , a highly elastic material , forms the ligaments connecting flight muscles to the wing apparatus .
In more derived orders of insects , such as Diptera (flies) and Hymenoptera (wasp) , the indirect muscles occupy the greatest volume of the pterothorax and function as the primary source of power for the wingstroke . Contraction of the dorsolongitudinal muscles causes the severe arching of the notum which depresses the wing while contraction of the dorsoventral muscles causes opposite motion of notum . Other more primitive insects , such as Orthoptera (locusts) , Coleoptera (beetles) , and Odonata (dragonflies) use direct muscles that are responsible for developing the needed power for the up and down strokes .
Insect wing muscle is a strictly aerobic tissue . Per unit protein it consumes fuel and oxygen at rates taking place in a very concentrated and highly organized tissue so that the steady @-@ state rates per unit volume represent an absolute record in biology . The fuel and oxygen rich blood is carried to the muscles through diffusion occurring in large amounts , in order to maintain the high level of energy used during flight . Many wing muscles are large and may be as large as 10 mm in length and 2 mm in width . Moreover , in some Diptera the fibres are of giant dimensions . For instance , in the very active Rutilia , the cross @-@ section is 1800 µm long and more than 500 µm wide . The transport of fuel and oxygen from the surroundings to the sites of consumption and the reverse transport of carbon dioxide therefore represent a challenge to the biologist both in relation to transport in the liquid phase and in the intricate system of air tubes , i.e. in the tracheal system .

= = = Coupling , folding , and other features = = =

In many insect species , the fore and hind wing are coupled together , which improves the aerodynamic efficiency of flight . The most common coupling mechanism (e.g. , Hymenoptera and Trichoptera) is a row of small hooks on the forward margin of the hind wing , or " hamuli " , which lock onto the fore wing , keeping them held together (hamulate coupling) . In some other insect species (e.g. , Mecoptera , Lepidoptera , and some Trichoptera) the jugal lobe of the fore wing covers a portion of the hind wing (jugal coupling) , or the margins of the fore and hind wing overlap broadly (amplexiform coupling) , or the hindwing bristles , or frenulum , hook under the retaining structure or retinaculum on the forewing .
When at rest , the wings are held over the back in most insects , which may involve longitudinal folding of the wing membrane and sometimes also transverse folding . Folding may sometimes occur along the flexion lines . Though fold lines may be transverse , as in the hind wings of beetles and earwigs , they are normally radial to the base of the wing , allowing adjacent sections of a wing to be folded over or under each other . The commonest fold line is the jugal fold , situated just behind the third anal vein , although , most Neoptera have a jugal fold just behind vein 3A on the forewings . It is sometimes also present on the hindwings . Where the anal area of the hindwing is large , as in Orthoptera and Blattodea , the whole of this part may be folded under the anterior part of the wing along a vannal fold a little posterior to the claval furrow . In addition , in Orthoptera and Blattodea , the anal area is folded like a fan along the veins , the anal veins being convex , at the

crests of the folds , and the accessory veins concave . Whereas the claval furrow and jugal fold are probably homologous in different species , the vannal fold varies in position in different taxa . Folding is produced by a muscle arising on the pleuron and inserted into the third axillary sclerite in such a way that , when it contracts , the sclerite pivots about its points of articulation with the posterior notal process and the second axillary sclerite .

As a result , the distal arm of the third axillary sclerite rotates upwards and inwards , so that finally its position is completely reversed . The anal veins are articulated with this sclerite in such a way that when it moves they are carried with it and become flexed over the back of the insect . Activity of the same muscle in flight affects the power output of the wing and so it is also important in flight control . In orthopteroid insects , the elasticity of the cuticle causes the vannal area of the wing to fold along the veins . Consequently , energy is expended in unfolding this region when the wings are moved to the flight position . In general , wing extension probably results from the contraction of muscles attached to the basalar sclerite or , in some insects , to the subalar sclerite .

= = Flight = =

Two groups of relatively large insects , the Ephemeroptera (mayflies) and the Odonata (dragonflies and damselflies) have the flight muscles attached directly to their wings ; the wings can beat no faster than the rate at which nerves can send impulses to command the muscles to beat . All other living winged insects fly using a different mechanism , involving indirect flight muscles which cause the thorax to vibrate ; the wings can beat faster than the rate at which the muscles receive nerve impulses . This mechanism evolved once , and is the defining feature (synapomorphy) for the infraclass Neoptera .

There are two basic aerodynamic models of insect flight . Most insects use a method that creates a spiralling leading edge vortex . Some very small insects use the fling and clap or Weis @-@ Fogh mechanism in which the wings clap together above the insect 's body and then fling apart . As they fling open , the air gets sucked in and creates a vortex over each wing . This bound vortex then moves across the wing and , in the clap , acts as the starting vortex for the other wing . Circulation and lift are increased , at the price of wear and tear on the wings .

Many insects can hover by beating their wings rapidly , requiring sideways stabilization as well as lift .

A few insects use gliding flight , without the use of thrust . It is found in some species of arboreal ants , known as gliding ants .

= = Evolution = =

Sometime in the Carboniferous Period , some 350 million years ago , when there were only two major land masses , insects began flying . How and why insect wings developed , however , is not well understood , largely due to the scarcity of appropriate fossils from the period of their development in the Lower Carboniferous . Three main theories on the origins of insect flight are that wings developed from paranotal lobes , extensions of the thoracic terga ; that they are modifications of movable abdominal gills as found on aquatic naiads of mayflies ; or that they developed from thoracic protrusions used as radiators .

= = = Fossils = = =

Fossils from the Devonian (400 million years ago) are all wingless , but by the Carboniferous (320 million years ago) , more than 10 different genera of insects had fully functional wings . There is little preservation of transitional forms between the two periods . The earliest winged insects are from this time period (Pterygota) , including the Blattoptera , Caloneurodea , primitive stem @-@ group Ephemeropterans , Orthoptera and Palaeodictyopteroidea . Very early Blattopterans (during the Carboniferous) had a very large discoid pronotum and coriaceous forewings with a distinct CuP vein (an unbranched wing vein , lying near the claval fold and reaching the wing posterior margin) .

Even though the oldest definitive insect fossil is the Devonian Rhyniognatha hirsti , estimated at 396 ? 407 million years old , it possessed dicondylic mandibles , a feature associated with winged insects .

During the Permian , the dragonflies Odonata were the dominant aerial predator and probably dominated terrestrial insect predation as well . True Odonata appeared in the Permian and all are amphibian . Their prototypes are the oldest winged fossils , go back to the Devonian , and are different from other wings in every way . Their prototypes may have had the beginnings of many modern attributes even by late Carboniferous and it is possible that they even captured small vertebrates , for some species had a wing span of 71 cm . The earliest beetle @-@ like species during the Permian had pointed , leather like forewings with cells and pits . Hemiptera , or true bugs had appeared in the form of Arctiniscytina and Paraknightia having forewings with unusual venation , possibly diverging from Blattoptera .

A single large wing from a species of Diptera in the Triassic (10 mm instead of usual 2 ? 6 mm) was found in Australia (Mt . Crosby) .This family Tilliardipteridae , despite of the numerous ' tipuloid ' features , should be included in Psychodomorpha sensu Hennig on account of loss of the convex distal 1A reaching wing margin and formation of the anal loop .

= = = Hypotheses = = =

Paranotal hypothesis : This hypothesis suggests that the insect 's wings developed from paranotal lobes , a preadaptation found in insect fossils that is believed to have assisted stabilization while hopping or falling . In favor of this hypothesis is the tendency of most insects , when startled while climbing on branches , to escape by dropping to the ground . Such lobes would have served as parachutes and enable the insect to land more softly . The theory suggests that these lobes gradually grew larger and in a later stage developed a joint with the thorax . Even later would appear the muscles to move these crude wings . This model implies a progressive increase in the effectiveness of the wings , starting with parachuting , then gliding and finally active flight . Still , lack of substantial fossil evidence of the development of the wing joints and muscles poses a major difficulty to the theory , as does the seemingly spontaneous development of articulation and venation , and it has been largely rejected by experts in the field .

Epicoxal hypothesis : This theory suggested that a possible origin for insect wings might have been the movable abdominal gills found in many aquatic insects , such as on naiads of mayflies . According to this theory these tracheal gills , which started their way as exits of the respiratory system and over time were modified into locomotive purposes , eventually developed into wings . The tracheal gills are equipped with little winglets that perpetually vibrate and have their own tiny straight muscles .

Endite @-@ exite hypothesis : The hypothesis with perhaps the strongest evidence is that which stems from the adaptation of endites and exites , appendages on the respective inner and outer aspects of the primitive arthropod limb . This was advanced by Trueman based on a study by Goldschmidt in 1945 on Drosophila melanogaster , in which a pod variation displayed a mutation transforming normal wings to what was interpreted as a triple @-@ jointed leg arrangement with some additional appendages but lacking the tarsus , where the wing 's costal surface normally would be . This mutation was reinterpreted as strong evidence for a dorsal exite and endite fusion , rather than a leg , with the appendages fitting in much better with this hypothesis . The innervation , articulation and musculature required for the evolution of wings are already present in podomeres .

Paranota plus leg gene recruitment hypothesis : The fossil larvae of Coxoplectoptera provided important new clues to the disputed question of the evolutionary origin of insect wings . Before the larvae fossil discovery the paranotal @-@ hypothesis and the leg @-@ exite @-@ hypothesis have been considered as incompatible alternative explanations , which have both been supported by a set of evidences from the fossil record , comparative morphology , developmental biology and genetics . The expression of leg genes in the ontogeny of the insect wing has been universally considered as conclusive evidence in favour of the leg @-@ exite @-@ hypothesis , which proposes that insect wings are derived from mobile leg appendages (exites) . However , the larvae of Coxoplectoptera show that the abdominal gills of mayflies and their ancestors , which are generally considered as corresponding structures to insect wings , articulated within the dorsal tergite plates . This cannot be seen in modern mayfly larvae , because their abdominal tergites and sternites are fused to rings , without any traces left even in embryonic development . If larval gills and wings are corresponding (" serial homologous ") structures and thus share the same evolutionary origin , the new results from Coxoplectoptera demonstrate that also wings are of tergal origin , as proposed by the classical paranotal @-@ hypothesis . Staniczek , Bechly & Godunko (2011) therefore suggested a new hypothesis that could reconcile the apparently conflicting evidence from paleontology and developmental genetics : wings first originated as stiff outgrowths of tergal plates (paranota) , and only later in evolution became mobile , articulated appendages through secondary recruiting of leg genes .

Suggestions have been made that wings may have evolved initially for sailing on the surface of water as seen in some stoneflies . An alternative idea is that it drives from directed aerial gliding descent ? a preflight phenomena found in some apterygote , a wingless sister taxa to the winged insects . The earliest fliers were similar to dragonflies with two sets of wings , direct flight muscles , and no ability to fold their wings over their abdomens . Most insects today , which evolved from those first fliers , have simplified to either one pair of wings or two pairs functioning as a single pair and using a system of indirect flight muscles .

Natural selection has played an enormous role in refining the wings , control and sensory systems , and anything else that affects aerodynamics or kinematics . One noteworthy trait is wing twist . Most insect wings are twisted , as are helicopter blades , with a higher angle of attack at the base . The twist generally is between 10 and 20 degrees . In addition to this twist , the wing surfaces are not necessarily flat or featureless ; most larger insects have wing membranes distorted and angled between the veins in such a way that the cross @-@ section of the wings approximates an airfoil . Thus , the wing 's basic shape already is capable of generating a small amount of lift at zero angle of attack (see Insect wing) . Most insects control their wings by adjusting tilt , stiffness , and flapping frequency of the wings with tiny muscles in the thorax (below) . Some insects evolved other wing features that are not advantageous for flight , but play a role in something else , such as mating or protection .

Some insects , occupying the biological niches that they do , need to be incredibly maneuverable . They must find their food in tight spaces and be capable of escaping larger predators ? or they may themselves be predators , and need to capture prey . Their maneuverability , from an aerodynamic viewpoint , is provided by high lift and thrust forces . Typical insect fliers can attain lift forces up to three times their weight and horizontal thrust forces up to five times their weight . There are two substantially different insect flight mechanisms , and each has its own advantages and disadvantages ? just because odonates have a more primitive flight mechanism does not mean they are less able fliers ; they are , in certain ways , more agile than anything that has evolved afterward .

= = Morphogenesis = =

While the development of wings in insects is clearly defined in those who are members of Endopterygota , which undergo complete metamorphosis ; in these species , the wing develops while in the pupal stage of the insects life cycle . However , insects that undergo incomplete metamorphosis do not have a pupal stage , therefore they must have a different wing morphogenesis . Insects such as those that are hemimetabolic have wings that start out as buds , which are found underneath the exoskeleton , and do not become exposed until the last instar of the nymph .

The first indication of the wing buds is of a thickening of the hypodermis , which can be observed in insect species as early the embryo , and in the earliest stages of the life cycle . During the development of morphological features while in the embryo , or embryogenesis , a cluster of cells grow underneath the ectoderm which later in development , after the lateral ectoderm has grown dorsally to form wind imaginal disc . An example of wing bud development in the larvae , can be seen in those of White butterflies (Pieris) . In the second instar the histoblast become more prominent , which now form a pocket @-@ like structure . As of the third and fourth instars , the histoblast become more elongated . This greatly extended and evaginated , or protruding , part is what becomes the wing . By the close of the last instar , or fifth , the wing is pushed out of the wing @-@ pocket , although continues to lie under the old larval cuticle while in its prepupal stage . It is not until the butterfly is in its pupal stage that the wing @-@ bud becomes exposed , and shortly after eclosion , the wing begins to expand and form its definitive shape .

The development of tracheation of the wings begin before the wing histoblast form , as it is important to note that they develop near a large trachea . During the fourth instar , cells from the epithelium of this trachea become greatly enlarged extend into the cavity of the wing bud , with each cell having developed a closely coiled tracheole . Each trachcole is of unicellular origin , and is at first intracellular in position ; while tracheae are of multicellular origin and the lumen of each is intercellular in position . The development of tracheoles , each coiled within a single cell of the epithelium of a trachea , and the subsequent opening of communication between the tracheoles and the lumen of the trachea , and the uncoiling and stretching out of the tracheoles , so that they reach all parts of the wing .

In the earlier stages of its development , the wing @-@ bud is not provided with special organs of respiration such as tracheation , as it resembles in this respect the other portions of the hypodermis of which it is still a part . It should be noted , however , that the histoblast is developed near a large trachea , a cross @-@ section of which is shown in , which represents sections of these parts of the first , second , third and fourth instars respectively . At the same time the tracheoles uncoil , and extend in bundles in the forming vein @-@ cavities of the wing @-@ bud . At the molt that marks the beginning of the pupal stadium stage , they become functional . At the same time , the larval tracheoles degenerate ; their function having been replaced by the wing tracheae .

= = Nomenclature = =

Most of the nomenclature of insect orders is based on the Ancient Greek word for wing , ?????? (pteron) , as the suffix -ptera .

= = Adaptations = =

= = = Variation = = =

Insect wings are fundamental in identifying and classifying species as there is no other set of structures in studying insects more significant . Each order and insect family has distinctive wing shapes and features . In many cases , even species may be distinguished from each other by differences of color and pattern . For example , just by position one can identify species , albeit to a much lesser extent . Though most insects fold their wings when at rest , dragonflies and some damselflies rest with their wings spread out horizontally , while groups such as the caddisflies , stoneflies , alderflies , and lacewings hold their wings sloped roof @-@ like over their backs . A few moths wrap their wings around their bodies , while many flies and most butterflies close their wings together straight upward over the back .

Many times the shape of the wings correlates with the type of insect flight . The best @-@ flying insects tend to have long , slender wings . In many species of Sphingidae (sphinx moths) , the forewings are large and sharply pointed , forming with the small hind wings a triangle that is suggestive of the wings of fast , modern airplanes . Another , possibly more important correlation , is that of the size and power of the muscles to the speed and power of flight . In the powerfully flying insects , the wings are most adapted for the stresses and aerodynamics of flight . The veins are thicker , stronger , and closer together toward the front edge (or " leading edge ") and thinner yet flexible toward the rear edge (or " trailing edge ") . This makes the insect wing an excellently constructed airfoil , capable of exerting both propulsion and lift while minimizing drag .

Variation of the wing beat may also occur , not just amongst different species , but even among individuals at different times . In general , the frequency is dependent upon the ratio between the power of the wing muscles and the resistance of the load . Large @-@ winged , light @-@ bodied butterflies may have a wing beat frequency of 4 ? 20 per second whereas small @-@ winged , heavy @-@ bodied flies and bees beat their wings more than 100 times a second and mosquitoes can beat up to 988 ? 1046 times a second . The same goes for flight ; though it is generally difficult to estimate the speed of insects in flight , most insects can probably fly faster in nature than they do in controlled experiments .

= = = Coleoptera = = =

In species of Coleoptera (beetles) , the only functional wings are the hind wings . The hind wings are longer than the elytra , folded longitudinally and transversely under the elytra . The wing is rotated forwards on its base into flight position . This action spread the wing and unfolded longitudinally and transversely . There is the spring mechanism in the wing structure , sometimes with the help of abdomen movement , to keep the wing in folded position . The beetle wing venation is reduced and modified due to the folding structure , which include :
Costa (C) , Subcosta posterior (ScP) ? at the leading wing marginal , fused for most of the length .
Radius anterior (RA) ? divided into two branches beyond the middle of the wing .
Radius posterior (RP) ? basal connection is lost .
Media posterior (MP) ? branches , long and strong vein .
Cubitus anterior (CuA)
Anal veins (AA , AP) ? veins behind the cubitus , separated by anal fold .
In most species of beetles , the front pair of wings are modified and sclerotised (hardened) to form elytra and they protect the delicate hindwings which are folded beneath . The elytra are connected to the pterathorax ; being called as such because it is where the wings are connected (pteron meaning " wing " in Greek) . The elytra are not used for flight , but tend to cover the hind part of the body and protect the second pair of wings (alae) . The elytra must be raised in order to move the hind flight wings . A beetle 's flight wings are crossed with veins and are folded after landing , often along these veins , and are stored below the elytra . In some beetles , the ability to fly has been lost . These include some ground beetles (family Carabidae) and some " true weevils " (family Curculionidae) , but also some desert and cave @-@ dwelling species of other families . Many of these species have the two elytra fused together , forming a solid shield over the abdomen . In a few families , both the ability to fly and the elytra have been lost , with the best known example being the glow @-@ worms of the family Phengodidae , in which the females are larviform throughout their lives .

= = = Lepidoptera = = =

The two pairs of wings are found on the middle and third segment , or mesothorax and metathorax respectively . In the more recent genera , the wings of the second segment are much more pronounced , however some more primitive forms have similarly sized wings of both segments . The wings are covered in scales arranged like shingles , forming the extraordinary variety seen in color . The mesothorax is evolved to have more powerful muscles to propel moth or butterfly through the air , with the wing of said segment having a stronger vein structure . The largest superfamily , Noctuidae , has the wings modified to act as Tympanal or hearing organs Modifications in the wing 's venation include :
Costa (C) ? not found in Butterflies .
Subcosta (Sc) + Radius 1 (Sc + R1) ? at the leading wing marginal , fused or very close for most of the length , in hind wing fused and well developed in the humeral area , subcosta never branches in butterfly .
Radius (R2 @-@ R5) ? radius divides into branches beyond the middle of the wing up to five

branches in Papilionidae . On forewing , the last R is stalked in all butterflies except Hesperiidae is separated .
Radius sector (Rs) ? in hind wing .
Media (M1 @-@ M3) ? the basal section has been lost .
Cubitus anterior (CuA1 @-@ CuA2) ? CuP section has been lost .
Anal veins (A , 1A + 2A , 3A) ? either one vein A , or two veins 1A + 2A , 3A .
Humeral vein ? The hind wing of most butterflies has the humeral vein , except Lycaenidae There is the enlargement of the humeral area of the hind wing which is overlapped with the fore wing . The humeral vein strengthened the hind wing overlapped area so that the two wings coupling better .
The wings , head parts of thorax and abdomen of Lepidoptera are covered with minute scales , from which feature the order ' Lepidoptera ' derives its names , the word " lepteron " in Ancient Greek meaning ' scale ' . Most scales are lamellar , or blade @-@ like and attached with a pedicel , while other forms may be hair @-@ like or specialized as secondary sexual characteristics . The lumen or surface of the lamella , has a complex structure . It gives color either due to the pigmentary colors contained within or due to its three @-@ dimensional structure . Scales provide a number of functions , which include insulation , thermoregulation , aiding gliding flight , amongst others , the most important of which is the large diversity of vivid or indistinct patterns they provide which help the organism protect itself by camouflage , mimicry , and to seek mates .

= = = Odonata = = =

Species of Odonata (Damselflies and dragonflies) both have two pairs of wings which are about equal in size and shape and are clear in color . There are five , if the R + M is counted as 1 , main vein stems on dragonfly and damselfly wings , and wing veins are fused at their bases and the wings cannot be folded over the body at rest , which also include :
Costa (C) ? at the leading edge of the wing , strong and marginal , extends to the apex of the wing .
Subcosta (Sc) ? second longitudinal vein , it is unbranched , joins C at nodus .
Radius and Media (R + M) ? third and fourth longitudinal vein , the strongest vein on the wing , with branches , R1 @-@ R4 , reach the wing margin , the media anterior (MA) are also reach the wing margin . IR2 and IR3 are intercalary veins behind R2 and R3 respectively .
Cubitus (Cu) ? fifth longitudinal vein , cubitus posterior (CuP) is unbranched and reach the wing margin .
Anal veins (A1) ? unbranched veins behind the cubitus .
A nodus is formed where the second main vein meets the leading edge of the wing . The black pterostigma is carried near the wing tip .
The main veins and the crossveins form the wing venation pattern . The venation patterns are different in different species . There may be very numerous crossveins or rather few . The Australian Flatwing Damselfly 's wings are one of the few veins patterns . The venation pattern is useful for species identification . Almost all Anisoptera settle with the wings held out sideways or slightly downward , however most Zygoptera settle with the wings held together , dorsal surfaces apposed . The thorax of Zygoptera is so oblique that when held in this way the wings fit neatly along the top of the abdomen . They do not appear to be held straight up as in butterflies or mayflies . In a few zygopteran families the wings are held horizontally at rest , and in one anisopteran genus (e.g. Cordulephya , Corduliidae) the wings are held in the typical damselfly resting position . Adult species possess two pairs of equal or subequal wings . There appear to be only five main vein stems . A nodus is formed where the second main vein (subcosta) meets the leading edge of the wing . In most families a conspicuous pterostigma is carried near the wing tip . Identification as Odonata can be based on the venation . The only likely confusion is with some lacewings (order Neuroptera) which have many crossveins in the wings . Until the early years of the 20th century Odonata were often regarded as being related to lacewings and were given the ordinal name Paraneuroptera , but any resemblance between these two orders is entirely superficial . In Anisoptera the hindwing is broader than the forewing and in both wings a crossvein divides the

discoidal cell into a Triangle and Supertriangle .

= = = Orthoptera = = =

Species of Orthoptera (Grasshoppers and crickets) have forewings that are tough opaque tegmina , narrow which are normally covering the hind wings and abdomen at rest . The hind wings are board membranous and folded in fan @-@ like manner , which include the following venation :
Costa (C) ? at the leading marginal of the forewing and hind wing , unbranched .
Subcosta (Sc) ? second longitudinal vein , unbranched .
Radius (R) ? third longitudinal vein , branched to Rs in forewing and hind wing .
Media anterior (MA) ? fourth longitudinal vein , branched in basal part as Media posterior (MP) .
Cubitus (Cu) ? fifth longitudinal vein , on forewing and hind wing dividing near the wing base into branched CuA , and unbranched CuP .
Anal veins (A) ? veins behind the cubitus , unbranched , two in forewing , many in hind wing .

= = = Phasmatodea = = =

Costa (C) ? at the leading marginal of the hind wing , unbranched , absent in forewing .
Subcosta (Sc) ? second longitudinal vein , unbranched .
Radius (R) ? third longitudinal vein , branched to Rs in hind wing , unbranched in forewing .
Media anterior (MA) ? fourth longitudinal vein , branched in basal part as Media posterior (MP) .
Cubitus (Cu) ? fifth longitudinal vein , unbranched .
Anal veins (A) ? veins behind the cubitus , unbranched , two in forewing , many in hind wing 1A @-@ 7A in one group and the rest in another group .
Stick insect have forewings that are tough , opaque tegmina , short and covering only the base part of the hind wings at rest . Hind wings from costa to Cubitus are tough and opaque like the forewings . The large anal area are membranous and folded in fan @-@ like manner . There are no or very few branching in Stick Insect wing veins .

= = = Dermaptera = = =

Other orders such as the Dermaptera (earwigs) , Orthoptera (grasshoppers , crickets) , Mantodea (praying mantis) and Blattodea (cockroaches) have rigid leathery forewings that aren 't used for flying , sometimes called tegmen (pl. tegmina) , elytra , or pseudoelytron .

= = = Hemiptera = = =

In Hemiptera (true bugs) , the forewings may be hardened , though to a lesser extent than in the beetles . For example , the anterior part of the front wings of stink bugs is hardened , while the posterior part is membranous . They are called hemelytron (pl. hemelytra) . They are only found in the suborder Heteroptera ; the wings of the Homoptera , such as the cicada , are typically entirely membranous . Both forewings and hindwings of Cicada are membranous , most species are glass @-@ like although some are opaque . Cicadas are not good fliers and most fly only a few seconds . When flying , forewing and hind wing are hooked together by a grooved coupling along the hind wing costa and forewing margin . Most species have a basic venation as shown in the following picture .
Costa (C) ? at the leading wing marginal , in forewing extends to the node and lies close to Sc + R.
Subcosta + Radius (Sc + R) ? in forewing Sc and R fused together to the node . Radial sector (Rs) arises near the node and unbranches .
Radius anterior (RA)
Radius posterior (RP)
Media (M) ? branches to M1 to M4 .

Cubitus anterior (CuA) ? branches to CuA1 and CuA2 .
Cubitus posterior (CuP) ? unbranches .
Anal veins (A) ? veins behind the cubitus , 1A and 2A fused in the forewing , CuP and 2A are folded .
Also notice there are the ambient veins and peripheral membranes on the margin of both wings .

= = = Diptera = = =

In the Diptera (true flies) , there is only one pair of functional wings , with the posterior pair of wings are reduced to halteres , which help the fly to sense its orientation and movement , as well as to improve balance by acting similar to gyroscopes . In Calyptratae , the very hindmost portion of the wings are modified into somewhat thickened flaps called calypters which cover the halteres .
Costa (C) ? not found in Diptera .
Subcosta (Sc) ? became the leading wing vein , unbranched .
Radius (R) ? branched to R1 @-@ R5 .
Media (M) ? branched to M1 @-@ M4 .
Cubitus anterior (CuA) - unbranched , CuP is reduced in Diptera . Some species CuA and 1A are separated , some species meets when reaching the wing margin , some species fused .
Anal veins (A) ? only two anal veins 1A and 2A are present , 2A is not distinctive in some species .

Discal Cell (dc) ? well defined in most species .

= = = Blattodea = = =

Species of Blattodea (cockroaches) have a forewing , are also known as tegmen , that is more or less sclerotized . It is used in flight as well as a form of protection of the membranous hind wings . The veins of hind wing are about the same as front wing but with large anal lobe folded at rest between CuP and 1A . The anal lobe usually folded in a fan @-@ like manner .
Costa (C) ? at the leading edge of the wing .
Subcosta (Sc) ? second longitudinal vein , it is relatively short .
Radius (R) ? third longitudinal vein , with many pectinate branches .
Media (M) ? fourth longitudinal vein , reach the wing margin .
Cubitus anterior (CuA) ? fifth longitudinal vein , with dichotomous branches occupy large part of tegmen .
Cubitus posterior (CuP) ? is unbranched , curved and reach the wing margin .
Anal veins (A) ? veins behind the cubitus .

= = = Hymenoptera = = =

The Hymenoptera adults , include sawflies , wasps , bees and non @-@ working ants , all of which have two pairs of membranous wings .
Costa (C) ? not found in Hymenoptera .
Subcosta (Sc) ? unbranched .
Radius (R) ? branched to R1 @-@ R5 .
Media (M) ? M is unbranched , in forewing M is fused with Rs for part of its length .
Cubitus (CuA) ? unbranched , CuP is absent in Hymenoptera .
Anal veins (A) ? only two anal veins 1A and 2A are present , 2A is not distinctive in some species .

Wing @-@ coupling ? Row of hooks on the leading edge of hind wing engage the hind margin of the forewing , strongly couple the wings in flight .
Line of wing folding ? Some species , including Vespidae , the forewing are longitudinally folded along the ' line of wing folding ' at rest .
Pterostigma ? is present for some species .

The forward margin of the hind wing bears a number of hooked bristles , or " hamuli " , which lock onto the fore wing , keeping them held together . The smaller species may have only two or three hamuli on each side , but the largest wasps may have a considerable number , keeping the wings gripped together especially tightly . Hymenopteran wings have relatively few veins compared with many other insects , especially in the smaller species .

= = = Other families = = =

Termites are relatively poor fliers and are readily blown downwind in wind speeds of less than 2 km / h , shedding their wings soon after landing at an acceptable site , where they mate and attempt to form a nest in damp timber or earth . Wings of most termites have three heavy veins along the basal part of the front edge of the forewing and the crossveins near the wing tip are angled , making trapezoidal cells . Although subterranean termite wings have just two major veins along the front edge of the forewing and the cross veins towards the wingtip are perpendicular to these veins , making square and rectangular cells .

Species of Thysanoptera (thrips) have slender front and hind wings with long fringes of hair , called fringed wings . While species of Trichoptera (caddisfly) have hairy wings with the front and hind wings clothed with setae .