

Insect Wings

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A wing, as its primary function is an organ of flight. Because wings have many secondary functions: camouflage, visual signaling, acoustic signaling, thermo-regulation, and structural protection– and there are others, they show a wide diversity of form and often represent a compromise between their primary and various secondary functions. **Read Chapman, Chapt. 9, sections 9.1- 9.7 inclusive.**

Wings operate along two axes, for this reason conventional morphological directional terms are not easily applied, i.e. in Orthoptera, the anterior margin of a fully extended wing might be a ventral margin when the wing is flexed or a dorsal margin in a late instar nymph. An independent set of wing surface and margin terms has been developed to overcome this problem. Using a *fully extended wing* for orientation, the anterior margin is the **costal margin**. The most distal anterior angle of the wing is the **apex**. The wing margin running parallel (often obliquely parallel) to the long axis of the body is the **outer margin**. The most distal posterior angle is known as the **ternus** (outer angle [fw], anal angle [hw]). The posterior wing margin is the inner margin (often called anal margin [hw]). The major flight surface of the wing is the **remigium**. When a posterior area of the wing is ‘set-off’ from the remigium by a fold (more on wing creases and folding later), this area is the **anal lobe** (vannus [Orthoptera], clavus [Hemiptera]). An additional area demarcated by a fold and posteriad of the anal lobe is the **jugal lobe**. This complete terminology is best applied to trigonate (trangular) winged insects, but most terms have wide application.

Wings are evaginations of the tergum or thoracic notum. Embryonically, each wing consists of two layers of cuticle surrounding and lined interiorly by a cellular epidermis (dermal cells). The two dermal layers in turn enclose a blood sinus containing a neural trunk (innervating the dermal cells) and a branched tracheal trunk. In a fully formed wing, the two cuticular layers have become conjoined and the only remaining sinuses being the veins– each of which is still a blood sinus with innervation and a tracheal trunk. Veins give structural support to the wing membrane. The network of veins has been categorized into three patterns of primary venation and six patterns of secondary venation.

Patterns of primary venation represent a phyletic sequence from ancestral to advanced in the evolution of the network of wing veins. The three types of primary venation are: archidictyon, polyneurous, and costaneurous.

Archidictyon: Believed to be the most archaic type of vein network. Areas between major veins are for the most part filled with pentagonal cells. Examples: wings of Odonata: Anisoptera.

Polyneurous: Derived from the archidictyon type. Cells are quadrate and parallel sided, the sided align with major veins and with adjoining cells form secondary longitudinal veins called **intercalary veins**. Examples: wings of Ephemeroptera: Ephemeridae, hindwings of Orthoptera: Caelifera.

Costaneurous: Derived from the Polyneurous pattern. Cells along the forward margin of the wing have been retained and cross-veins form a ladder-like pattern. On the remaining wing surface, many cross-veins have been lost. Examples: Neuroptera: Sisyridae, Corydalidae. Note the costal cross-veins here are not homologs of those found in Odonata (or Ephemeroptera) which are flattened and triangular when viewed laterally– and act as brace veins to keep the foreword wing margin upturned in flight. Costaneurous cross-veins are cylindrical support struts to keep the foreword wing margin ridged– the angle of attack with the air being under muscular control via the pteralia. See following lecture.

Patterns of secondary venation represent derivations from the three primary patterns and do not necessarily have phyletic significance. The six types of secondary venation are: false archidictyon, false polyneurous, oligoneurous, tegmin, hemelytron, and elytron.

False archedictyon: Cells between major veins tend to be hexagonal in shape with pentagonal cells found near longitudinal veins. Example: Neuroptera: Ascalaphidae.

False polyneurous: Cells between major veins are rectangular due to the loss of many cross-veins, tend to be at least twice as long as wide, and are usually not uniformly distributed over the flying surface. Example: forewings of Plecoptera: Perlidae.

Oligoneurous: Could be termed a 'tertiary pattern' as the loss of cross-veins and even longitudinal veins can come from one of the primary venation types or from the preceding two patterns. Example: Cecidomyiidae (extreme) or Ephemeroptera: Oligoneuridae.

Tegmen: Derivable from any of the primary types or preceding secondary types. Forewings show increased sclerotization and the original venation pattern is obscured. Example: forewings of Orthoptera: Caelifera, or Homoptera: Cercopidae.

Hemelytron: Could be termed a 'tertiary pattern' derivable from any of the above. The basal two-thirds of the forewing are more heavily sclerotized leaving the distal third membranous. Examples: Hemiptera: Pentatomidae.

Elytron: Could be termed a 'tertiary pattern' derivable from any of the above patterns. Forewing sclerotization has produced a forewing functioning as a protective device, the flight function given-over to the hindwings.

Insect wing venation

Insect wing venation consists of longitudinal support veins connected by cross-veins. The principal longitudinal veins from anterior to posterior, from the costal to inner margins, on an archetypical insect wing (with standard abbreviations) are: **Costa (C.)**, **Subcosta (Sc.)**, **Radius (R)**, **Radius Sector (RS)**, **Medius Anterior (MA)**, **Medius Posterior (MP)**, **Cubitus Anterior (CuA)**, **Cubitus Posterior (CuP)**, and as many as five **Anal veins (A)**.

These veins form pairs, each with a convex anterior and concave posterior element. These pairs are: C and Sc, R and Rs, MA and MP, CuA, and CuP. Anal veins are convex veins with secondary derived concave intercalary veins between— see polyneurous venation (above). The resultant arrangement which adds strength to the wing is known as **fluting**. A Japanese fan and the hindwings of a macropterous grasshopper possess a similar form.

Longitudinal veins may possess branches which ultimately terminate at the wing margins. The branching sequence is always dichotomous. Vein branches reaching the wing margins are designated by numerical subscripts, i.e. Sc₂, or MP₃. Numbering of the terminal branches is from costal to inner margins. Typical terminal branching venation of an insect wing is as follows: Costa— unbranched, Subcosta— two branched, Radius— unbranched, Radius sector— four branches, Medius anterior— two branches, Medius posterior— four branches, Cubitus anterior— two branches, Cubitus posterior— unbranched. Anal veins— unbranched. Longitudinal veins often fuse together such that one or more branches are lost, or, even major veins may fuse. In the wings of Diptera a common arrangement of the forewing Rs veins is Rs₁₊₂₊₃. This nomenclature indicates that these three branches have united to form a single vein. On the hindwings of most Lepidoptera the second most anterior veins is designated as Sc+ R. This indicates that the Subcosta and Radius veins have fused to form a single vein.

Some 'anomalies' of insect wing venation are as follows: Ephemeroptera possess both the MA and MP vein stems, Odonata possess the MA stem only, other insects possess only the MP veins. The MP vein *stem* (but not branches), is lost in many Diptera, Lepidoptera, and fused with Cu stem in Hymenoptera. Because of the above anomalies, when referring to the medius veins in insects other than the Paleoptera (Ephemeroptera and Odonata), the word posterior is taken to be understood and commonly dropped. The medius posterior vein is simply referred to as the medius and its branches as M_{number}. Similarly, because the Cubitus anterior frequently plays an important role in insect identification but the CuP does not, the word anterior is frequently omitted in discussion as understood and is omitted when cross-veins are designated— see below.

The major longitudinal veins are connected by cross-veins. Usually there is a cross-vein linking every major vein to its anterior and posterior neighbors. The major cross-veins are then designated as follows: **c- sc** (sometimes called humeral vein), **sc- r**, **r- rs**, **rs- m** (also **r- m**), **ma- mp**, and **m- cu**. Note that the cross-veins are designated in lower case letters, hyphenated, and the vein closest to the costal margin is listed first.

Wing areas bounded by veins are called **cells**. If the distal boundary of a cell is a wing margin, the cell is termed an **open cell**. If a cross-vein separates a cell from the wing margin, the cell is termed a **closed cell**. Wing cells take the name of the subtended branch *above* them starting from the base outward. A cell bordered anteriorly by vein Rs_4 , basally by the m cross-vein, and posteriorly by vein M_1 would be called the Rs_4 cell. In those cases in which an anterior vein is followed by multiple cells along its length, these would be designated as 1st, 2nd, 3rd, etc, from proximal to distal followed by the vein name, i.e. cells in a polyneurous wing below Rs_1 would be from the most basal outward: 1st Rs_1 , 2nd Rs_1 , 3rd Rs_1 , etc. to the end of the series.

Wing venation systems.

In various entomology textbooks, and among the various insect orders, different systems of wing venation have been used. Part of this is tradition, part is disagreements of morphological interpretation (see below), and part is convenience. In the following table, equivalents of the most widely used systems— those you are likely to run across in major references to either insect morphology or systematics are presented. Most disagreements as to vein designations have resulted from the misinterpretation of wing articulations and sclerites. In the table, homologous veins occur in the same row— this is only approximate as in the different orders every single branch may not be an exact homolog, but rather serial homologs or homoplasy. Bold and underlined entries are those with a nomenclature different from the left-hand column. Shaded areas within a column indicate that the same vein is named twice within a given venation system— also due to problems of determining exact homologies across different orders.

Insect wing articulation.

Note that *The designation of insect veins is based upon their articulation to the pteralia, i.e. axillary sclerites.* The typical insect wing has three axillary sclerites (four in orthopteroid insects) and two median plates. At the base of the costal margin are two additional sclerites: the **humeral plate** and the **tegula**. Also, within the pleural membrane below the wings are the **alariae** or **epiplurites** (basalar, subalar). Collectively these wing sclerites are known as the **pteraliae**. The axillary sclerites articulate with wing veins distally and with each other or the notal wing processes proximally. The alariae are connected via ligaments to the axillary sclerites and their inserted muscles originate from the coxa or internal thoracic wall or apophyses— (see below). The **pteraliae** and their articulations are as follows:

Humeral plate. Could be considered an additional axillary sclerite (as does Kukulová-Peck— see below).

Articulates with the costal vein stem distally and the tegula proximally.

Tegula. Usually a scale-like sclerite articulating with the humeral plate distally and the alar arm of the notum basally. In the Lepidoptera, the tegula is developed into a large ‘leaf-like’ flap which covers the wing bases and most of the alinotum.

1st axillary sclerite. (Often ‘F’ shaped in the orthopteroid orders) articulates with the subcosta stem, the 2nd axillary sclerite, and the anterior notal wing process.

2nd axillary sclerite. (Weakly ‘S’ shaped in many insects) articulates with the radius stem, the 1st axillary sclerite, and the posterior median plate.

Anterior median plate. Articulates with the posterior median plate and the medius, cubitus, and postcubitus vein stems. A line of flexure running between this plate and the posterior median plate and extending to the costal margin between the humeral plate and the tegula is the costal fold— see below.

Posterior median plate. Articulates anteriorbasad with the 2nd axillary sclerite, distad with the anterior median plate, and postiobasad with the 3rd axillary sclerite. A wing fold running from its juncture with the 3rd axillary sclerite to the outer margin is the vannal fold— see below.

3rd axillary sclerite. (Inverted ‘T’ shaped in most insects) articulates with the 2nd axillary sclerite, the posterior median plate, the anal veins, and the posterior notal wing process. In the orthopteroid insects this sclerite is divided into a distal v-shaped 3rd axillary sclerite, and an oval **4th axillary sclerite** which then articulates

with the 3rd axillary sclerite and the posterior notal wing process.

Insect wing coupling

Most winged insects possess two pair of wings; Diptera and Strepsiptera with a single pair of wings and Coleoptera, at least functionally possessing a single pair of wings. Greater efficiency in flight energetics is achieved by wing coupling mechanisms. Although the pterothorax is a functional unit, the greatest development of musculature for flight is in the mesothorax, the metathoracic wing movement is, via wing coupling, governed by the mesothorax. Among the 'four-winged insects' only Odonata and Neuroptera appear not to possess any serviceable wing coupling mechanism.

The simplest wing coupling device is an enlarged **humeral lobe** of the hindwing. This underlaps the inner margin of the forewing and provides a unified flight surface, especially on the downstroke. Examples: Occurs in many families of Ephemeroptera: Ephemeroidea, Heptageniidae, etc.; Lepidoptera: Bombycoidea, Papilionoidea.

Wings may also be coupled by **hamuli**, which are, often uncinata, setae found along the costal margin of the hw and the inner margin of the fw. The setae interlock much like velcro. Very often the inner margin is turned down while the costal margin is turned up providing an additional physical support. This is the common wing lock occurring in Hymenoptera and also in the Sesiidae of the Lepidoptera, and in Trichoptera.

A third type of wing lock consists of one or more humeral spines on the hindwings (**frenulum**) which then hooks to a membranous flap or patch of bristles (**retinaculum**) on the ventral fw. This coupling device occurs in the Lepidoptera: Noctuoidea, Geometroidea, Pyraloidea, Tortricoidea, and most minor superfamilies. A variant is a **jugal lobe** or a **fibula**. In each case an attenuated lobe (jugal) or triangular flap (fibula) extends from the basal region of the inner margin of the fw on to the dorsal hw. Stiffened scales of these fw extensions mesh with those on the dorsal surface of the hw to provide a wing lock. This system is found in the 'mandibulate moths', for example: Hepialidae and Eriocraniidae, respectively.

Certain groups of insects may have more than a single wing-lock system. Hamuli and frenulum-retinaculum occur in the Trichoptera and Sesiidae of the Lepidoptera. In the hemipteroid orders more than a single mechanism may be involved although the systems have yet to receive names.

Neuroptera wings are somewhat asynchronous in that the hws are fractionally behind the fws at each wing beat: photographed for Chrysopidae. Odonata with f/hws independently controlled by direct flight muscles have no requirement for a wing lock.

Chapman, 1998 Wooton, 1979	Comstock & Needham, 1899, etc.	Snodgrass, 1935	Hamilton, 1971/2	Kristenson & Neilson, 1991	Hampson (European system), 1901
stem	branches				
-	<u>Precosta</u> <u>Pc</u>	<u>Pc</u>	-	-	-
Costa C	C	C	C	C	-
Subcosta Sc1	Sc1	Sc1	Sc	Sc1	<u>12b</u>
Sc2	Sc2	Sc2	-	Sc2	<u>12a</u>
Radius R1	R1	R1	R1	R1	<u>11</u>
Radius Sector Rs1	<u>R2</u>	<u>R2</u>	<u>S1</u>	<u>S1</u>	<u>10</u>
Rs2	<u>R3</u>	<u>R3</u>	<u>S2</u>	<u>S2</u>	<u>9</u>
Rs3	<u>R4</u>	<u>R4</u>	<u>S3</u>	<u>S3</u>	<u>8</u>
Rs4	<u>R5</u>	<u>R5</u>	<u>S4</u>	<u>S4</u>	<u>7</u>
Medius Anterior MA1	MA1	MA1	<u>M1</u>	MA1	-
MA2	MA2	MA2	<u>M2</u>	MA2	-
Medius Posterior MP1	M1	M1	-	M1	<u>6</u>
MP2	M2	M2	-	M2	<u>5</u>
MP3	M3	M3	<u>M3</u>	M3	<u>4</u>
MP4	M4	M4	<u>M4</u>	M4	-
Cubitus Anterior CuA1	<u>Cu1a</u>	<u>Cu1a</u>	<u>Cu1</u>	CuA1	<u>3</u>
CuA2	<u>Cu1b</u>	<u>Cu1b</u>	<u>Cu2</u>	CuA2	<u>2</u>
-	<u>Cu2</u>	<u>Cu2</u>	<u>Plical P</u>	-	-
Cubitus Posterior CuP	<u>A1</u>	<u>Post cubitus</u> <u>PCu</u>	<u>Plical P</u>	CuP	-
-	-	-	<u>Empusal E</u>	-	-
Anal vein 1A	<u>A2</u>	1A	1A	1A	<u>1c</u>
2A	<u>A3</u>	2A	2A	2A	<u>1b</u>
3A+	<u>A4+</u>	3- 5A	3A+	3A	<u>1a</u>

Wing movement. The insect wing has lines of flexion to allow flapping and wing folding. These are the wing folds or furrows. Authors have (as with wing venation) their own interpretations and the same terms is often applied quite differently by various authors. The following list is based upon Hamilton (1971/2) with equivalents of other authors provided.

Costal fold. (Basal fold of Chapman). Extends anteriorly from the juncture of the median plates and the third axillary sclerite to the costal margin between the humeral plate and the tegula. Allows wings to be folded 'tent-like' over the abdomen.

Median fold. (Median flexion line of Chapman) Extends from the anterior median plate to the outer margin between the Rs and MP veins. Allows the posterior half of the remigium to be folded underneath the anterior portion, i.e. Hymenoptera: Vespidae.

Vannal fold. (Claval furrow/fold auct., anal fold, vannus dividens). Extends from the juncture of the median plates and the third axillary sclerite to the outer wing margin between the post cubitus and first anal veins. Allows the anal lobe (clavus, vannus) to be folded underneath the remigium.

Jugal fold. Extends from the third axillary sclerite to the wing margin between the anal veins and any additional basal jugal veins. In most insects homologous to the posterior portion of the basal fold— see below.

Basal fold. Extends from the juncture of the anterior notal wing process and first axillary sclerite posteriorly to the juncture of the third axillary sclerite (fourth in orthopteroids) with the posterior notal wing process to the inner margin. Allows wings to be folded backwards, overlapping and laying on top of the abdomen.

Direct flight muscles and wing folding.

Control of insect wings orientation, angle of attack, and flexion along the horizontal (x-) axis and wing twisting, is accomplished via the direct flight muscles. The first axillary sclerite is connected by ligaments to the basilar. Muscles inserted on the basilar(es) originate at the base of the coxa and episternum. The wing 'pivots' on the pleural wing process/ second axillary sclerite which has ligaments to both a basilar and subalar. The third axillary sclerite is connected by ligaments to the subalar(es) and by muscle originating at the pleural apophyses (muscle terms origin and insertion refer to the immobile and mobile connection points, respectively). Muscles inserted on the subalar have their origin at the base of the coxa. See figure 9.16 in Chapman (p. 197) and note that these diagrams are oriented with the head to the right.

A typical insect wing folds in the following sequence of events. Muscles to the basilar relax while muscles of the subalar (SaC) contract. This pulls the second axillary sclerite (2nd axl) backward on its pivot of the pleural wing process and stretches ligaments to the 1st axl. Muscles inserted on the basoposterior arm of 3rd axl. with origin on the pleural apophyses contract. This action rotates 3rd axl. such that the basoposterior arm is now the most distal arm (see model, also note that 3rd axl., as well as the alariae are *proximal* of the pleural apophyses). The wing flexes along the costal and vannal folds. Finally, muscles to the subalariae and basilariae from the thoracic wall or coxal bases contract, pulling the 3rd, 2nd, and lastly 1st axl. (via connecting ligaments) inward and downward, respectively. This causes wing flexing along the basal fold and the wings reach their resting position. The 2nd axl. often has a 'wing-lock' engaged with the pleural wing process to keep the wing flexed and recall that ligaments to the 1st axl. are stretched when wings are in repose. This stored potential energy is used to aid in wing extension.

Indirect flight muscles and flight.

Wing flapping is typically mostly under the control of indirect flight muscles. Recall that the pterothorax is a box with ridged sides and bottom. The top is a sclerotized area 'floating' on (surrounded by) a membrane. In flight, the up-stroke is produced by the contraction of tergal-sternal muscles and the down-stroke by contraction of the longitudinal dorsal muscles. Contraction of the tergal-sternal muscles pulls the alinotum down and so also the wing membrane (remember that it is an evagination of the notum) but the pleural wing process acts as a fulcrum for the wing via the 2nd axl and the whole process is much like a teeter-totter; the wing base is pulled down and the wing itself is elevated. In the down-stroke the dorso-longitudinal muscles originating and inserting on the phragma

(enlarged antecostae) contract, since the alinotum is a convex unified structure without flexion lines, contraction can only result in mechanical deformation– the top bulges, pulling the wing base up and the wing itself down as it moves on its fulcrum.

Variations on a theme: In Odonata and Blattodea, the downstroke is accomplished by contraction of muscles inserted on the basilar and originating on the pleural apophyses– i.e. direct flight muscles. In the Orthoptera and Coleoptera, the downstroke is a combination of the direct flight and indirect flight muscle action.. **The evolution of insect wings**

The various proposals for the evolution of insect wings are usually centered around three sets of ideals: 1) Morphological evolution, i.e. from what structures did wings develop; 2) Co-option/exaptation, i.e. what is the natural selection pathway for wing development; and finally 3) Is the origin of insect wings a monophyletic or di-/polyphyletic event, i.e. did wings evolve more than once in the Insecta?

Wing origins as mono- or di-/polyphyletic.

- 1) Monophyletic origin– most authors.
- 2) More than one origin for wings– Matsuda 1981, other 19th century authors.

Co-option/ exaptation theories of wing development.

- 1) Wings derived from lateral lobes used in courtship display or as stridulatory organs. Proponents: Alexander & Brown, 1960.
- 2) Wings derived from abdominal gills used for swimming. Proponent Carpenter 1916.
- 3) Wings derived from lateral lobes used in camouflage. Proponents: Hamilton 1971/2, Kukulová-Peck 1991.
- 4) Wings derived from thermo-regulatory organs. Kingsolver & Koehn, 1994.
- 5) Wings derived from gliding/ parachuting lobes. Proponents– See #4 above and also next.

Morphological evolutionary theories can be broadly categorized as follows.

- 1) Wings as tergal evaginations or paranotal lobes. Traditionally the most widely accepted theory. Proponents: Snodgrass 1954, Hamilton, 1971/2, Matsuda, 1981, Wootton 1992,
- 2) Wings as the serial development of abdominal gills– pleural in origin. Proponents: Carpenter 1916, .
- 3) Wings as excites of a basal leg segment. Theory steadily gaining acceptance. Proponents: Kukulová-Peck, 1991 and earlier, Turner, 1982.

The question of monophyly frames the discussion of evolutionary development and natural selection/ behavioral pathways to wing development. All theories mentioned above have positive and negative elements. For each, I will give a brief summary and list positive and negative features.

Monophyletic wing origin: Wings evolved once in the insects, probably in the Carboniferous period (but possibly mid Silurian). Fossil winged insects occur in Upper Carboniferous deposits; dicondylic mandibles of the type associated with winged insects has been found in Silurian deposits. There is a wide homology of wing veins throughout extant and extinct orders. Objections (see below) Some morphologist believe that the dragonfly wing articulation cannot be derived morphologically or sequenced chronologically with respect to the development of wings in other pterygote insects.

Di-phyletic wing origin: Wings of the orders Odonata and Protodonata are highly specialized from the earliest fossils. The three (or four) axillary sclerite formula found in the most ancestral insects clearly related to other extinct or extant orders are not found in the odonate orders. Similarities in wing venation between odonates and other insect orders are strictly due to evolutionary parallelism from a common ancestral stock. Odonate orders are held to have evolved from the Archaeognatha– Machelid like ancestor, all other pterygote insects from Thysanura like ancestors. Supporting evidence: Presence of direct flight muscles in Machelids which move notal lobes, can be homologized with odonate direct flight muscles. Large compound eyes. Lack of wing folding and axillary sclerites. Note that molecular data would split the Thysanura, separating the Machelidae from the Lepismatidae. Objections: homologizable muscles are also found in the Thysanura. Eye size could easily be convergent. Authorities are in disagreement as to whether

the odonates possess true axillary sclerites.

Co-option (Darwins' term) or exaptation (Gould's term) refers to the evolution of a structure for one function and 'co-opting' it for another, i.e. What good is a partially formed complex organ such as an eye or a wing? Evolutionary theory requires this principle for the development of novel characters. A structure is gradually selected for and becomes specialized for a specific function and simultaneously this structure is serviceable for another unrelated function. Example: fish swim bladders are also serviceable lungs. Some of the ideas advanced below are not as yet scientifically falsifiable.

Wings derived from courtship display or stridulatory organs. Because there are flightless insects with wings—although reduced in size, it is postulated that wing-like structures could evolve as a consequence of sexual selection. Supporting arguments: Point(s) of wing origin would be confined to one body region—a focus for signaling. Also, sexual selection is regarded as a more potent operant than simple natural selection as traits generally detrimental can be preserved due to short term benefits. Objections: What about wings in the opposite sex? A 'co-factor' is needed such as escape from predators *from the first* for efficient opposite sex flight to develop. This is at present then a teleological argument.

Wings derived from gills used in swimming. See morphological discussion below as relates to the pleural wall. Supporting argument: provides a readily observable explanation for development of wing movement. Objections: oxygen uptake is increased by beating, but not by increase in gill surface area beyond a relatively small area increase since oxygen circulates through an insect respiratory system largely by diffusion. This theory does not explain the lack of abdominal wings in insects.

Wings derived from lateral lobes used in camouflage. Both nymphs and adults of fossil insects show pronounced dorsal-ventral flattening (before fossilization) with prominent paranotal lobes on all segments, but especially on thoracic segments. Such structures could be linked to the development of gliding or parachuting—see discussions below. Supporting arguments: dorsal-ventrally flattened free-living insects in a wide variety of habitats today exhibit lateral lobes. Objections: As with gills, a second function is required but the theory is not teleological. Note that it is possible to derive a flapping mechanism here if the structure is linked to a function. Oribatid mites of the Superfamily Gallumoidea have lateral flanges known as pteromorphs which can be outspread to allow for walking or folded down to conserve moisture. This latter function could merit a special category but is combined here under camouflage in that it is difficult to envision a *small* organism developing wings *initially* when anemotaxis would suffice. This pteromorph idea may also be applicable to improved efficiency in thermal-regulation as a natural selective pathway to produce a flapping wing.

Wings developed from thermal-regulatory lobes. Because early fossils show prominent paranotal lobes, these could have arisen as thermal-regulators and secondarily been co-opted as wings. Supporting arguments: Lobes on the thorax do (in models) substantially increase the temperature of a limited body volume (such as a thorax where other locomotor organs occur). This, of itself is a selective advantage. Also, such a development again addresses the question as to development of wings on the thorax only. Objections: insect integument is not a good heat conductor, consequently (as with gills and oxygen uptake) while there is great thermal-regulatory advantage in a small surface area increase, the diminishing returns point is quickly reached.

Paranotal lobes as gliding or parachuting organs. Lobes developed as a direct selective advantage in escape from predators or even dispersal are advantageous since a controlled descent allows a larger body size (if parachuting) or a means to reach another portion of a discontinuously distributed habitat. Supporting arguments: Prominent paranotal lobes are found in many fossil insects and specifically, those occurring on the meso/ metathoraces are often elongate in nymphs. Objections: Out of more than a million species of described insects today, *not one* species glides using an immovable foil. The pathway to flapping is difficult to envision—hinging a parachute. Finally, a certain size lobe is required *before* any appreciable advantage is accrued in parachuting or gliding. *But important* note: experimental tests on cylindrical objects with 'paranotal lobes' show that the lobe size required to derive the benefit of a controlled descent begins just about where the point of diminishing returns in lobe size is reached for thermal-regulation!

Morphological origins for insect wing development are circumscribed by observations on the present-day insect fauna and the necessity for agreement with the fossil record. Because of the great diversity of insect form and the mode of development *and* embryology, observations on one group are not always directly applicable to another. This lack of universality, perhaps more than any other factor has contributed to the wide variety of theories above and in the continued support for each of the differing theories which follow.

Paranotal lobe theory of Insect wing development. Insect wings are derivatives of the definitive thoracic tergum or notum. At some point a 'rubicon' was reached, whether by gradual selective pressure or co-opting of functions such that wings were developed from such lobes. Supporting evidence: Again paranotal lobes are present in fossils of the most ancestral of pterygote insects. Embryology of Orthoptera clearly shows gradual wing development from the thoracic tergum. Objections: Embryology in different insect groups apparently shows differing sequences— see below. Also, paranotal lobes in fossils shows a line of possible flexion— in nymphs and adults. This could be interpreted either as: lobes were at their inception were movable structures, or these lines may represent sulci and the lobes as such are then not articulated at all. See above under the co-option category.

Gill theory of Insect wing development. Wings are the serial homologs and development in the thorax of the sequence of lateral gills present on the abdomen of aquatic insects such as the Ephemeroptera. Wings are evaginations of the pleural wall. Supporting arguments: Abdominal gills and thoracic wings are innervated and moved by means of serially homologous nerves and muscles (at least in Paleopteran insects). The same muscles and nerves can be found and homologized on the first two or three abdominal segments of Orthoptera. The origin of wing flapping is accounted for by this theory. Koehn and Kingsolver postulate an intermediate stage with a form taxiing along the water surface— as adult stoneflies will do when their wings are partially clipped. Objections: Lack of abdominal wings not explained. Embryology clearly shows gill development from either the tergum or from an area immediately above the coxa and subsequent gradual displacement of the developing gill to its present 'mid-pleural' location. Finally, gills contain branched tracheae which indicates a terrestrial origin for the organism and these terrestrial organisms had paranotal lobes. This theory has the underlying supposition that pterygotes are aquatic in origin when the oldest pterygote fossils known are terrestrial, all apterygote fossils known are of terrestrial types *and yet* aquatic creatures are preferentially preserved as a direct result of taphonomy. Also, at present there are no apterygotes confined to aquatic/limnic habitats.

Exite theory of insect wing development. In its present form this theory states that the ancestral arthropod limb consists of the following segments from distal to proximal: pretarsus, tarsus, basitarsus, tibia, patella, femur, prefemur, trochanter, coxa, subcoxa, and epicoxa. In the Hexapoda, it is widely accepted that the subcoxa is incorporated to form the pleural wall (epimeron/ episternum) and that the prefemur (usually) and patella (always) are lost. The present theory adds and accounts for an additional leg segment (epicoxa) which leaves the definitive number of leg segments in the Insecta at eight. The remnants of the epicoxa form the pteralia (basal wing articulating sclerites) and the wing itself is the exite lobe of the epicoxa. One modification is the suggestion that the dorsal wing surface is formed by the exite while the ventral surface by the endite of the epicoxa. Supporting arguments for the exite theory: Embryology of Odonata (Coenagrionidae) clearly shows the embryonic wing migrating from a coxal position to a position high on the pleural wall. Libellulid wings show a derivation from the terga, Ephemeroptera gills show embryonic migration from tergum or near coxa to pleuron. Conclusion, throughout the more primitive insects a tergal migration of wing/gill embryonic structure is observed with occasional secondary migration of structures so that the present ontogeny represents 'snippets' of past phylogeny. Earliest fossil pterygote insects show exites on leg segments and the pleural wall. Wing bases in these same fossils show a very large number of pteralia (a bauplan of 32 is postulated in this theory) and, the thoracic notum is not a single sclerotized unit but shows numerous distal sutures indicating a composite origin. Objections: Because of the universality of the bauplan presented, a combination of characters not able to be derived from it is difficult to postulate.

Other features of this theory: bauplan gives 32 pteralia arranged in eight rows of four 'columns' each. The four 'columns' from proximal to distal are collectively termed proaxalaria, axalaria, fulcalaria, and basivenaria. The eight rows correspond to a homologized system of eight major wing veins, each with anterior (convex) and posterior

=sector (concave) elements-- see handout. The veins from anterior to posterior in an extended wing are: precosta, costa, subcosta, radius, medius, cubitus, anal, and jugal. Fusion of various combinations of the 32 pteralia form all combinations of wing articulation seen in the insects; loss or fusion of various components of the elemental eight veins accounts for all venational patterns seen in modern insects. How would you homologize this system by Kukulová-Peck with that of Chapman/Wootton?