

# The Origin of Wings and Venational Types in Insects

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There have been many theories as to how the wings of insects arose, and from what parts of the body they were derived, but with increase of knowledge of the morphology most of them are either wholly abandoned or considered very improbable. Most insect morphologists now agree that the wings are in some way derived by the extension of the lateral edges of the dorsal sclerites of the two segments (mesothorax and metathorax) to which they are attached, and that they served to plane through the air, more or less like a flying squirrel or a flying fish, before true flight was developed.

In a similar way the theories as to the pattern of wing veins have evolved with increasing knowledge of the details, until we now have agreement that there is a fundamental pattern from which all the insect venations are derived, though there is still a good deal of argument as to the equivalence of particular veins in the different orders. The remaining points of argument have come to be mainly the following: 1, whether the dragon flies and may-flies can be properly compared to each other, and, whether or not, the relation of their veins to those of other winged insects; 2, whether the difference between convex and concave veins is more or less significant than the patterns of the pupal and nymphal tracheae, and if important, which veins were originally concave; 3, whether the front branch of the vein called *media* is homologous in all orders of insects, and if not, whether the vein called  $R_{4+5}$  in some orders is the equivalent of the one called "*media anterior*" in others by some authors; 4, whether the "*axillary*" or "*anal*" veins can be directly compared in the different groups of orders, or whether they must be considered to be several different selections from an originally amorphous series; and 5, to what extent the veins in the various fossil insects loosely grouped as "*Palaeodictyoptera*" can be homologized to those of living insects.

The following account is planned to give a key to the present state of our knowledge, and attempts an answer to these questions. I have assumed that the illustrations in three standard works are at hand: Comstock's "*Wings of Insects*," Snodgrass's "*Principles of Insect Morphology*," and Handlirsch's "*Die Fossilen Insekten*," but believe that the figures included in this paper are enough to explain the general line of the argument.

## The Origin of Wings

We must start with the condition of the two posterior segments of the insect thorax as it was shortly before the beginning of wings. Figure 1 is so drawn as to be comparable with Snodgrass's figure 91, p. 165, in the "*Principles of Insect Morphology*." The *tergum* (T) formed a broad plate, the whole width of the body, ending in a flange, *W*, along each side (shaded in the

figure), whose lower as well as upper face belongs to the tergum. On the side of the body below this lies the *pleura*, bisected by a vertical infolding, the *pleural suture* (*Pls*) dividing it into the anterior *episternum* (*Eps*) and posterior *epimeron* (*Epm*). Internally this infolding was a heavy flange (Snodgrass Fig. 92), ending in a knob above, the *wing process* (Fig. 1, *W. P.*), which supports the lateral flange of the tergum at a single point near its middle, that we shall call the fulcrum (its position marked by an asterisk\*, in Figs. 2 and 3). The tergum was also subdivided, but only the *scutum* (*Sct*) and *scutellum* (*Scl*) have relation to the developing wing, for the lateral flange is an extension of them only, and the postscutellum and phragmas are excluded. The musculature of body wall and legs was, of course, already highly developed, but we must call special attention to two leg-muscles running from the upper edge of the pleura to the coxa, a *basalar* (3E' of Snodgrass's Figs. 102C, 103, etc.) and a *subalar* (3E''), respectively muscles E and F of Snodgrass's "Morphology and Mechanism of the Insect Thorax," *Smiths. Misc. Coll.* vol. 80, no. 1, 1927.

A third preëxisting structure that is drawn into the formation of the wing is the tracheal system. A characteristic of the insect tracheation except in a few of the lowest Apterygota is that longitudinal trunks are formed on each side by the anastomosis of a branch of the leg trachea of each segment with the anterior trachea of the following; this compound trachea becomes very large, and in the abdomen of the caterpillar runs in a distinctive way ectal to the deepest fibre or two of the transverse lateral muscles. In the thorax the large longitudinal trachea that takes its place runs ental to the *entire* musculature, even the fibre which corresponds to the innermost one on the abdomen, but comparative study shows that there is another more ectal trachea, in the position of the abdominal one, and this trachea is produced in some forms by the anastomosis of a leg trachea in front with a primary trachea of the segment behind.<sup>1</sup> This one is the tracheal loop which supplies the wings, and is shown in diagrammatic condition by the very primitive Neuropteran, *Chauliodes* (Chapman in Comstock's "Wings of Insects" p. 32, fig. 20). I would suggest that this one was originally the continuation of the longitudinal trunk of the

1 Šulc in *Acta Soc. Sci. Nat. Moraviae* iv, pp. 283, etc., 1927 (*Zool. Rec.* 1930), would equate the two main tracheal stems of the wing to the two main tracheae of the paranotal lobes of *Machilis*. Unfortunately for his theory the basal connections are entirely different. In the winged insects the anterior stem comes from the leg trachea of the same segment, the posterior from the anterior side of the spiracular tuft of the following segment. But in *Machilis* as figured by Šulc the first comes from the dorsal and the second from the leg trachea of the same segment. I incline to the theory that the wing-tracheae have developed from the longitudinal trunk after it was formed, and that it is not homologous with the more dorsal series of anastomoses in *Machilis*, though the latter may become the *definitive* longitudinal trunk of the thorax, as it obviously is in the cockroach (Comstock, *Wings of Insects* 31, fig. 18). It would still be possible to save Šulc's plan by modification—assume that the anterior trunk of *Machilis* was wholly lost, that the posterior trunk, which *does* come from the leg trachea, and does supply most of the paranotal lobe, becomes the anterior one of winged insects, and that the posterior trunk is secondary. In fact this is minute and almost always overlooked in the may-flies, and was omitted by Šulc in his may-fly figures.

abdomen, and that its smallness and late appearance was a secondary effect of its having become involved in the wing, — so sharing its late development.

The nerves to the sensory organs of the wings are probably of at least equal importance, and in the finished wing accompany the tracheae within the veins,<sup>2</sup> but we know too little about their history and basal connections to bring them into our history. This nerve is morphologically the anterior lateral one, and supplies most of the segmental muscles as well as the wing.

Before the commencement of wings, then, we have on each thoracic segment a chitinized shelf-like extension of the tergum, supported a little behind the middle by the pleural ridge, and with an important longitudinal trachea running along it within, and supplying it with tracheal twigs. The shape of the flange would doubtless cause these twigs to take the form of a single longitudinal series.

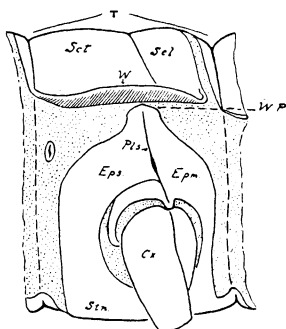


Fig. 1. Hypothetical Segment of Thorax, before Wings; side view.

### First Stage of Development

Present theories of the first rudimentary approach to flight may be divided into two groups. According to one school the pre-flying condition took the form of a strongly flattened insect, essentially like an apterous cockroach or *Machilis*, that developed the habits of climbing up the trunks of the Devonian trees and planing off to a new locality, as many of the apterous cockroaches are still in the habit of doing. Others would have in mind an insect that was at home in the water, and developed the habit of leaping out from time to time like a flying fish. One may call these two the flying squirrel and the flying-fish schools. What follows is developed on the squirrel theory, but its application to the flying-fish theory would call for merely minor changes.

We have then a flat insect, — a pre-cockroach, — with the habit of leaping and planing like a flying squirrel. In such a creature any increase of width of the lateral flanges would make for longer flight, and a special widening rather

<sup>2</sup> See e.g. Racięcka, O unerwieniu skrzydeł u *Rhopalocera*. *Prace Zakładu Zoologicznego Uniwersytetu St. Batoregu w Wilnie*, vol. iv, no. 12.

in front of the center of gravity would be very useful for control. So I postulate an insect in which a couple of segments (the meso- and metathorax) are specially extended in the form of lobes such as are shown in top view in Fig. 2. In this figure I have shown the longitudinal trachea (the ancient one, not the one of modern larvae) with the portion marking the link between its two original trunks dotted. I have shown the tracheal twigs which support the flange, now at least arranged in a single series, and with the usual tendency of tracheae to dichotomize. I have figured the one in the middle of the series, where the flange has become widest, as already having a double dichotomy, but this may perhaps be an anticipation of a later condition. An important feature of this stage, however, is that the foremost twig supplied by the trunk from

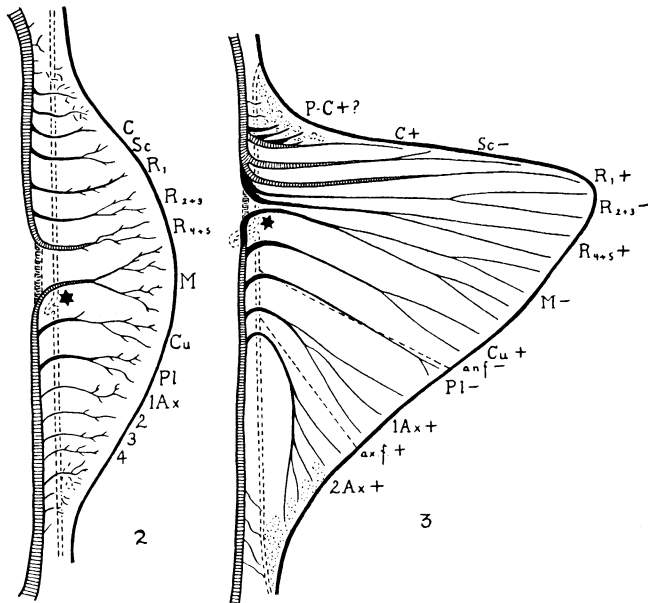


Fig. 2. Hypothetical planing wing with tracheae; early stage. Fig. 3. Same; fully functional stage.

the spiracle behind runs around *in front* of the fulcrum (\*), a fact very noticeable in later evolution, and one indicating that at this stage the pleural suture did not have its forward slant, so characteristic of all flying insects except the Odonata, but had its upper as well as its lower end well behind the middle of the segment. This is still the condition in *Thysanura* (e.g. *Japyx*, Snodgrass, Sm. Misc. Coll. lxxx (1) fig. 10.) or to a less degree even in Heterometabolous nymphs (l.c. fig. 13).

We can assume that muscular action will be of some slight effect even at this stage, if as is probable, the chitine was somewhat flexible. Even though the material later to become the basal and subalar sclerites, was doubtless

still the upper edge of the pleura, contraction of the basalar muscle (3E' of Snodgrass '35, E of Snodgrass '27, p. 65, fig. 28) would obviously pull the front of the wing down as well as move the leg, and by this warping would produce a turn toward the side whose muscle should contract. A simultaneous contraction of the subalar muscle, serving to immobilize the leg, would also aid the warping of the wing, even at this stage.

### Second Stage

The line of evolution would obviously go in the direction of greater support and more effective steering, since true flight would hardly yet be possible. The first need would lead to a direct increase of area, the second to the specific lengthening, concentration and strengthening of the portion of the "wing" controlled by the basalar muscle. We may assume that by this time the tracheae (and their accompanying nerves, of course) had come to a definite number in the broader portion of the flap, though still indefinite in front and behind; and we may now tag them with the familiar names (Fig. 3). I have applied the traditional names to the two figures.

This new step, as compared with figure 2, has involved the following changes: 1, the flap is longer, broadening the body for better sustentation; 2, the fulcrum has moved forward, concentrating the part of the wing controlled by the basalar muscle; 3, 4, the tracheae in the anterior portion of the wing have presumably enlarged, and this portion has doubtless come to be more chitinized (stronger and stiffer) than the posterior portion; 5, this same portion has become relatively longer, and the 4-forked *M*, which was the center of a symmetrical wing, has slipped back to a subordinate position in the thin part of the wing; 6, the veins which are to become *R*s may well have suffered the same fate; but 7, the fulcrum and tracheal supply have kept their old relation, so that the foremost trachea supplied by the posterior trunk (*M*) now begins to take its characteristic wide loop around the fulcrum.

We now have a really efficient organ of gliding flight, and there is no reason why this stage might not have become a dominant and efficient insect type. If the *Psilotum* of the insect world has survived in some neglected corner of Malaysia, I should expect it to look like this.

### Third Stage

The conversion of the wing just described (Fig. 3) into an actual organ of flight is a simple but distinctly odd process. All that is needed is to change the steady tonic contraction of the basalar muscle (3E') into a vibratory, clonic type. As this muscle is attached to the stiffened front portion of the wing, already developed for steering, the immediate result will be a sculling motion, and actual though weak flight. Stating it teleologically an insect that started to alight (contracting muscle 3E' to bring it down) and then countermanded the order, but so inefficiently as to throw the muscle into intermittent contraction, would automatically find itself flying. At this stage

of development we must assume that the subalar muscle ( $3E''$ ) does not share in the clonus, but merely contracts enough to antagonize  $3E'$  at the coxa and prevent the leg from moving. As long as the wing-process remained longitudinally in line with the insertions of the two muscles (as in Fig. 2) it would perhaps increase the curvature of the wing, but as soon as the wing-process had moved back into the body (as in Fig. 3) its synergistic contraction with  $3E'$  would depress the wing as a whole, and it could then have served as a minor flight muscle.

At what stage of this evolution the indirect wing-muscles would begin to function as flight muscles I would hardly venture to guess. They would of course contract to fix the thorax as a concomitant to any use of other thorax muscles, but I cannot say whether they would aid the warping of the "wing" in its planing stage. The fact that they are non-functional in the Odonata

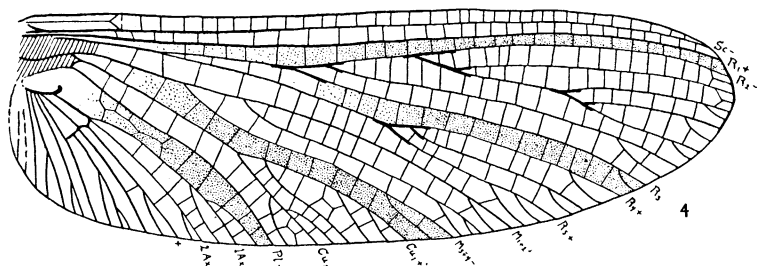


Fig. 4. Ephemera. Venation of *Prottereisma*.

suggests that perhaps they were only added to the flight muscles at a relatively late stage, by a secondary spreading of the vibratory impulse intended to activate  $3E'$ , in some form where the shape and elasticity of the thorax made such a spreading useful.

About at this point we get the modification of the wing bases which converts a series of merely bifurcated tracheae into the definitive system on which the hypothetical venation is built. An important modification of the wing as it becomes an efficient organ is the narrowing of the base, and with this the forming of a membranous hinge dorsally as well as pleurally. As a result of this the bases of the veins naturally become much crowded, and I assume that, as usual with tubular organs in such cases, there is lateral fusion of the tracheal-bases, and of the veins which come to surround them. But at this stage we get a divergence of development, which is as I believe fundamental. The veins which fuse are not the same in three main subdivisions of the winged insects: in the Odonata and Ephemera, and also in the fossil Protodonata and Ditaxineura,  $R_1$  remains a free and practically unbranched vein; in all the residue, therein including the so-called Protphemera, — and all the varied lot now grouped as Palaeodictyoptera, — the next one or two veins have joined as posterior branches of  $R$ , and form the "sector." These latter again divide into two series, in the first, represented only by fossils, — *Stenodictya* and a

few related genera, — there is a single forked concave vein attached to R, and the following main stem of media starts with a strongly convex anterior branch; in the residue, including all living forms except the Ephemera and Odonata, Media is wholly a concave vein, and Radial Sector is more richly branched; I believe in the former case the second original vein behind  $R_1$  has joined media, where it becomes the so-called media anterior (of Lameere), while in the latter it has joined radius, and become  $R_{4+5}$ . If this is correct the terms  $R_{4+5}$  and MA are mutually exclusive and should not be used in the same orders. So I should make three main venation groups: 1,  $R_1$  free, Rs, M and Cu either free (Ephemera) or combined on a single stem (Protodonata and Odonata, including *Ditaxineura*); 2,  $R_{2+3}$  forming the sector of R,  $R_{4+5}$  joined to M as MA; 3,  $R_{2+3}$  and  $R_{4+5}$  both joined to  $R_1$ , making a fundamentally 4-branched sector, and M wholly concave.

In a few primitive Neuroptera we see  $R_{4+5}$  still in a neutral state, since while it is clearly joined to R, the connection to base of M is still visible, looking like an oblique cross-veins, especially in the hind wing of Hemerobiidae and fore wing of Myremeleonidae.<sup>3</sup>

Since all these three types have fully functional wings, we must assume that in the ancestral fully winged insect the main veins (or at least  $R_{2+3}$  and  $R_{4+5}$ ) were still independent at the base.

#### Development of Texture

It is obvious that the first stage of the wing-flap is a mere extension of the body-cavity, containing as a matter of course all the normal components: blood-space, tracheae, and nerves leading to the tactile setae on the skin. Perhaps there may also have been portions of muscle and fat body which would later be eliminated, and it is obvious that there were structures of auditory type, for scolopalaee are still to be found in the large veins of most insects. The progress from this would not be the formation of veins, as usually stated, but the forming of the intervening membranes, for the veins are still extensions of the body cavity, with the essential blood-space, tracheae and nerves. There will then be two controls of the formation of the vein-patterns: 1, there must be a sufficient supply of spaces to accommodate the tracheae and nerves, to supply blood for the living tissues, and especially to expand the wing at the last moult, while between the tracheae the exoskeleton as well as the space could be thinned to save weight. The veins then were not places where the exoskeleton was thickened, but places where it was not thinned, and this probably explains the curious fact that where an injury to the nymph or pupa forms an abnormal blood-space, there is formed not a defect of the wing but a supernumerary vein (whether a trachea is present or not), while a supernumerary trachea may often fail to form a vein, if it fails to prevent the

<sup>3</sup> *Permonera* (Carpenter, Am. Jour. Sci. (5) 22, 125, fig. 6) shows this condition strikingly. I suspect it is no longer a true Anisaxian, like *Dunbaria*, but already belongs to the Neuroptera, where it combines features of both Megaloptera and Planipennia with a point unique to itself (the loss of Cu).

collapse of the original blood-space. The tracheae, being preëxistent, however will obviously be the normal reason for blood-spaces to remain and then for veins to be formed.

2. With the thinning of the intervening areas the veins obviously also become the main strength of the wings. It is plain that this need is equal but different to the other, though both require a certain minimum of space between veins, and both require a similar connection to the base. In general we may assume that the two needs are compatible, and that a vein can take a position useful for both, though in many of the higher orders the temporary need of blood for expansion of the wings is supplied by un-chitinized veins that collapse and disappear as the wing dries, — striking cases being the fugitive net-veining of the cicadas (*Am. Nat.* 56, 191, 1922) and 1st A and the base of M in all but the lowest Lepidoptera. The reverse condition obviously cannot exist, since blood will be necessary in any case for the secretion of the hard skeleton (sclerotization) *after* expansion is completed.

It is an interesting question whether the cockroaches may not owe the thickness of their elytra to the incompleteness of this process; for they are the only living order whose continuous history goes back to the beginning of our record. In them the distinction between vein and cell exists, but is one of degree, not kind, the interspaces being thinner than the veins, but still supplied with a blood-space. The Coleoptera, which show the same condition even more

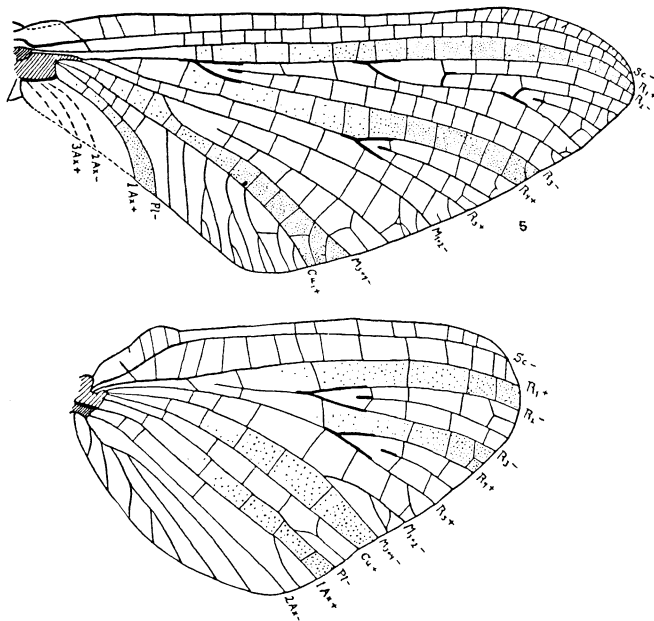


Fig. 5. Ephemera. Venation of modern type (*Siphonurus*). The hind wing drawn on a larger scale.



strikingly, must be a case of degeneration, since they are obviously from the Holometabolous stem, which certainly had a long history of fully membranized wings in their ancestral Palaeodictyoptera or Anisaxia, and Megaloptera.

### Development of the Hinge

We started with a long flap of elastic chitin (Fig. 2). The line of progress of such a structure as it becomes more movable is always the formation of an articulation. Obviously in the present case the need is first for a pivot, for the vertical motion which we assume in steering, and then a longitudinal hinge to serve the wing-stroke as soon as true flight is developed. The second of these needs could be served by a mere dechitinization of the line where the wing attaches to the tergum, but the first requires the shortening of the long chitinous base. We need to get a firm point of attachment at the middle of the wing, or a little in front, then a loosening of connections both in front and behind this point. The attachment is formed in fact of two structures. The *fulcrum* (\*), where the wing rests on the pleural wing-process, serves to resist the down-stroke, and the media drops below the general wing-level to associate itself with the fulcrum and take the main function of support. The remaining attachment to the tergum is taken by radius, which rises and becomes the principal convex vein of the wing; it also moves back, so as to be as near as possible to media and the wing-process and form an efficient pivot. I believe it is this coming together of radius and media that crowds out sector and media anterior (or the fuller sector with  $R_{4+5}$  as well as  $R_{2+3}$ , and forces their branches to migrate onto the stem of either radius (higher insects,  $R_{2+3}$  of *Stenodictya*) or media (Odonata,  $R_{4+5}$ =MA of *Stenodictya*). Only in the Ephemera does sector keep its independence, and it does so at the cost of its base.

At about the same point of evolution we may assume the basalar and subalar sclerites became independent of the episternum and epimeron, respectively; and became small sclerites, merely serving the two direct wing-muscles. Even the Ephemera have reached this condition, though the basalar is inconspicuous and the subalar is very large and has often been mistaken by morphologists for the epimeron. In the Odonata, which are also commonly said to lack basal sclerites, the pleural ones are fully developed, but so deeply imbedded as to be easily overlooked, — they form mainly large muscle-tendons, — and are connected directly to the wing by bands of tough membrane.

We have noted that the basalar muscle ( $3E'$ ) is now the principal if not the only flight-muscle, as well as the principal if not the only muscle for the down-warping of the wing on landing. It makes its connection to the base of the next vein in front of R, which we can now call subcosta, and causes it to become a second concave vein. The vein in front of this again makes connection (through the tegula) with the small muscle which pulls the wing forward (one of the tergo-pleurals), and becomes the front edge of the functional wing in all forms above the Orthoptera. In these latter a few *precostal* veins may intervene, but in all other winged insects the precostals degenerate to minor twigs or disappear.

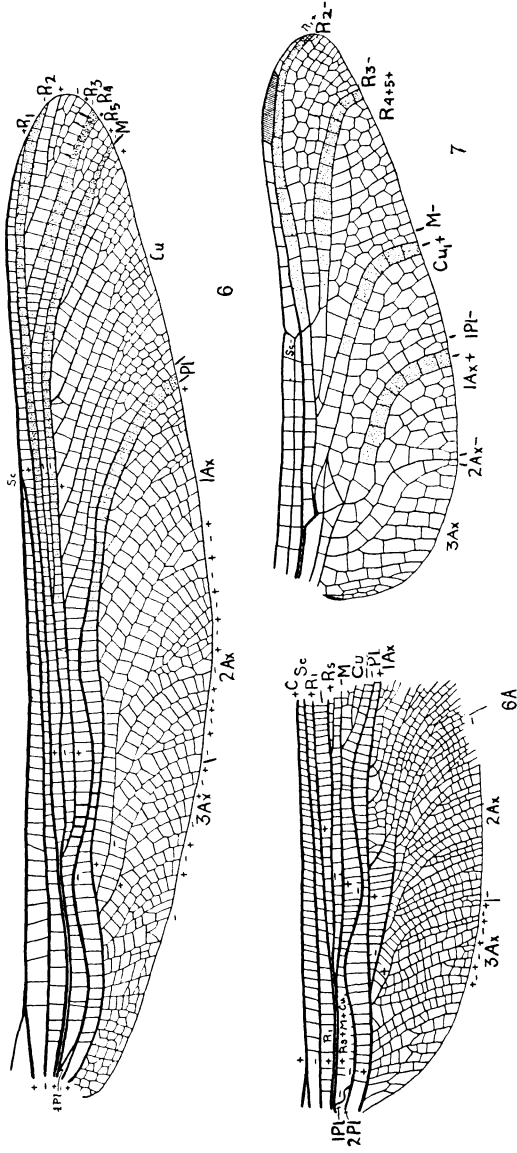


Fig. 6. Protodonata. Fore wing and base of hind wing of Typus. Fig. 7. Odonata. Libelluline hind wing.

Behind the fulcrum further development takes quite different directions in the various main lines. We must first divide the flying insects into those which can fold the wings back over the body (Neoptera) and those that can only lift them up above the back, or occasionally not even that (Palaeoptera, including of living forms only the Ephemera and Odonata). In the latter there is only one step of progress in the machinery; the bases of the veins (cubital and anal-axillary group) become concentrated close behind the fulcrum

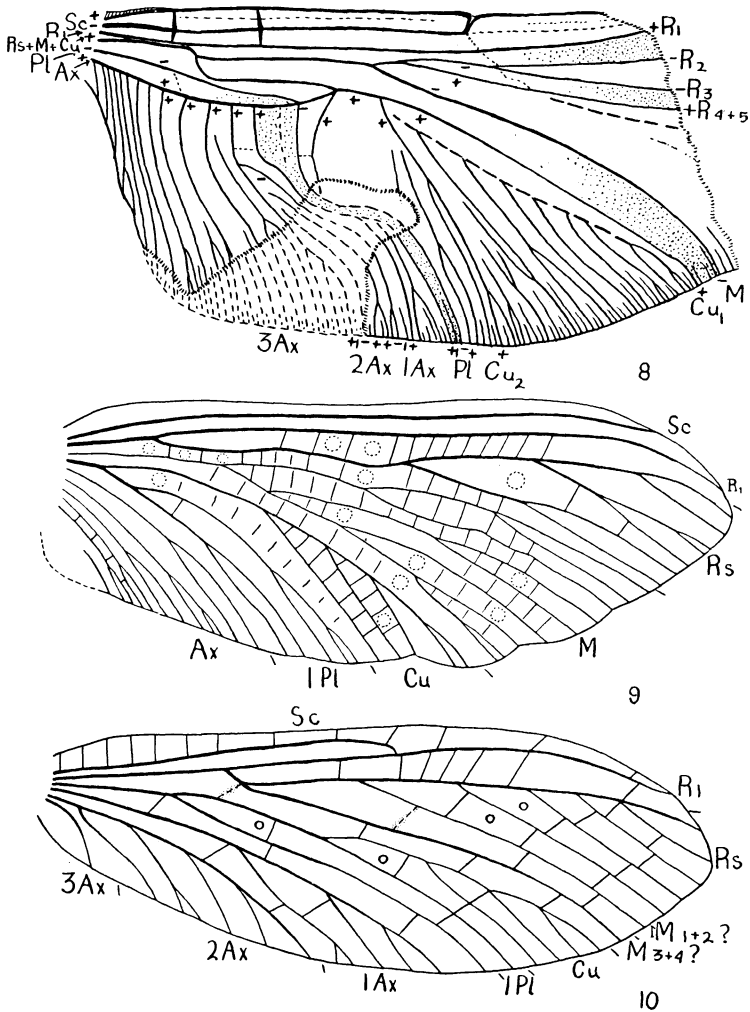


Fig. 8. Odonata. *Æschnidiopsis flindersensis* (Wood). Hind wing. Fig. 9. Anisaxia. Lamproptilia. Fig. 10. Neuroptera Megaloptera. Diaphanoptera.

to aid the pivot-motion of the wing (rotating on a transverse axis), and at the same time are cut off from the body by a band or area of membrane which serves as the hinge for motion on the longitudinal axis. In some forms they remain numerous, though the most posterior always fuse together to a certain extent, and the second (plical, in some orders commonly called first anal, in others treated as a branch of Cu) often fuses at the base with the first (true cubitus). At this same time the extreme bases of the veins are modified into a series of thickened knobs, the *axillary sclerites*. In the Odonata and doubtless the Protodonata these remain continuous with the veins, and in the Ephemera are somewhat amorphous, but in the Neoptera the portions of the veins just beyond them become flexible, at least from front to back, and in the case of the veins behind radius often become completely membranous. In the first two cases the contraction of the axillary muscle (Snodgrass Fig. 103, *D*) merely pulls down the axillary sclerite to which it is attached and thereby raises the wing, in the Neoptera a further contraction pulls the sclerite in deeply, folding the wing down and back over the body, as explained more fully by Snodgrass. In the Ephemera the number of axillary veins (of somewhat uncertain homology) which reach the base of the wing or nearly so, remains large (Figs. 4 and 5); in the Protodonata and Odonata the whole axillary system fuses into a single main stem at the extreme wing-base, and its three branches a little further out may or may not represent the three axillaries of Neoptera. In the Protodonata these three main branches are clearer than in the modern Odonata (Fig. 7) and are convex, concave, convex. In the broader-winged Odonata this region is involved in a complicated system of truss-bracing, producing the *anal loop* or "boot." My own interpretation of this is based on the condition of the Protodonates, and differs from that accepted by Odonate specialists (see below) but we both agree that there is a single basal anal main stem which forks into the two or three anals further out.

The entire Neoptera, both Orthopteroids and Holometabola, agree on the pattern of axillary sclerites and the mechanism of wing folding, for the details of which see Snodgrass. Here again the axillary muscle pulls on sclerites formed by the partial fusion of the bases of the cubital and axillary veins, which are now almost independent of their outer portions. The first pull has the same effect of raising the wing, but further contraction causes it to swing back over the body, developing a convex fold through the midst of the axillary area (ax.f.+ of Fig. 3) and a second concave fold close to the body. In the hind wing of the Orthopteroids this axillary fold is close behind the Cu and Pl, only one more vein intervening (which I have called 2d Pl), but in the Holometabola the fold is frequently lower, in the middle of the anal fan. There are also frequently further lesser folds (very numerous below the ax. fold in the Blattoids other than Corydiidae s.l., Dermaptera, and Orthoptera), but these vary from order to order. In the outer part of the wing it is a question whether the so-called axillary folds are homologous (see 5th Ent. Congress, pp. 277-284) but their basal portions and functions agree absolutely. In the Holometabola, also the Psocidae and their kin, no second plical can be identified.

Another development, present at least in all the Neoptera, is a concave furrow (not a fold as often called) from base to margin of the wing just below Cu. This lies close along the (1st) plical vein, and causes it in turn to be a concave vein. It is also a line of weakness, and when it coincides exactly with the plical vein tends to obliterate it (as also does the discal "fold" when it happens to lie on a portion of media). This, as well as the discal fold when present, have no obvious function in the adult wing, and I suspect are somehow concerned in the packing of the unexpanded wing in the pupal pad. In any case they are present in all orders of Neoptera which have an ample posterior part of the wing, and in almost all members of those orders. It is my personal belief that the second or third main concave vein of the Palaeoptera can also be treated as homologous. It has the same relation to neighboring veins and to the basal articulation, and in the Protodonata is plainly supplied by a vein running sharply back from near the base of the convex vein in front of it in the same way. For this reason I interpret the so-called Cu+A of the Comstock-Needham Odonata scheme (*Wings of Insects* Fig. 230 etc.) as Pl. and the so-called R+M (which is really two veins closely parallel in all Odonata, Protodonata and related forms) as  $R_1$  and  $Rs+M+Cu$ .

In the Ephemera the same approach will require us to choose a simple concave vein as Pl, and the obvious one is the one so labelled in Tillyard's later papers, and in Needham and Knox's "Biology of the May-Flies"; this is the vein that earlier works (e.g. Comstock in the "Wings of Insects") called 2nd A in the fore wing and  $Cu_2$  in the hind wing. By this interpretation  $R_1$  will be free and  $Rs+M+Cu$  will form a single fan, just as in the Odonata, while in both wings the remaining axillaries will arise from a single transverse basal bar exactly as in many Orthopteroids, and the second main axillary will be a concave vein.

By this interpretation we reach a position intermediate between those persons who regard the system of convex and concave veins as fundamental (e.g. Adolph and recently Lameere) and those who ignore it. If we are right there are three fundamentally concave veins, Sc because of the basalar muscle attached indirectly to it, media from its articulation with the wing-process, and Pl, from whatever mysterious cause produced the anal furrow. There is one fundamentally convex vein,  $R_1$ , because it carries the basal articulation with the tergum, and the residue are fundamentally neutral, but tend to become convex when they lie between two concave veins. This alternation of convex and concave veins also serves to strengthen the wing, and we believe that in the preanal region of the common ancestor of Odonata, Ephemera and Protodonata it had gone further, involving most of the wing in a system of alternate convex and concave veins. In these types we believe we can call  $R_{2+3}$  also concave,  $R_{4+5}$  convex, Cu convex and 2d Ax concave, though we are not prepared to carry these homologies over into the Neoptera as confidently. In the latter in particular we do not believe there were originally any concave axillaries, the concave folds in the axillary region lying between veins, and

only developing into I-veins secondarily. We accept the usual interpretation of other I-veins, but note that they are almost limited to the Palaeoptera.<sup>4</sup>

Besides the three orders which we have repeatedly mentioned, palaeontologists list several fossil types as Palaeoptera. These will be discussed more fully at the end of this paper, but we do not feel sure these are related either to each other or to the living Palaeoptera. No one has claimed that the true Palaeodictyoptera could fold their wings, — such forms as *Dictyoneura*, *Stenodictya* (Comstock Fig. 77), *Eurhythmoptyx*, Figs. 92, 100, *Hadroneuria*, Fig. 96, etc. And in these types even the nymphs held their wing-pads extended straight out (Comstock, p. 92, figs. 80, 81, from Handlirsch). In these types we believe the forces narrowing the base of the wing were the same as in the Odonata, but that fusion took place independently and in a different way, — namely MA (alias  $R_{4+5}$ ) fused with M, and  $R_{2+3}$  with  $R_1$ , producing the regular series of convex veins, each with a concave posterior branch, on which Lameere puts so much weight.<sup>5</sup> But we believe this state is secondary to an original condition in which only Sc and M were independent concave veins, that *Stenodictya* had never had an anal furrow, and that the slightly concave or convex condition of the anals or axillaries was due to minor causes. Whether this is due to the fact that these are the only known insects whose pupal wing pads are not folded back can only be decided when we discover the reason for the “anal furrow.”

As to the higher so-called Palaedictyoptera, taking *Lamproptilia* (Fig. 9) and *Dunbaria* as examples, we find an axillary area of the Holometabolous type, fundamentally as in *Corydalis*, even to the grouping of the bases of the axillary veins in a fan. It is wholly unlikely that these could not fold their wings. Other features are also Neuropterous, e.g. the ample anal area of hind wing, and nygmata (indicated in *Dunbaria* and *Lamproptilia* by conspicuous pattern elements, though not actually reported from the fossils). The plical vein is still branched in some forms, but so is it in a few primitive Neuroptera *Planipennia*, and only the convex MA and well developed cerci<sup>6</sup> show links to the true Palaeodictyoptera.

As to *Diaphanoptera* (Fig. 10) I believe it is merely a primitive relative of *Corydalis*. There is absolutely nothing incongruous, even the nygmata being shown in their proper places in Brongniart's figure. *Homaloneura* (Comstock Fig. 105) is to my eye related to it, though it still has long cerci.

### Differentiation of Types of Venation

We have arrived at an insect with fully functional wings, but not yet one that can be matched by any actually known, whether living or fossil. Each of

<sup>4</sup> The principal exceptions are certain cockroaches, themselves one of the most primitive groups of insects. In some Neuroptera, e.g. the Hemerobiidae, we have also the so-called trichosors; tiny bits of chitin bearing groups of sensory setae, alternating with the veins at the margin. These may also be extremely rudimentary intercalary veins.

<sup>5</sup> But at least in *Stenodictya* the last of these (Cu with CuP or Pl) is followed by a purely concave vein.

<sup>6</sup> A few beetle larvae still show equally well developed cerci.

the known types of wing has some further specialization, and we can cite four of these, three still living and at least one wholly fossil; typified by the Odonata, the Orthoptera, the Holometabola and (let us say) Stenodictya. In the hypothetical ancestor we had an articulation capable of movement up and down, — upwards even to the vertical position, pivoting on a longitudinal line of weakness at the base, and with some power of rotation, pivoting on a strong point formed by the junction of Radius with the tergum above and of Media with the wing-process below. Between these two joints were crowded (perhaps even crumpled) the bases of  $R_{2+3}$  and  $R_{4+5}$ , but these must have still been independent, though perhaps cut off from direct connection with the base (compare the May-Flies). Behind media again the veins must have been cut off by a flexible articular strip of membrane, through which passed blood-veins containing tracheae and nerves to supply the veins further out. The base was narrowed both in front and behind, and the most posterior veins (axillaries) and any surviving anterior ones (precostals) were gathered each into a diverging bundle. We may assume that the posterior bundle comprised a forked cubital, then a vein that was either free or already fused at its extreme base with the cubital, and behind this a homogeneous series arising from a heavy basal bar, of unknown or even indefinite number. If we forget the true Palaeodictyoptera for the moment we can say further that the wings when held vertically could be thrown back (as in resting may-flies or butterflies) and that then, at least in the hind wing two folds appeared, radiating from the articulation behind, a concave one close to the body, and a convex one through the midst of the fan of axillaries. For muscle attachment and to govern the various motions there was a system of so-called basal sclerites: and the following, which are shared by may-flies and higher insects, must be credited to the archetype. Below the wing there were two sclerites (originally cut off from the episternum and epimeron), the basalar before the wing-process and the subalar behind, each bearing the insertion of the corresponding "direct wing-muscle" and connected by strengthened membrane to subcosta and the cubito-axillary group of veins respectively. On the dorsal side it is not so clear, but it would appear that the membranous line forming the joint fell farther in than the point of articulation of the wing to the pleura, and that this overlapping portion contained swollen and distorted bases of the main veins (at least radius and one more, and the common base of the axillary mass) which served as the attachment of the muscles that lifted the wings. This is still essentially the state in the Odonata. Between the second and third was a plate of lighter chitinization, doubtless representing the vestige of the base of media, perhaps combined with what later became Rs. This plate is the median sclerite; it folds diagonally in the middle when the wing is folded back, even in *Siphonurus*.

From this point on we must follow several lines of evolution separately. What we have just described is practically the condition in the primitive may-fly, *Siphonurus*.

### Palaeoptera

In the early twenties it gradually became evident that the may-flies and dragon flies stood in contrast to other living orders of insects, and this condi-

tion was put on record in 1924, independently by Martynov in Russia<sup>7</sup> and by Crampton.<sup>8</sup> I am not sure which name has priority, but will accept Martynov's since it is simpler and equally appropriate. Each proposed the term to include the insects known (living) or believed (fossil) to be unable to fold the wings back over the abdomen. For the latter they chose secondary evidence differently, Martynov emphasizing the arrangement of the anal-axillary veins and Crampton the basal sclerites. In fact both characters break down, and we will use the term in a more restricted sense, basing it partly on other characters.

We will limit the term Palaeoptera to the Ephemera and Odonata with their fossil kin, chiefly the Protodonata. They show the following characters, most of which have occasional exceptions on one side of the line or the other: Wings without basal sclerites dorsally (vestigial in lower Ephemera and presumably present in fossil types), not capable of being folded back rooflike over the abdomen (so folded in nymphs of Ephemera and perhaps ancestrally in the adults); wings generally plaited in a characteristic way, with four special *crucial plaits* (see below); costal space with true cross veins instead of veinlets branching off Sc and R<sub>1</sub>; wing of imago not bearing setae (but with marginal setae in subimago of Ephemera); R<sub>1</sub> wholly free and unbranched;<sup>9</sup> 2d Ax a concave vein. In the living species there are always triangular brace-veins near base of wings, crossing from costal edge to R, but these are not always visible in fossils.

The fluting of the wing-membrane reaches an extreme in the may-flies and Protodonata, where practically every vein and branch enters the fluting system, and practically every fork of a vein contains a prompt second fork or intercalary vein of opposite sign.

In particular note what I shall refer to as the four *crucial plaits* (stippled in the figures): — in these cases two veins of opposite sign run closely parallel for a distance, with usually only a single series of cells between them, and one or both giving off a series of branchlets on the other side; these are (as I interpret the venation, see below): R<sub>1</sub> and the serial Rs—R<sub>2</sub>, the serial R<sub>2+3</sub>&R<sub>3</sub> and R<sub>4+5</sub>&R<sub>4</sub>; M<sub>3+4</sub> and Cu&Cu<sub>1</sub>; Pl and 1st Ax. These occur identically in Odonata, Protodonata and the earlier Ephemera (Protereisma) though in some later Ephemera the number of intervening rows of cells is increased, but are absent in forms with much reduced venation, such as Zygoptera, the highest may-flies, and Ditaxineura.

Another character that both may-flies and dragon-flies have in common,

7 Rev. Russe Ent. 18, 145-174, 1924, translated in Psyche 37, 245-280, 1930; Zeit. Morph. Ök. Tiere 4, 465-501, 1925. He proposes the name Palaeoptera (misprinted Paleoptera in the translation).

8 Jour. Ent. Zool. 16, 33, 1924. He proposes the name Archipterygota.

9 The figures in Needham's "Biology of May-Flies" show Rs stalked with R<sub>1</sub> on the hind wing, but all the specimens of fully veined may-flies examined show them completely separated. In Siphonurus there is actually a slender clear space between them. In the Odonata all species examined show them separate, while practically all figures published show them fused.



but which is not strictly limited to them, is the extremely smooth wing-membrane, with neither fixed hairs nor setae; but if we can trust the preservation of our fossils, some of the types related to the Anisaxia also show the character. I have not seen it in any other living form, though often setae are limited to the veins and margins and very minute. And these two orders agree, and differ from other types of insects, in the nymphs being highly specialized for aquatic life and far different from the adult. In all early aquatic Neoptera the nymph is fundamentally much like the adult, and has probably been in the water for a much shorter period.

Enough of these characters mentioned are definite specializations so that we must assume these two Palaeopterous orders, with their fossil kin, have had a common stem, though certainly they had already separated when our fossil record begins. Beyond this point we must consider them separately.

### Ephemerida

It is quite impossible to determine which is more primitive, the Ephemerida or the Odonata. Each has unique primitive features, and each shows not only its own specializations, but features suggestive of higher forms, though on the whole the may-flies have the more of both.

As primitive features we may just mention the paired reproductive outlets, presence of two winged instars, free though minute terminal segment of the larval mandible (the so-called lacinia), and in the wing the presence of more than three axillary veins (in a few of the lowest types) the 4th as well as the second being concave. Most striking of all is that the veins which make up Rs, M and Cu in higher forms are still a floating fan-like mass, — though they have lost their bases, they have not yet joined up with  $R_1$ . There is definitely no MA of Lameere, since the convex  $R_{4+5}$  while free from the base of R has already joined with  $R_{2+3}$ .

The only feature that definitely connects with Neoptera is the presence of the complete set of basal sclerites in primitive types, though no may-fly is known to fold its wings roof-like, and perhaps the gathering of the axillary branches on a basal transverse chitinization (emphasized as a black bar in the figures).

To derive this scheme from the general Palaeopteran type we need only this gathering of axillaries, for the joining of  $R_{4+5}$  (MA) to  $R_{2+3}$ , and the limiting of terminal branching to certain fields, leaving the four crucial plaits free, are shared by the Odonata, and therefore already Palaeopteran.

In the two figures, one of the hind wing of the fossil *Protereisma*, the other of the primitive modern *Siphonurus*, I have emphasized the four triradii and the crucial folds for easier comparison, but it is easy to see they are almost identical, even to the pectinate  $Cu_1$ .

The history of the Ephemerida begins in the Permian, and we have no idea what may have lain behind them. *Triplosoba* (known by a single specimen) has been suggested as the ancestor, but its venation is of quite a different

type with simple MA out of the stem of M, R<sub>1</sub> already stalked on Rs, and quite different cubito-axillary system. It certainly belongs in the company of Palaeodictyoptera.

### Protodonata and Odonata

#### Comparative Nomenclature of Venations

Present Scheme	Comstock-Needham * <i>Bases</i>	Tillyard (later)**
C	C	C
Sc	Sc	Sc
R <sub>1</sub>	R + M	R + M
R <sub>s</sub> + M + Cu		
Pl †		
Ax	Cu + A	Cu <sub>2</sub> + 1A
	A' & A ††	A' & A
	<i>Terminations</i>	
C	C	C
Sc	Sc	Sc
R <sub>1</sub>	R <sub>1</sub>	R <sub>1</sub>
R <sub>2</sub>	M <sub>1</sub>	R <sub>2</sub>
R <sub>3</sub>	M <sub>2</sub>	R <sub>3</sub>
R <sub>4</sub>	R <sub>s</sub>	IR <sub>3</sub>
R <sub>5</sub>	‡	
M	M <sub>3</sub>	R <sub>4+5</sub>
Cu <sub>1</sub>	M <sub>4</sub>	MA
Cu <sub>2</sub>	‡	
Pl †	Cu	Cu <sub>2</sub>
1Ax ‡‡	Cu	1A
1Ax <sub>a</sub>	A <sub>1</sub>	‡
2Ax	§	Aspl
3Ax <sub>1</sub>	A <sub>2</sub>	‡

\* As given in the "Wings of Insects."

\*\* As given in the "Insects of Australia and New Zealand."

† Note that the designations Pl of my system, CuP of Lameere and Cu<sub>2</sub> of Neuropterists are concededly merely different designations of the same veins.

†† Not so labelled, but basal part shown (in black) as a cross-vein.

‡ Obscure veins, usually broken up where the supplements cross them, figured but not named by Comstock-Needham *et al.*

‡‡ Reviving the term "Axillary" for the veins often called "anal" but distinct from the original anal vein (which was usually Pl of my system).

§ Absent in forms figured.

VARIANT SYSTEMS: *Ris* considers the bisector of the anal loop (my 2 Ax) a true vein, labelling my 1Ax, 2Ax and 3Ax, A<sub>1</sub>, A<sub>2</sub> and A<sub>3</sub> respectively. He also accepts the whole base of this stem as a true vein (A).

*Tillyard* in earlier papers follows Comstock, except that he counts Comstock's Rs as a secondary branch of M, labelling it Ms and later IR<sub>3</sub>.

*Carpenter* follows Tillyard's later system, except that he accepts Tillyard's  $IR_3$  as the true  $R_3$ .

*Handlirsch* follows Comstock in the Odonata, but in the Protodonata he only marks main vein-areas, assigning C, Sc, R, as I do, assigning both my M and Cu to M, Pl and 1Ax to Cu, and 2Ax and 3Ax to A, — with no attention to basal connections.

All workers except Comstock and Tillyard (after his earliest papers) consider the roundabout course of the anal trachea as secondary; they treat the apparent base of A as its base and the "anal crossing" as merely a modified cross-vein.

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In the Protodonata and Odonata the crux is the interpretation of the venation. I have assumed that the tracheation is more plastic than the venation, as in other orders, and as would be expected from the less precise adjustment biologically necessary. So I have accepted the so-called "radial sector" as a purely tracheal modification, and treat the vein which it occupies (being the first convex one of the sectorial area) as  $R_4$ , as in all other orders with well differentiated convex and concave veins, — in this I follow Tillyard; but I also accept the anal tracheation as secondary (as Tillyard has shown, it varies from genus to genus) and so follow Needham in viewing the 'anal crossing' as a cross-vein only secondarily occupied by a trachea.

I have interpreted the whole system on the assumption that the plaiting is fixed in these strongly plaited forms, and in particular that the four crucial plaits (stippled) are homologous with those of the may-flies, — like them, the first is convex before concave, the other three concave before convex; and the last one, alike in Ephemera, Protodonata, and Zygoptera and Anisozygoptera, is doubly sinuate in the same way.

None of the living Odonata and Ephemera can fold the wings back, but this character is weakened by the presence of the axillary sclerites in some Ephemera, our lack of knowledge in the case of fossil types, and the reappearance of the same character as a degeneration in many Lepidoptera.

Against the features which show plainly a common ancestry for the three orders we have the fact that there is no convergence between them in the fossil record, and that Odonata and Ephemera each have primitive features not shared by the others: the Odonata having only direct wing-muscles, and no trace of the dorsal axillary sclerites as separate elements.

To derive the Protodonata from the common Palaeopteran we must add the following specializations: wing much narrowed, the main veins running roughly parallel, M and Cu fused at base with  $R_s$  (though *not* with  $R_1$ !); the three anals fused though each with a separate system of terminal branching; the more basal branches of the third with any surviving more posterior axillaries appearing as parallel posterior branches of the main stem: M reduced to a simple vein. The family figured (Meganeuridae) and most forms known show

a tendency to reduction of the apical part of wing, reaching an extreme in *Paralogus*, but only slight in *Protagrion*.

To derive the Odonata only moderate further modifications are necessary, mainly the forming of the nodus by the development of a strong cross vein at tip of Sc, and a definite stigma. The other features generally thought of as Odonate appear within the history of the Order. The Mesozoic *Aeschnidiopsis*<sup>10</sup> (Fig. 8) does not yet have an arculus, but only a sharp bend in Cu at the proper point, and still has a dozen free posterior branches of the anal stem. Unfortunately the anal loop area is lost, but *Aeschnidium*<sup>11</sup> shows the same condition as in the Meganeuridae, — a moderately branched 2d Ax as well as 1st Ax; though in this genus a secondary vein has developed parallel to the base of Ax (obviously an 'anal supplement') cutting off the bases of the axillary branches, just as the R and Cu supplements often cut off the bases of their respective branch veins.

As to the further development of the anal loop, *Synthemis* shows the exact condition of *Aeschnidium*, and the rest of the Macromiinae and Aeschnids could easily come from it by reduction, but the true Libellulinae come much closer to the true Protodonates, and presumably to the unrecorded condition of *Aeschnidiopsis*, for their "boot" could be derived directly from the Meganeurid merely by the reduction of 2 Ax to a single vein and resulting convergence at the margin of branches of 1 Ax and 3 Ax, as suggested in the figures. It is interesting to note that a few genera (possibly degenerate) do not have this convergence, though the bisector of the loop (i.e. 2Ax) is always simple. The best developed of these are *Nannothemis* and a few relatives, which also do not yet have the "triangle"; in *Bironides* and *Tetrathemis* the veins which are to become arculus and triangle are still three ordinary cross-veins.

Note also that in the Zygoptera and Anisozygoptera (both fossil and living) the structures that are to be the triangle, subtriangle and supertriangle remain ordinary cells, and the corresponding junction of Pl and Ax does not take place, but we have two parallel sinuous veins to bound the fourth crucial plait just as in the Protodonata.

In all living Odonata the anal area is much reduced, the Anisoptera with one to at most three (*Tramea*) free posterior branches, and the Zygoptera with mere stubs, but the Aeschnidiidae of the Mesozoic still had a good number (7 in *Aeschnidium*, 12 in *Aeschnidiopsis*). *Agrion* has the most of any living Odonata (apparently toward a dozen) but is believed to have a secondary increase in the number of veins generally.

Practically all the fossils that may belong to this series are recognized Ephemera, Protodonata or Odonata. The only exception is *Ditaxineura*, which still has the oblique costal brace of the Ephemera with the wing form of the Odonata and reduced venation. The separate R<sub>1</sub> is obvious in all fossils actually examined, though often not figured, and all other types sometimes called Palaeoptera are excluded by this character.

<sup>10</sup> See Tillyard, Proc. Linn. Soc. N.S.W. xlii, Pls. 42, 43, 1917.

<sup>11</sup> See Handlirsch, Foss. Ins. pl. 47 fig. 16, 1908.

### Palaeodictyoptera

There is a complex of types, all fossil, in which both radius and media are formed of a convex anterior and a concave posterior branch. I believe these are separately derived from our hypothetical type by the junction of the potential  $R_{2+3}$  to  $R_1$ , making its concave posterior branch, but of the next (convex)  $R_{4+5}$  to the following medial stem, to which it gives a convex anterior branch. I do not agree with Lameere that this is a primitive condition, or one from which the living Hemimetabola are descended (as to the Holometabola, see further). It represents approximately the Palaeodictyoptera of Handlirsch, but within the long series of families we have two distinct types, which I believe should stand as separate orders. The true Palaeodictyoptera are marked by a nymph with the wing-pads extending directly out, unlike all other insects (Wings of Insects, Fig. 80), simple convex media anterior, rarely forked close to the margin, and then much less richly than the concave media posterior or true media; simple or rarely two-branched Cu (anterior) with a more richly branched CuP (not developed as a plical) attached to its posterior side; first axillary vein (in Stenodictya) also concave, but widely separated from CuP, the following ones apparently convex; but none of the plaiting as well marked as in the preceding orders, only Sc being really deeply concave. There is no evidence that this series ever folded their wings, and the hind wings have the same simple series of anals as the fore, so far as preserved, with no grouping in an anal fan. The nymphs have been assumed to be aquatic, but I think on no evidence whatever.

This series is characterized from Stenodictya, the only type on which I have seen evidence of the convexity and concavity of the veins. It will include the whole Dictyonuridae as limited by Handlirsch (these being the original Palaeodictyoptera of Goldenberg), also Peromaptera, Megaptilus, Hypermegethes, Mecynoptera, the Lithomantidae, Lycocercus, the Homiopteridae, etc., in Handlirsch's series to Spiloptilus, inclusive, but excluding Fouquea, and finally Polycreagra. The only divergence, except for varying degree of imperfection of the record is in a few genera where Cu becomes (or remains) more richly branched, particularly Mecynoptera, Heolus and some Homiopteridae. I have seen no evidence on the plaiting of these types, but the sparse and rather evenly spaced axillaries of these are still of the Stenodictya type.

This series contrasts with the Palaeoptera, with which they have been associated, in the stalking of  $R_{2+3}$  on  $R_1$ , presence of costal veinlets, narrow plaits with a convex in front of a concave vein (unlike the crucial plaits of the Palaeoptera), and much less defined plaiting generally, lack of a definite plical vein, the concave vein on the posterior side of Cu being an ordinary branched vein, and followed (in Stenodictya at least) with a second but widely spaced concave vein and then a convex one. They differ from these and from all living insects as well in the absence of a posterior convex branch of Rs, with correlatively the presence of a convex anterior branch of M, and the nymph with wing pads sticking straight laterally. Obviously they must have been derived from a separate line far before our fossil record begins, and

the evidence is on the whole that they have left no descendants. Eubleptus and Eugereon have all the essential features of this group, and Triplosoba shows the characteristic simple MA. They should not be associated with the Hemiptera or the Ephemera.

### Orthopteroidea

The great majority of the remaining living Hemimetabolous insects have another definite type of wing. The fluting is less definite than in the Palaeoptera, and tends to fade out, though in this case it is Sc rather than Pl which tends to lose its concavity. On the fore wing M is easily identified from the under face of the wing, but on the upper side is sunk into a sharp depression, that most often closes over as a deep fold, typically covering the bases of all the veins from M to Pl (2 Pl in this series). The cockroaches and most Orthoptera have the closed fold, the Gryllacrididae, Plecoptera and Hemiptera have the open groove, but in the latter an axillary sclerite slips into it and fills it in the folded position. In this series  $R_{4+5}$  is fundamentally a portion of radius, which shows a convex posterior branch whenever the plaiting is recognizable in the outer part of the wing, and M is wholly concave, so we judge that we again have a distinct way of grouping the original veins into a definitive pattern:  $R_1 : R_s : MP$  in the Palaeoptera;  $R_{1-3} ; MA+MP$  in the Palaeodictyoptera;  $R_{1-5} : MP$  in the Orthopteroids. Another unique feature is the anal furrow: in all the forms with fairly complete venation there are *two* plical veins, i.e. besides the concave vein which normally appears as a basal posterior branch of Cu, there is a second independent concave vein in the anal furrow, which I will call 2 Pl, before we come to the first member of the true axillary series. The hind wing lacks the basal furrow or fold but has the second plical, — in fact in the cockroaches there is even a third plical, which comes out of the base of the axillary system, but is plainly of a different kind from the usually branched true first axillary.

This venation pattern obviously includes the Plecoptera and the Hemiptera as well as the Orthoptera in the broadest sense, and like the two preceding types is distinct from the beginning of our fossil record. Whether it also includes the Psocidae and their kin does not appear from wing-characters: the Psocids lack the basal fold and the second plical vein, which would seem to favor the stem of the Holometabola, but the venation is too reduced to make the connection compelling. On the other hand the incomplete transformation is against this, though the ancestors of the Holometabola must have had it once, the body characters are generally considered Orthopteroid, and the oldest recognized fossils look almost exactly like Homoptera of the same period, until we note the position of the base of Cu. In the Psocidae there is a wide space between Cu and the common stem of R and M, filled with flat membrane, in the more reduced Homoptera the basal fold brings them in contact, and then in the Psyllidae and probably the Archescytinidae they actually fuse. In the Homoptera the two plicals fuse in the fore wing at the same stage (between the Auchenorhyncha and Sternorhyncha), whereas there is only a single weak (first) plical in even the most primitive Psocidae.

### Holometabola

In placing the Holometabola we are faced with a dilemma, which the known fossil record cannot clear. At first glance the grouping of radial veins is just as in the Orthopteroids, and the fate of the second (and possibly third) plical could be easily explained by comparison of the Trichoptera with the Plecoptera (Forbes, 5th Ent. Congress, p. 282, 1933). Also the folding of the wings is exactly the same, even to the detailed way in which the axillary sclerites work (see Snodgrass, Principles of Ins. Morph. 215 ff.). But the fossil record seems to show a different connection, from the Palaeodictyoptera, through a series of annectant types to the true Neuroptera, by a late transfer of MA to the radial stem, — in fact many Neuroptera still have a slanting vein out of the base of M running across to the base of R or Rs (r-m of recent authors), plainest in the hind wing.

We must now bring up a series of fossils which have been grouped with the Palaeodictyoptera, but show all but one of the characters of the Holometabola, and to emphasize their fundamental importance I indicate for them a new Order:

### Anisaxia, new order

Insects with so far as known the general body type of the Palaeodictyoptera, with ample wings, slender body and long many-segmented cerci. Wings with radial sector wholly concave, media with a several-branched anterior convex branch (MA), Cu also several-branched, the concave posterior fork (CuP or 1 Pl) not more richly branched and often simple; following vein a true axillary, convex and normally branched, often pectinately, the following axillaries (usually imperfectly preserved) more crowded, and in the few cases visible arising from a transverse basal bar, as in all richly veined types which fold their wings. Hind wing noticeably broader than fore wing, especially toward inner margin.

This group differs from the Palaeodictyoptera in having richly branched anterior forks on both M and Cu (i.e. MA and true Cu) and especially in having all the signs of true wing-folding, the proportions being about as in the *Corydalis* group, with true anal furrow and associated plical vein. It differs from the true Holometabola in having long multisegmented cerci, and a convex MA attached to M and not to Rs. The nymph is unknown, but we may guess that the wing-pads were folded back and down as in Holometabolous pupae. It is also natural to assume that the transformation was incomplete and the nymph aquatic, but our evidence is nil. It would appear that the modern Neuroptera have been derived from it by two separate stems, since the Myrmeleonid shows a several-branched Pl<sup>12</sup> (as in *Lamproptilia*, *Compsoptera* and *Homaloneurina*) while the Megaloptera like all other Holometabola have a simple one like *Spilaptera* and *Dunbaria*.

This order will contain Handlirsch's *Spilapteridae* (including *Dunbaria*)

<sup>12</sup> Best shown on the fore wing of *Palpares*.

and Lamproptilia. Fouquea is not completely enough known to place for certain, but also appears to belong here.

A feature of several orders of Holometabola, but of no other insects is the presence of nygmata (Forbes, Ent. News xxxv, 230, 1924). These are not generally shown in figures of fossils, but the pattern of Lamproptilia (Fig. 9) strongly suggests their presence. In Diaphanoptera (Fig. 10), which Handlirsch would make a separate order related to this series, they are plain, but I believe Diaphanoptera is merely a primitive genus close to Corydalis.

The Megasecaptera show the same body type, though with much reduced venation, eliminating most of the distinctions between the Palaeodictyoptera and Anisaxia; but the fact that at least Asthenohymen folded its wings points strongly to the latter. The names "Protohymen" and "Protohymenoptera," applied to a section of this order, are based on a superficial resemblance that has no basis in more important features.

### Summary

1. Wings arose in insects as extensions of the lateral edges of the terga.
2. Flight developed in 4 stages: *a*, leaping, *b*, gliding, *c*, steering, *d*, true flight.
3. The "direct" wing muscles are more immediately adapted for flight than the "indirect" ones, and probably gained their function first.
4. The adaptations in structure of the wings were: *a*, extension in length, perpendicular to the body, *b*, moving forward of the ventral pivot (top of pleural suture) *c*, crowding of anterior veins (C to M), *d*, thinning of wing substance to membrane, with closure of its cavities except at veins for support and blood supply, *e*, formation of a hinge by *f*, loss of chitinization of bases of veins, and *g*, narrowing of base with resulting crowding of vein-bases.
5. The narrowing of the wing-base resulted in basal fusion of neighboring veins (and their tracheae).
6. This fusion in the radial region took place in three different ways: *a*,  $R_1$  (convex) free,  $R_{2+3}$  (concave) fused with  $R_{4+5}$  (convex); *b*,  $R_1$  fusing with  $R_{2+3}$ ,  $R_{4+5}$  fusing with M (concave); *c*,  $R_{2-5}$  fusing with  $R_1$  at base, M (concave) free.
7. These three types of reduction of the wing base represent three lines which separated before the beginning of our fossil record: Palaeoptera, Orthopteroidea, Palaeodictyoptera.
8. The Holometabola make a fourth group older than our record, but could have been derived from either Orthopteroidea or the Palaeodictyoptera.
9. The Psocidae and their kin are similarly ambiguous and may be related to the Holometabola. They lack two distinctive features of the Orthopteroidea: the groove at base of fore wing and the second plical vein.
10. The principal orders of winged insects fall into these groups as follows:



- a, *Palaeoptera*: Ephemera, Protodonata, Odonata.
- b, *Orthopteroidea*: Orthoptera, Dermaptera, Plecoptera, Hemiptera.
- c, *Palaeodictyoptera*: (restricted), with Protephemerida and Protohemiptera.
- d, *Psocoptera*, perhaps with Parasitica and Thysanoptera.
- e, *Holometabola*: Anisaxia (now separated from Palaeodictyoptera), Megasecaptera (with Protohymenoptera), Neuroptera (with Diaphanopteroidea), Coleoptera, Hymenoptera, Mecoptera, Diptera, Trichoptera, Lepidoptera.

## NOTES ON FIGURES

Fig. 1. is hypothetical, drawn and lettered to be comparable to Snodgrass: "Principles of Insect Morphology" fig. 96.

Figs. 4-7. Slightly diagrammatic and partly composite. The "crucial folds" are emphasized by stippling, and the four most important triradii of the may-flies by thickening the bases of the veins.

Figs. 4 and 6 after figures by Carpenter.

Fig. 8. mostly after Tillyard, in Proc. Linn. Soc. N.S.W. xlii, pls. 42, 43, 1917, completed where broken from *Aeschnidium densum* Hagen, Handlirsch "Die Fossilen Insekten" pl. 47, fig. 16, 1908. Most crossveins omitted and crucial plaits stippled.

Figs. 9 and 10 after Brongniart, somewhat simplified; the markings indicating position of nygmata in Fig. 9 and nygmata in Fig. 10 accented.

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