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THE INSECT WING, PART I. ORIGIN AND DEVELOPMENT OF WINGS FROM NOTAL LOBES[1]

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ABSTRACT

The paranotal theory of wing origin receives support from morphological studies on Thysanura and fossil insects. It is proposed that the first winged insects, the Archaeoptera, had wings that resembled notal lobes in many respects. Studies of recent Paleoptera offer insights into the origin and development of the axillary sclerites and basal plates which permit the articulation of the wing. Six separate sclerites, arranged in two longitudinal rows of three, were probably the basic configuration of these structures. Their subsequent modifications in the Odonata and Neoptera are noted. Wing folding probably evolved from the flexion folds between these rows of sclerites. The erection of two major groups of the neopterous orders, Pliconeoptera and Planoneoptera, is necessitated by the evidence derived from a brief phylogenetic analysis.

The study reported here is the result of a reexamination of the wing venation of insects. This began as an effort to establish the homologies of the venation of Homoptera. Existing literature proved inadequate for this task; it was found that the scope of the study had to be expanded to include the venation of other orders, and eventually led to a reexamination of theories of the primitive venational type. It became apparent as the study progressed that the archetype of the insect wing could be better understood if certain observations by Snodgrass and other workers were added to the basic Comstock-Needham system (1898–1899). These concepts have met with little acceptance as yet. Of particular interest is the work of Forbes (1943), which, when added to the information on the paleopterous wing deduced by Edmunds and Traver (1954), gives a coherent picture of the origin of the wing, and a clearer understanding of the functional relationships of the parts.

The question of the homologies of vein systems relies heavily upon understanding of the nature of wing fluting, and the structure and function of the basal sclerites and wing tracheae. Accordingly, the first part of this series of four papers deals with the origin and development of the wing with special reference to these structures. The venational homologies must be left to a later section to permit full discussion

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of the topic, although these vein systems will be mentioned here to facilitate discussion and permit fuller understanding of the interrelationships of the wing parts.

EVOLUTIONARY STAGES OF WING DEVELOPMENT

The most widely accepted theory of the origin of the insect wing is the "paranotal theory" advanced by Woodward (1876). This theory is accepted for the purposes of this study, with additional support of it found in certain morphological features. The alternative theories of wing origin were compared with this theory by Crampton (1916) and by Alexander and Brown (1960).

Paranotal flanges. According to the paranotal theory, the wing precursors were flangelike lateral outpocketings of the thoracic tergites that served as gliding planes before they acquired a line of flexion to permit flapping motions. The main evidence in support of this theory is derived from the development of wing pads in immature winged insects. Further evidence is seen in the high degree of development of the prothoracic notal lobes in the very primitive pterygote order Paleodictyoptera. The structure of these resembles short wings, as will be shown later. The phylogenetic studies of Ross (1955) showed that the two apterygote orders most closely related to the winged insects are the Thysanura and Microcoryphia (Machilidae). This lends support to the paranotal theory, as both these groups are peculiar in possessing short but distinct lateral flanges of the thoracic segments that closely resemble the wing buds in early instar nymphs, such as those of Plecoptera. These lobes are provided with two sets of large muscles that insert just beyond the base, outside the plane of the thoracic pleurites, in a manner similar to the direct flight muscles of winged insects. Ide (1936) studied rudimentary paranota of certain nymphal Ephemeroptera, and concluded that these are homologous with the wing pads on other segments.

Why did insects acquire lobes of sufficient size to permit gliding? The answer can be found in recent insects that also possess such flanges.

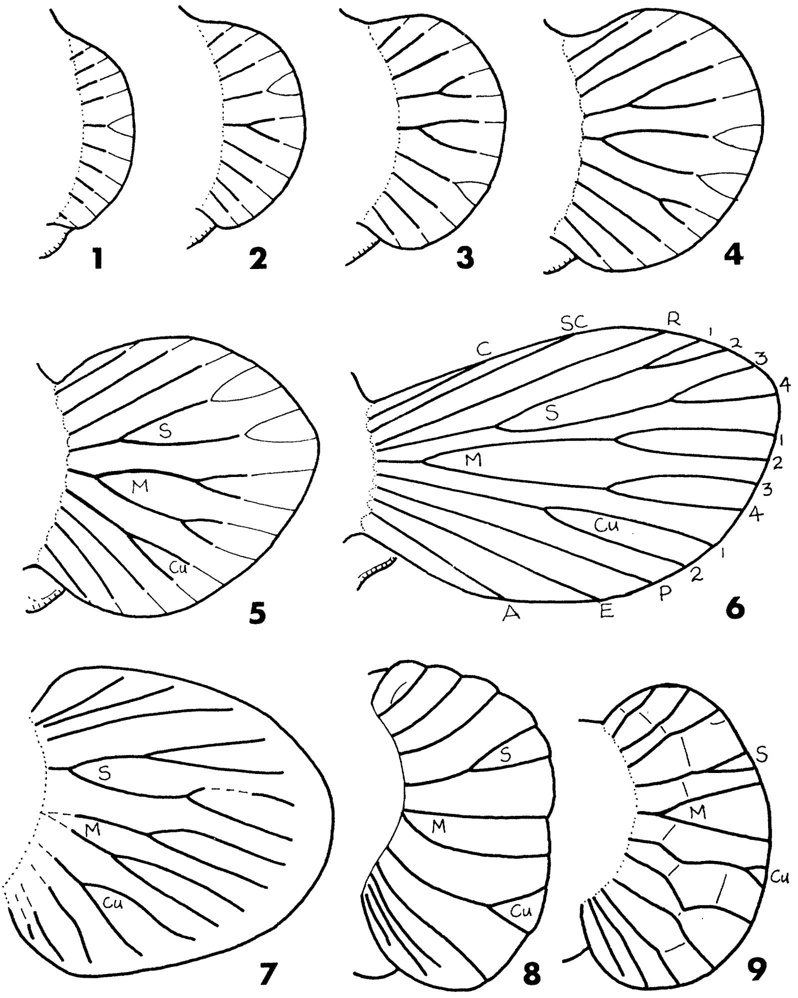
There are quite a few winged insects with large pronotal flanges. Some examples of these can be found in the Cicadellidae, Silphidae, and Chrysomelidae, while these "paranota" are characteristic of all Blattoidea, Peloridiidae, and Tingidae. With the exception of the paranota of cockroaches, all are probably secondarily derived. They occur in widely unrelated groups and have close relatives that show no evidence of such structures. Almost without exception, these lobes are found in insects that are strongly dorsoventrally flattened, and presumably aid in concealing them. Thysanura are generally rather flattened; I therefore postulate that some group of these creatures, more highly flattened than the rest, expanded their thoracic lobes to conceal themselves. Such lobes would be of sufficient size to make gliding jumps possible in these small insects (Flower, 1964).

Gliding lobes. According to the paranotal theory, the gliding planes must have originally been equally developed on all three thoracic segments. The form of these lobes is thought to have resembled the prothoracic paranota of the Paleodictyoptera and the meso- and metathoracic wing buds of immature winged insects. These lobes would thus be directed backwards, least strongly so on the prothorax and most strongly so on the metathorax. This agrees well with the shape of the lateral flanges of the Thysanura. Presumably, the prothoracic planes would be needed to balance the insect, compensating for the other planes being turned backwards.

These paranota would carry tracheae derived from the superficial notal trachea that existed before the lobes developed (Forbes, 1943). It seems most likely that all these tracheae originally arose from a single trunk. Thysanura have a single such trunk servicing their notal flanges (Barnhart, 1961). The wings of most Ephemeroptera are also serviced by only a single such trunk (Comstock and Needham, 1898–1899). Higher insects have the wing tracheae arising from a loop, the "alar arch," evidently formed by the fusion of a posterior trunk to this branching anterior tracheal trunk (Ander, 1938). Most insects have the posterior trunk continuous with the end of the anterior one, setting off only the anal tracheae on a common stem. Tillyard (1923) reported an alar arch in *Nesameletus* (as *Ameletus*) (Ephemeroptera), which differs in having the posterior trunk fused to the anterior one between the cubital and median tracheae. The alar arch must therefore have been evolved twice from the condition with two free trunks.

The superficial branches of the main trachea would be carried outward as the paranota enlarged. As the lobe widened to form the gliding planes, the apical tracheal branches would become further apart, and would have to branch to service the entire lobe. Since the tip would expand most rapidly, the first branch would occur at the tip (Fig. 1). The trachea immediately in front of this would branch next, as the wing precursors, resembling wings, would be broader in the costal region (Fig. 2). Still further enlargement of the lobes would result in the branching of the trachea immediately behind the first branched trachea (Fig. 3). Elongation of the lobes would necessitate further branching of these same tracheal systems (Figs. 4–5).

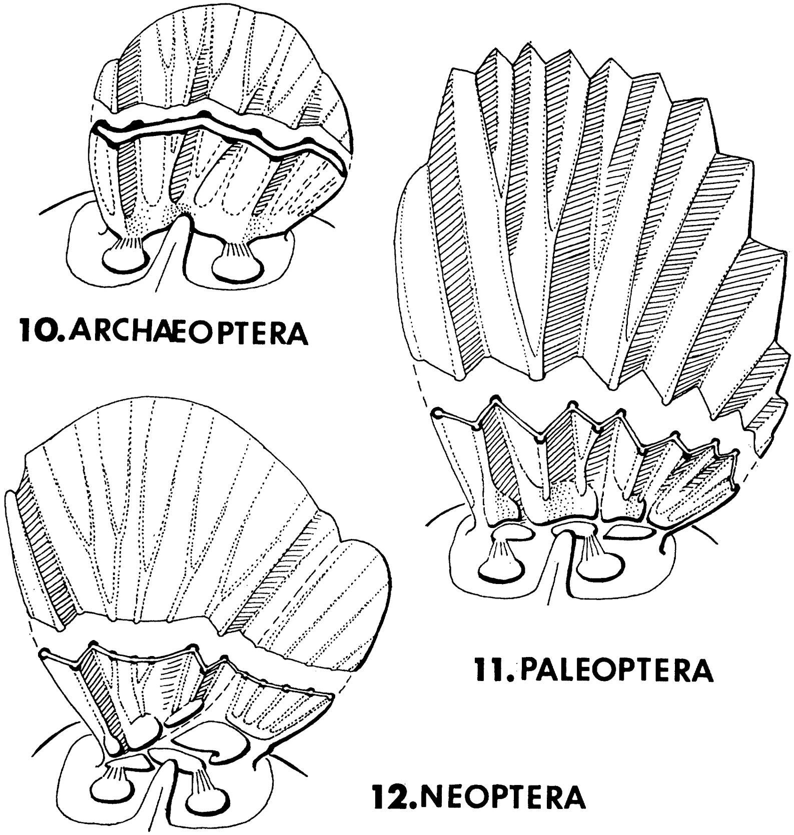
Most of the pronotal paranota preserved in fossils show little structural differentiation. Tillyard (1928) studied the paranota of *Lemmatophora typica* Sellards (Fig. 9) and noted that its twelve setose ridges closely resemble the thickenings around the tracheal trunks in nymphal wing pads. These structures branch in exactly the same manner as those in Figure 3, the longest forkings corresponding to the earliest branchings, as outlined above. These tracheational branchings are similar to those apparent in the paranota of *Stilbocrocis heeri* Schlectendal (Fig. 8). *Lithomantis carbonaria* Woodward (in Bolton, 1921) has much more highly developed paranotal lobes; the venational branchings (Fig. 7) repeat the sequence apparent in other fossils, but in addition have the complete set of branchings of the tracheae, as in Figure 5. The



FIGS. 1–9. 1–5, Developmental stages in the tracheation of paranotal lobes (hypothetical); 6, veins of a primitive wing; 7, vein precursors of the paranotal lobes of *Lithomantis carbonaria* Woodward (drawn from Bolton); 8, same, of *Stilbocrocis heeri* Schlectendal (after Laurentiaux); 9, same, of *Lemmatophora typica* Sellards (after Tillyard).

tracheal branches of these lobes have the same features as the primitive venation of insect wings (Fig. 6).

Archaeopterous wings. The earliest wings must have been thick and heavy. Their sole support would necessarily have been their heavy



10. ARCHAEOPTERA

11. PALEOPTERA

12. NEOPTERA

FIGS. 10–12. Wing types of groups as labeled, cross-sectioned at midlength.

sclerotization. As demonstrated by Forbes (1943), the rudiments of fluting would probably have been present. The media (M) would be raised by the pressure of the pleural pivot beneath it, while subcosta (SC) and plical (P) veins would be drawn down by the attachments of the muscles from the basalare and subalare (Fig. 10). These wings would have been very clumsy by modern standards. Understandably, the Archaeoptera would not have been able to compete with the more efficient Paleoptera, and would soon have become extinct.

A Devonian fossil, *Eopterum devonicum* Rohdendorf (1961), may represent this stage.[3] The very thick veins, fine marginal veinlets,

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[3] E. F. Riek (personal communication) is of the opinion that this fossil represents a crustacean telson.

and thick wing membrane are characteristic. The convex veins are apparent on the exposed surface; a portion of this surface is broken away, exposing the subcostal vein on the lower surface.

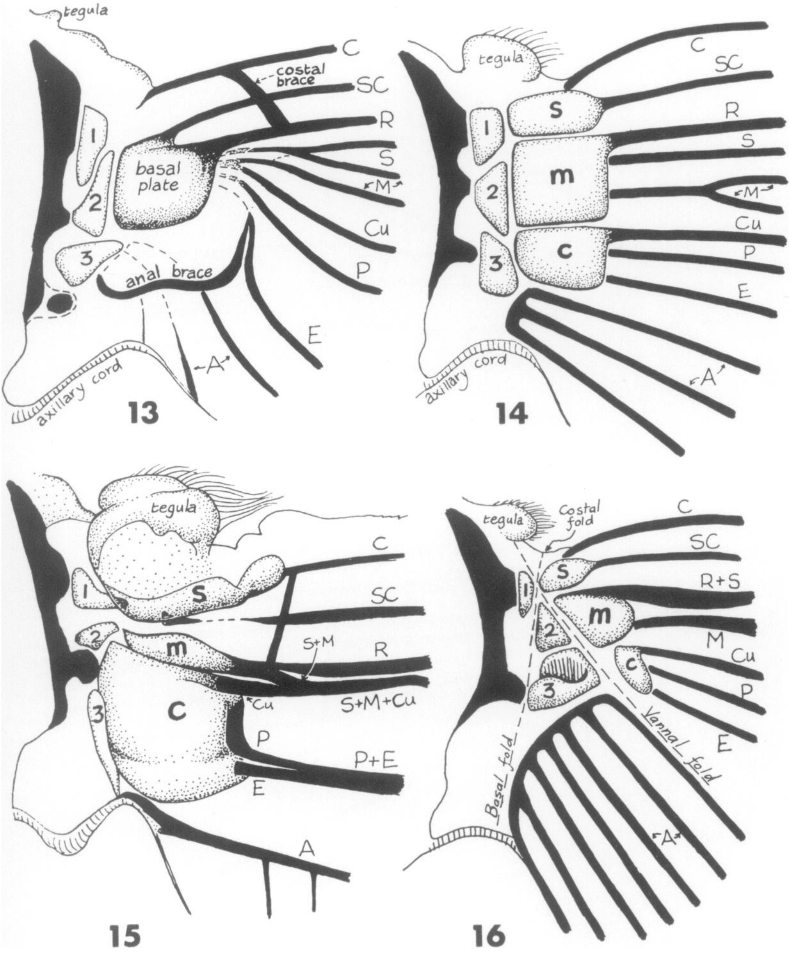
Paleopterous wings. The heavy lobelike wings that the earliest insects must have possessed could have been greatly improved by a reduction in sclerotization. Only the basal part of the wing and the region around the tracheae need retain sclerotin for supporting the wing. Weakening of the intertracheal membrane would define the true veins; hence the veins would be laid down around the tracheae, making the relationship one-to-one. The primitive venation (excepting crossveins) would then take the same form as the tracheation.

Lightening of the wings could proceed further if some of the support of the wings were supplied by the membrane itself. Edmunds and Traver (1954) showed that great structural strength is conferred by the alternation of convex and concave veins beyond the wing base, and suggested that the paleopterous condition is thus the ancestral type of all modern wings. This fluting is apparently an extension of the flexion of the archaeopterous venation, at least on the basal half. The fluting at the tip is accomplished by the addition of untracheated intercalary veins (Fig. 11).

The Ephemeroptera are the most primitive winged insects living today. Their flight is mainly a simple flapping motion, the tip of the wing bending on the upstroke (Edmunds and Traver, 1954). They retain the single tracheal trunk to the wing base. Their large number of indirect tergosternal flight muscles is similar to those of the Thysanura (Matsuda, 1970). Their wing base is especially primitive, consisting of a single heavily sclerotized plate from which all the veins arise (Fig. 13). This basal plate is probably homologous to the original heavy sclerotization between the tracheal ridges, retained for structural strength. The basal plate articulates against three small, ill-defined axillary sclerites. These can be demonstrated to be homologous with these sclerites in higher insects by musculature and by their relation to the thoracic processes (Matsuda, 1970). Their arrangement relative to each other is simpler, and all have a pivot point with the tergum.

The Odonata are the only other extant paleopterous order. They, like members of the other higher orders, have the basal tracheal trunks fused to form the alar arch.

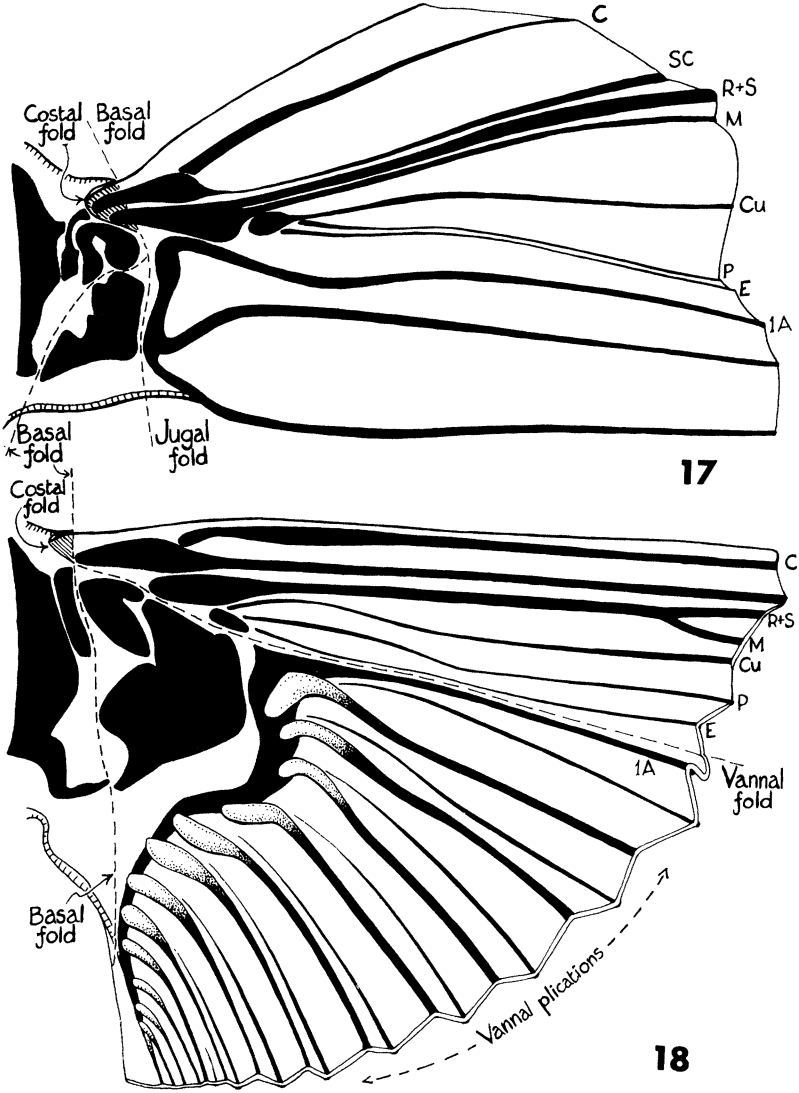
The wing base of Odonata consists mainly of several large, bulbous, rather amorphous plates to which the wing veins fuse (Fig. 15). This has misled several workers, some stating that the axillary sclerites are absent, while others recognize only the first axillary sclerite. These sclerites are to be found in the same position as those of the Ephemeroptera, essentially vertical in position below the basal plates. The axillary sclerites are small, but highly mobile, permitting considerable rotation of the wing base. Only two tergal points of articulation remain, as in other higher insects. The second of these is strongly produced, and



FIGS. 13–16. Basal sclerites of wings. 13, Ephemeroptera (Heptageniidae); 14, theoretical ancestral type; 15, Odonata (Aeschnidae); 16, generalized Neoptera. 1, 2, 3, first to third axillary sclerites; s, m, c, subcostal, median and cubital plates.

articulates directly with one of the basal plates; the displaced third axillary sclerite is largely non-functional.

The basal plate itself is considerably modified. The main body of this plate is divided into two adjacent parts, each giving rise to three vein systems. A rather remote portion of the basal plate, articulating solely with the first axillary sclerite, is fused to the heavily sclerotized tegula, and is closely associated with the costal and subcostal veins.



FIGS. 17–18. Basal part of wings of Orthoptera (Acrididae). 17, fore wing with jugal fold; 18, hind wing with vannal fold and vannal plications.

These three sections of the basal plate appear to be homologous with some of the basal sclerites in neopterous wings, and are here designated the cubital plate, median plate, and subcostal plate ("basisubcostalis" of Matsuda), respectively.

The considerable similarity of these structures in the Odonata, Ephemeroptera, and Neoptera suggest a common evolutionary origin. The Ephemeroptera retain the simplest, and hence probably the primitive structure. Later, the basal plate apparently broke up into three sections, corresponding functionally to the three axillary sclerites (Fig. 14). The types characteristic of both Odonata and Neoptera can be derived from this form. In this connection, it must be noted that the "proximal median plate" (Snodgrass, 1935) is actually a flange of the third axillary sclerite (Snodgrass, 1952), which is found only in Neoptera and is not a primitive feature.

Neopterous wings. The single feature that best characterizes the Neoptera is their ability to fold the wings over the back. This is made possible by the aligning of the axillary sclerites and basal plates of the wing to make the basal flexion folds cross one another (Fig. 16). This pair of opposite folds permits the inversion of a portion of the wing upon retraction of the muscle to the third axillary; this pulls the remigion back against the body. Extension of the wing results in a small complementary fold just below the tegula.

Two types of folding are known. The vannal fold (Fig. 18) extends between the axillary sclerites and their corresponding basal plates, and so resembles the main articulating fold in the base of the paleopterous wing. Because the third axillary sclerite is very large, this folding plane is directed posterolaterally across the wing between the anal vein system and the other veins (Snodgrass, 1935), separating the wing into the anterior remigion and the posterior vannus. Folding of this type results in the whole vannus turning over. This folding mechanism is found in the hind wings of most Neoptera.

The second type, the jugal fold, is found in all fore wings and also in the hind wings of the Holometabola. This fold merely inverts the region of the third axillary sclerite, the jugum (Fig. 17). Retraction and extension of the wing produce a sliding motion around the second axillary sclerite, rather than a simple pivoting of the subcostal plate against the first axillary, as in the vannal fold.

Sculling flight in the Neoptera requires the elimination of most of the wing fluting characteristic of the Paleoptera (Edmunds and Traver, 1954), and the replacement of this form of support with modification of a few veins to bear the force of the downstroke. The radius (R) and cubitus (Cu) typically retain a slight convexity, probably by virtue of being the only convex veins that attach near the insertion of the muscles from the basalare and subalare (Fig. 12). The only rigid area needed is the costal area, which leads the wing in its stroke; the vein fluting is retained there. For reasons unknown to me, the plical vein (P) also retains its concave position. This plical furrow has been confused with the vannal fold, but is not usually an articulation fold. All other veins are essentially neutral in position.

PHYLOGENY

Most authorities regard the winged insects as having arisen only once in the course of evolution. This is based on the close resemblance of all known insect wings. No data discussed here appear to contradict this view, or even render it necessary to maintain other theories as viable alternatives.

Lemche (1940) found that unfolding the inverted wing pads of Odonata makes them project at right angles from the body, instead of backwards, as in other insects. Therefore, he postulated that the Odonata evolved wings independently of other insects. This concept has found favor with some other workers (Wille, 1960; Matsuda, 1970), making it necessary to reexamine these data.

Nymphs of Odonata have the same thoracic pleura as the adult, which are high and slope steeply backwards. Modification for an aquatic habitat has resulted in the thorax being flattened, so that the tops of these very large pleura take up a dorsal position. This makes the tergopleural line run obliquely from near the meson anteriorly to the edge of the body posteriorly. The wing pads thus lie at a peculiar angle relative to the sides of the body, with their costal margins drawn inwards. These pads may be seen to arise from the posterolateral angles of each segment (as in other insects) if one unfolds them sufficiently to bring them into a perpendicular relation to the pleura. Thus Lemche's hypothesis is untenable. The Odonata cannot be disassociated from the Paleoptera on the wing pad attitude.

The oldest lineages of winged insects living today are represented by the Odonata and Ephemeroptera, both paleopterous; all other winged insects are neopterous. Of the two orders, the Ephemeroptera clearly represent the earliest lineage to have arisen from the main line of pterygote evolution. Their peculiar primitive features have already been discussed.

Both the Ephemeroptera and Odonata are highly specialized orders and probably do not retain the original wing form of their common ancestor. It is likely that careful scrutiny of numerous fossil paleopterous insects will aid in understanding the relationships of members of this diverse group, and it may be possible eventually to ascertain the exact nature of the primitive paleopterous wing.

The first Neoptera must have been able to fold both wings along the vannal fold, despite the lack of such a fold in the fore wings of modern insects. This conclusion is based on the form of the basal sclerites; in all neopterous wings the basal plates are directed strongly outward (Figs. 17, 18). This modification is essential to the functioning of the vannal fold, but unnecessary for the jugal fold. This theory is also based on the form of the vannal and associated basal folds, which lie in the same orientation as those of the main flexion folds of the paleopterous wing. The jugal fold and its accompanying basal fold, by contrast, both represent modifications of these simple longitudinal folds.

Two evolutionary lineages are apparent within the Neoptera. The *Pliconeoptera* are characterized by complex, often reticulate venation that differs considerably between the wing pairs, and by a large vannal field of the hind wing that is folded fanwise along the numerous anal veins (Fig. 18). The members of this line differ from those placed in the "Panplecoptera" or "Polyneoptera" of authors in excluding the superficially similar order Plecoptera. Other morphological data also show the Plecoptera to be more closely related to the neuropteroid and hemipteroid orders than to the orthopteroid orders (Ross, 1955).

The other lineage, the *Planoneoptera*, is characterized by simple venation with at most five veins on the vannus, wing pairs with basically similar venation, and the lack of anal plications, the hind wings folding only once between the veins, along the vanal or jugal fold. Reticulate venation is represented in this group only in the higher Neuroptera, the Fulgoroidea, and the Pteronarcidae; all are considered to be specialized from ancestors with simple venation.

The extinct Protorthoptera (or Paraplecoptera) are neopterous, yet do not fit either of these lines. Their venation is complex and often reticulate, but the wings are basically similar in most forms, and there is not a trace of fan folding of the hind wings. The vannus typically bears seven anal veins, more than the Planoneoptera and fewer than the Pliconeoptera. On the basis of these characters, it seems likely that they are more primitive than either of the groups of modern Neoptera, and probably represent the common stock from which both evolved.

SUMMARY

The paranotal theory of the origin of wings receives support from the possession of paranotal flanges by the Thysanura and Microcoryphia. These paranotal flanges resemble wing buds. Winged insects are thought to have evolved from a group related to these insects which enlarged these flanges to form gliding planes.

The theoretical order in which the trachea branchings occurred as notal lobes developed agrees well with the observable "vein precursor" structures of paranotal lobes. These veinlike ridges in turn are precisely comparable to the postulated primitive venation of insect wings.

The first wing type, Archaeoptera, is postulated on theoretical grounds as intermediate between the pronotal paranota and paleopterous wings in structure. This hypothetical type agrees well with the known insect fossils from the Devonian period that possess wings. The more highly evolved Paleoptera are first represented from the Upper Carboniferous.

The origin and development of the axillary sclerites and basal plates of the wing are traced through the Ephemeroptera and Odonata to the Neoptera. The axillary sclerite modifications between the first form and that of Neoptera are loss of articulation of the second axil-

lary, and enlargement of the third axillary. The basal plate of the ephemeropteroid type gave rise to three fragments, each corresponding to their adjacent axillary sclerite. Homologies of these sclerites are as in Snodgrass (1952), but I recognize the subcostal and cubital plates as well as the median plate. The "proximal median plate" (Snodgrass, 1935) is a flange of the third axillary, as pointed out in his later work.

The vannal and jugal wing folds are redescribed, and it is noted that they are alternative types, and are thus not found together in the same wing. Typical Neoptera have the vannal fold in the hind wing and the jugal fold in the fore wing; the Holometabola fold both pairs of wings along the jugal fold. The plical furrow is a remnant of the paleopterous fluting, and does not represent a functional fold. Vannal plications occur in the orthopteroid orders; this and other characters set this group of insects off as the Pliconeoptera, in contrast to other extant Neoptera, the Planoneoptera.

ACKNOWLEDGMENTS

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DEVELOPMENT OF MALE REPRODUCTIVE ORGANS OF CHRYSOCORIS STOLLII[1]

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ABSTRACT

The vasa deferentia, formed as posterior continuations of the primordia of the testes, have an entirely mesodermal origin and the paired mesadenia arise as tubular evaginations from their ampullar extremities. Each of the phallic lobes, developed from the ninth sternum in the anterior part of the primary genital invagination, divides rather obliquely into an outer 'paramere' lobe forming the 'paramere' and an inner 'mesomere' lobe. The fusion of the mesomere lobes of the opposite sides results in the formation of two concentric hypodermal tubes, the outer of which is differentiated into the phallobase and conjunctiva, while the inner one forms the vesica. The rudiment of the ejaculatory duct is derived from a tubular invagination arising from between the bases of the mesomere lobes.

Despite a number of valuable works on the morphology of male reproductive organs of Hemiptera and especially the external genitalia, there is much confusion regarding the true morphologic nature and homology of these structures. Clearly, an understanding of the morphology of the different parts of the external genitalia is impossible without study of their development. Only a few workers have studied this development in Hemiptera; Christophers and Cragg (1922) in *Cimex lectularius*, Pruthi (1924) in *Idiocerus atkinsoni*, George (1928) in *Philaenus leucopthalmus*, Metcalfe (1932) in *Philaenus spumarius*, Rawat (1939) in *Naucoris cimicoides*, and Qadri (1949) in various

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