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THE FORMATION OF THE MIDDLE MEMBRANE IN THE WINGS OF PLATYPHYLAX DESIGNATUS WALK.

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There appears to be some difference of opinion regarding the terms middle membrane and "Grundmembran," their first formation and ultimate fate, and, at what stages in the development of the insect's wing they occur. Semper (10), from whose paper the word "Grundmembran" comes chose for his work the later stages of some Lepidoptera and found, between the two hypodermal layers of the developing wing, a membrane-like structure which he called the "Grundmembran"—this name has been adopted by others. Semper's view as to the origin of this membrane from "Bildungszellen" has been followed by some; we believe, however, the more widely accepted view to be that of Schäffer (9) who, speaking of the development of the wing in the Lepidoptera says: "Sehr fruh, etwas sobald die Schuppen sich anlegen, beginnt in ganz eigenartiger Weise die Verschmelzung der Flügelblatter." Again: "Est is eine von Plasmen gebildtee continuirliche Membran vorhanden die ich als 'Grundmembran' des Epithels bezeichnen will." Later the same worker says: "die Grundmembranen bei der Flügelblatter sich bereits dicht auf einander verschmolzen sind. Der Flügel erscheint so aus zwei Epithelien zusammensesetzt, von denen gegen eine in der Mitte gelengene Membran pfeilartige Fortsatze auslaufen."

What one might call the generally accepted view regarding the middle membrane is this: The basement membrane covering the hypodermis of the young developing wing is similar to that

on other parts of the body and, in the very young wing bud, the continuation of the one into that of the other can be easily seen. The young wing is formed by a fold of the hypodermis which at first remains unchanged and the two walls of the fold come to lie adjacent to each other, they finally come together and the two opposed basement membranes fuse to form the middle membrane. This happens early in the development of the wing and has been seen, clearly by some observers, indistinctly by others. Later in the development when the hypodermal cells have assumed their characteristic spindle shape this middle membrane persisting, or a new one forming, has been clearly seen as a well marked layer passing through the median portion of the wing and connected at either side to the hypodermal cells by long strands. This is the layer first described by Semper (10) and Schäffer (9) and it has been seen by nearly all those who have studied the development of an insect's wing by means of sections.

It might be well to give a few views of those who have studied the development of the wings of insects although not trying to make such a series of quotations complete. Comstock and Needham (1) working with beetles say: "It is also important to note that the basement membrane of the hypodermis of the wing differs in no respect from that of the hypodermis of the body wall, and is continuous with it. In the thinner parts of the wing the two basement membranes melt and fuse, this forming what has been termed the middle membrane of the wing."

Mercer (6) in speaking of the Lepidoptera says: "In sections of the wing buds made at this time (fifth larval stage) the so-called middle membrane is seen only with difficulty. This has given rise to the belief that it disappears at this time. Later when the wings become more opaque, i. e., in the pupa stage, the two basement membranes are again easily seen." Again the same author says: "Students of the subject have been confused by descriptions of three different structures, the basement membrane of the hypodermis, the middle membrane of the larval wing buds, and the 'Grundmembran' of the pupal wing; when in reality there is only a single structure, the basement membrane."

Mayer (5), who worked with Lepidoptera, says: "The middle membrane has disappeared as such, and in its place one

finds a delicate membrane lining the whole interior of the wing bags. This is the 'Grundmembran' of Semper." The figure to which Mayer refers for illustration of the middle membrane is taken from what he labels a mature larva; it is very similar to what we have shown in figure eight which is of an early pupa, this does not show any thing so membrane-like as Mayer has drawn and called the 'Grundmembran' in several of his later figures. Again he says: "The inner ends of these spindle-shaped cells are often seen to be fused to a double membrane (middle membrane), occupying the space between the two walls of the wing pad. In very old larvæ, however, this membrane is usually absent, and the inner portion of the cells which constitute the wing tissue end free."

Tannreuther (11), working with Lepidoptera found that "the basement membrane of the larval hypodermis is continuous over the sides of the evaginated cavity, which in later stages of development becomes the middle membrane of the larval wing. The hypodermal cells with their long fibre-like threads remain attached to the basement membrane which is continuous with that of the hypodermis." Again, in speaking of the larva in the fourth instar, he says: "The basement membrane is not so distinct, as the larva (e) at this stage differ in the sharpness of this membrane. In some individuals it is scarcely visible, in others it can only be determined by the ends of the hypodermis cells or fibres." In speaking of the prepupal wing he says: "The basement membranes of the evaginated cavity become united to form the middle membrane of the adult wing."

The following quotations are from Krüger whose work was principally with Coleoptera. "Dort wo die beiden Flügellamellen aneinanderstossen, zeigt sich schon, wie bemerkt, die erste, schwache Bildung einer Grundmembran. Sie geht offenbar aus den Zellen der Hypodermis hervor, was allerdings erst in spateren Entwicklungsstadien klar erkannt wurde. Die Grundmembran ternnt noch als deutliche Scheidewand bei die Flugellamellen."

Powell (7) in his work on the development of the wings of certain beetles, speaking of the larvæ shortly before pupation. "The basement membrane which throughout the development of the wing is very thin and not easily discernable, becomes

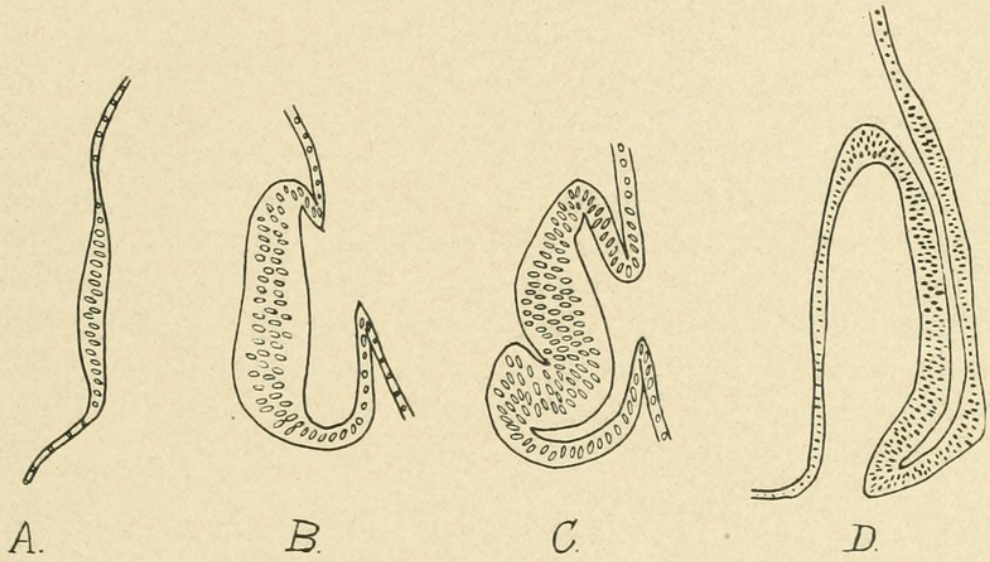
more or less degenerated during the prepupal period and in places the bases of the cells either end free or become fused and anastomosed with each other."

It might also be well to give a very brief account of the early development of the wings of *Platyphylax* taken from an earlier paper, Marshall (4).

In the earliest, newly hatched, larvæ sections through the thorax fail to show any modifications of the hypodermis at those areas where the wing rudiments will later appear. Very soon, probably in the second instar, four small, disk-like thickenings can be seen; they are formed by the elongation of a few cells of the hypodermis (Text-figure I, A) and are found on each side of the wing-bearing segments, dorsal to the legs. These disks, which remain continuous with the hypodermis, soon invaginate and each, sinking below the surface, forms a small pocket, the peripodial cavity, at the bottom of which the disk is situated (Text-figure I, B). The hypodermis consists of a single layer of cells with a basement membrane along its inner surface, this membrane is the same on the disk and on the surrounding hypodermis both of the peripodial cavity and that covering the thorax. The disks never recede far from the surface from which they invaginated and soon commence to evaginate (Text-figure I, C). The peripodial cavity remains in communication with the exterior through the peripodial pore, the opening formed by the original invagination. At first the invaginated disk was, from a surface view, circular, it gradually elongates and when evagination takes place the wing rudiment is like a flattened sack; each wall of this sack consists of a single layer of hypodermal cells and a basement membrane which forms the inner, adjacent, part of each wall. In this way the basement membrane of each wall comes to oppose and lie adjacent to that of the other wall, and, as the walls come closer and closer together, the two basement membranes lie against each other, touch, and apparently fuse. This is not true over the entire inner surface as here and there this fusion of the two layers has not occurred and certain elongated free spaces remain, these are the developing wing veins.

The wing rudiment increases in size and a slight bending is necessary in order that it may remain within the peripodial cavity; the expulsion from this cavity takes place shortly after the larva has closed its case preparatory to pupation and the

young developing wings become external (Text-figure I, D). The wing veins become clearly discernable from a surface view and in section they appear as empty spaces alternating with those parts where the two layers of the wing remain connected. While still within the last larval skin the wings become so large that, confined as they are by this covering, a second folding becomes necessary; during this period the wings attain their greatest thickness. When the last larval skin splits and the pupa is free the wings straighten and grow much thinner. The cuticular covering now formed by the wings soon becomes too small for their growth and another period of folding ensues, the wings remain thus folded until the emergence of the imago when they unfold and assume their definite form and shape.



TEXT-FIGURE I.

Four views of the young developing wing of **Platyphylax designatus.** A, thickening of the hypodermis; B, after invagination of this same thickened portion; C, the wing rudiment has evaginated, but still lies within the peripodial cavity; D, soon after the wing rudiment has left the peripodial cavity and become external. In all figures the external surface of the larva is to the right; the hypodermis only is represented, the cuticula not drawn. Figs. A, B and C, × 220; D, × 105.

After evagination of the imaginal disk each wing rudiment consists of two layers of hypodermal cells folded down into the peripodial cavity and each wall of the fold is a layer of cells similar, except in its greater thickness, to the continuous hypodermal layer forming the wall of this cavity. The two layers of the rudiment lie close to each other but in the early stages of development do not touch along any part of their opposing surfaces (Fig. 1, A). Each layer is seen in section to be com-

posed of a single row of cells with ovoid nuclei which are arranged in two or three apparent rows. The long narrow cells are so crowded together that the nuclei have lost their regular linear arrangement and have been pushed towards one end in the cell to which they belong. The nuclei are situated more in the basal half of each layer so that there is a thicker portion of protoplasm along the free surface of the hypodermis than between the nuclei and the basement membrane. In the specimens of *Platyphylax* examined the cell boundaries, which have been figured by other observers in different insects, could not be found with any great regularity and only here and there could traces of any boundaries separating the cells be seen. The hypodermis covering the thorax and that forming the peripodial membrane has a distinct basement membrane, this can also be seen on that part of the hypodermal layer forming the wing rudiment although in this last place it is not distinct (Fig.1,B.m).

The two layers of the wing rudiment, as its development proceeds, approach each other and pass through a stage in which there is but a narrow open space separating them from each other; here and there this open space is wider forming large openings, the developing wing veins. Narrow open spaces are also noticed between the cells of each layer, these do not as yet entirely separate the cells but appear only in the basal region; this is, however, the beginning of that separation of the cells which finally results, with the migration of the nucleus and protoplasm to one end, in the formation of the elongated, spindle-like cells which have been described in the developing wings of a number of insects. An endeavor to find a basement membrane in the wing rudiment shows that it is not distinct and continuous, it can sometimes be seen but cannot be traced for any considerable distance along the basal surface of either layer. Other workers have observed the basement membrane at this stage in different insects although, as quoted in the introductory remarks, all have not seen it with equal distinctness.

As the development of the wing goes on its two layers finally approach each other and their inner surfaces touch except where the developing wing veins are present. The two basement membranes should now lie adjacent to each other and fuse to form the middle membrane. An examination of sections at this stage shows however, that a continuous median membrane separating the two layers of the wing from each other cannot

with certainty be found. One does however find, running through the middle of each section, a continuous, narrow, lighter zone which is connected with and separates the two layers of hypodermis from each other (Fig. 3). This zone is without definite boundaries, and, from the darker protoplasm of the adjacent hypodermal layers, there are numerous small processes extending into it so that it is impossible to trace any definite line which might separate the parts from each other. Another change one notices at this stage is in the gradual moving of the nuclei of each layer towards the outer surfaces of the wing; most of these nuclei are no longer, as formerly, grouped in the basal half of each layer but are now fairly well scattered in all its parts. This is well shown by comparing figures one and three.

It is apparent that this light median zone remains for but a short time during the development of the wing. Slides through wings a little older than the last described fail to show any median zone which can be recognized as lighter in shade than the rest of the wing, but, in the same median position, one can still see the same zone but it is now darker than the rest; the sections showing this were prepared and stained in the same way as the slides showing the lighter median zone. The two layers of the hypodermis no longer lie close against this median zone but have moved slightly away from it, not leaving a clear entirely open space, but each layer of the hypodermis is connected with the median zone by numerous protoplasmic strands separated from each other by vacuoles which are irregular in outline. This makes each side of the median zone much lighter and this contract coupled with a probable increase in the density of the protoplasm of the middle zone, might account for its now appearing darker than the other parts of the slide (Fig. 4). There are now, excepting the cuticular covering, five layers shown in each section of the wing: 1, two outer layers, the original hypodermis, which have decreased in width and now form but a part of the entire section; 2, along the inner surface of each of these is a lighter layer composed of numerous vacuoles separated from each other by protoplasmic strands which connect the two outer layers, 1, with 3, a median layer which appears slightly darker than the other parts of the section. None of these layers has a distinct boundary. This last median layer is present in the developing wing of *Platyphylax* and forms what is commonly known as the middle membrane; this,

as will be shown, disappears and is replaced by a second one which is Semper's "Grundmembran." The accepted name, middle membrane, is so well established that the introduction of a new term, such as middle lamella or middle layer, would be futile; the old term will be adopted both for the earlier and the later layer although we cannot see in *Platyphylax* that there is a true membrane present in the median part of the developing wing.

In many sections at this age, and later, there can be found running through this middle layer small darker dots and short lines which would correspond to the middle membrane of other observers (Fig. 5). These are more or less distinct in different sections but do not show continuously for any great distance in any section and we are unable to find any regular structure strictly homologous to a membrane. The strands of protoplasm which connect this middle layer to the outer layers will be spoken of as the perpendicular strands.

All the stages so far described can be found in the developing wing while it is still within the peripodial cavity, in fact many internal rudiments show stages more advanced than these. We also find in these stages as well as later ones a number of dividing nuclei, the mitotic figures were nearly all found near the outer surface of the developing wing and away from that portion where the nuclei are most crowded together.

The middle membrane can be recognized when the perpendicular strands and the vacuoles between them first become clearly differentiated as layers of the wing. With the growth of the wing changes take place in the relative thickness of the different layers, the two original hypodermal layers decrease in thickness and the layers just inside of them, composed of the perpendicular strands and vacuoles, increase in thickness to finally, as will be seen later, occupy by far the largest part of the wing. The perpendicular strands are not straight but branch and divide and are generally curved for part of their length, such irregularities are more noticeable in the older stages when the strands are longer. Each strand appears to pass from the middle membrane to a nucleus in the hypodermal layer (Fig. 6). In sections such a connection is not always discernable but no doubt holds true for a great majority of the strands. Mayer (5) says: "Each of the hypodermis cells gives rise to one, and only

one, of these processes"; and later, "occasionally a hypodermis cell is seen without any such process."

At first the increase in width of the clearer layers, that is the elongation of the perpendicular strands and the clear spaces between them, causes no appreciable changes except in the relative width of the different layers. In certain slides one can see that, scattered rather irregularly in the middle membrane, there are a number of small ovoid bodies not well stained but clearly marked off from the surrounding protoplasm. At first it was difficult to understand just what these small bodies were but from a study of different stages of development it became apparent that they were nuclei of the hypodermal layers which had wandered into the middle membrane. In wings of about the age we are now considering, (Fig. 6), one can see that many of the nuclei of the hypodermis lie along its inner margin, some are noticed protruding into the adjacent clear layer and a few are seen on the perpendicular strands. Those nuclei occupying the two first mentioned positions and some of those on the strands are similar in size and structure to the normal nuclei of the hypodermal layer, some of those on the strands however are seen to be much smaller and lighter stained than normal but are still easily distinguished by their rather distinct boundaries which mark them sharply off from the surrounding cytoplasm (Fig. 7). This enlarged view will show more clearly what happens during this wandering and that many of the hypodermal nuclei pass from their original position to the middle membrane going from one layer to the other along the perpendicular strands. During this change in their position they lose their characteristic nuclear appearance and become much reduced in size. In this last figure (7) one sees, to the right, the inner ends of a few normal nuclei (entire nuclei not drawn) that are still within but at the inner edge of the hypodermal layer, adjacent to these are two entire nuclei that have started to move towards the middle membrane; the latter nuclei are as yet normal in appearance and size. Along some of the perpendicular strands can be seen other nuclei that have already decreased in size and lost their nuclear characteristics in a breaking up and disappearance of their reticulum and in their failure to stain. Finally, in the middle membrane, can be seen many of the nuclei which have wandered from the hypodermal layers, these have entirely lost their nuclear appearance but can be distinguished by the

rather definite boundary with which each is surrounded; they persist as small, fairly regular ovoid bodies within the middle membrane, remaining visible until a considerably later stage, continually decreasing in size to finally disappear.

Comstock and Needham (1) give a different origin for the nuclei in the middle membrane. They say: "In later stages, when, after the expansion of the wing, it (basement membrane) contains distinct nuclei, there is evidence that some of these at least are derived from the hypoderm cells whose nuclei once crowded up to this level, have remained stranded here after the expansion of the wing." Later in the same work they say: "When through excessive crowding, some of the innermost nuclei have come into contact with the basement membrane at the subsequent expansion of the wing, these, seem instead to remain where they are, and to attract to themselves the slender prolongations of the neighboring cells."

In the stages which have already been described (Figs. 1 to 7), the wing, except in the earliest stage, (Fig. 1), remains of about the same thickness and any changes taking place during the formation of the middle membrane and of the perpendicular strands go on during a partial rearrangement of the contents of the wing and an increase of its area. Before the larva closes its case preparatory to pupation the wing has grown down against the base of the leg and subsequent growth in a ventral direction is checked; covered, externally, by the cuticular layer the wing is confined within a limited area which it finally fills, it then starts to fold and this is noticed in both small and large folds along the surface (Fig. 8), giving it a fluted appearance, Verson (13). During this period and also after the larval case has been closed a surface view will show another system of very much larger folds; these start at the anterior margin of the wing and finally extend entirely across it, at first there are but one or two but an increase in their number soon occurs and gives to the wing a complicated folded appearance Marshall (4, Fig. 23). This is now that stage in the development of the wing when it has reached its maximum width and the perpendicular strands their greatest length.

Sections through the wing at this period of its greatest thickness show that there has been a considerable change in its internal structure. The outer layers which have been very distinct since the beginning of the formation of the clear layers

have nearly disappeared and are now seen restricted to a narrow layer along the surface of the wing just under the cuticula. It is seen from this section (Fig. 8) that the earlier clear layers now form nearly all of the wing, the long clear spaces still separating the perpendicular strands which extend nearly to the cuticula. The middle membrane is much narrower than in the last stage but occupies the same median position and still shows a number of the nuclei which have wandered into it.

During the growth of the wing in the latter part of larval life and while the insect is in a period in which the wings would be of about the ages found in figures six and eight the middle membrane shows, in some specimens, traces of what might be taken for the remains of a membrane. Running through the center of the middle membrane there can often be seen small dark dots and rods which may in some specimens be so numerous as to show a more or less linear arrangement (Fig. 8), this is only continuous for a short distance. Most of the slides examined did not show this central linear arrangement of dark dots and rods and one could see only a few darkened dots in its place; in most of the sections examined nothing of the kind could be found. We do not believe that this corresponds to a membrane although it occupies exactly the position in which the basement membrane would be found if present.

The meaning of the wandering of some of the nuclei from the hypodermal layers to the middle membrane is not clear. As will be shown later these nuclei finally disappear and there is no apparent reason why they should leave those parts of the wing where the other nuclei are found and wander to a portion of the wing in which it is impossible to see that they are of any use. The crowding of the nuclei due to the increase in width and folding of the wing might necessitate a decrease in their number but at this stage there still remains a thin outer layer along the surface of the wing which is nearly free from nuclei (Fig. 6) and into which other nuclei might be pushed. That an accretion to the mass of the middle membrane is needed and supplied in this way is not possible as the middle membrane soon after the nuclei have wandered into it, begins to decrease in thickness and to ultimately disappear. During the stages already described dividing nuclei can often be seen within the hypodermal layer so that nuclei are both being formed in this layer and also lost to it from this change in their position.

The wings, after the last larval skin has finally been cast, remain for a short time in their folded condition; they then unfold, decrease in thickness with an increase in their area. As a result of this the old hypodermal layers, just under the cuticula, are spread as a continuous layer in this position and have apparently received a considerable amount of the cytoplasm which was formerly in the perpendicular strands when these became shorter and thinner (Fig. 9). The nuclei, which in the last stage were all in the perpendicular strands, have nearly all wandered into the layers under the cuticula; a few still remain in the strands from which they later disappear. The middle membrane has become much thinner and, instead of being a fairly continuous layer, it here and there now assumes a zigzag shape; along its course can be seen very small and somewhat ovoid bodies, these are all that remain of those nuclei which, at an earlier stage, wandered into this layer from the hypodermis.

During that period in the life of the pupa in which its body contracts and shortens the changes, noted in the last paragraph, are continued and become more marked. The nuclei of the perpendicular strands have all passed from these into the old, outer, hypodermal layers in which they now are arranged in a fairly even layer. The protoplasm does not in these layers become even but in many places surrounds each nucleus in a triangular mass, these at the base are connected with each other but the apex of each points towards what remains of the middle membrane and is, in most cases, extended out into one of the perpendicular strands (Fig. 10). The perpendicular strands have become thinner and most of the protoplasm that they contained has entered the outer layers of the wing. The middle membrane no longer extends as a continuous layer through the median part of the wing but its zigzag course becomes more marked until finally it separates into a number of strands and can no longer be followed continuously as in all the earlier stages. This disappearance of the middle membrane becomes more marked until all traces of it are lost, the perpendicular strands then either pass across the wing from one surface to the other or they end blindly at some place along such a course. The failure to see all of the strands connected with both layers of the hypodermis is undoubtedly in part due to a study of thin sections. Many of the nuclei which earlier wandered into the middle membrane from the hypodermal layers

are still present but now restricted to the perpendicular strands (Fig. 11).

The wings reach their maximum thickness after the contraction of the pupa and they then lie stretched over and at the sides of its body; this chitinous case which now encloses them while ample in extent for the wings in their present condition is not sufficient to allow of the next growth, that of an increase in surface area. When this occurs it is necessary for the wings to decrease in thickness and become very much folded which folding continues until the imago is ready to issue from the pupal skin. To the perpendicular strands that pass across the wing from one surface to the other Mayer (5) has assigned a probable contractile power and to this attributed the drawing together of the two surfaces of the wing. This would account for the decrease in thickness and the limited area of the cuticular sack which now encloses the wings would necessitate the folding which becomes so marked during the remainder of pupal life. The narrowing of the wing is noticeable before its folding has commenced.

During the process described above certain changes take place in the different layers of the wing, of these the most noticeable is the reforming of the middle membrane which again occupies its old place in the median part of the wing (Fig. 12) and is now thinner and more membrane like than during the earlier stages before its disappearance. The perpendicular strands again pass from the hypodermis to the middle membrane and are irregular and branched. The degenerated nuclei which earlier wandered from the hypodermal layers to the middle membrane and which, upon the disappearance of the latter, remained on the perpendicular strands (Fig. 11) are again found in the middle membrane. In the hypodermal layers many nuclei are seen which have wandered away from the outer surfaces of the wing and come to lie between the hypodermis and the middle membrane. These are the nuclei of those cells, trichogens, from which later will develop the hairs upon the surface of the wings. It is at once noticed that these trichogens are more abundant upon one side of the sections than upon the other; this fact, knowing that there are many more hairs upon the dorsal than upon the ventral surface of the wing, enables one to distinguish these surfaces from each other rather early in pupal life.

The wing, as this last folding continues, decreases more and more in thickness (Fig. 13) but structurally there is no noticeable change. Here and there places are seen in the sections where the hypodermis and middle membrane have increased in thickness (Fig. 14) but such places are apt to be near the margin of the wing. The cause of this is not known unless it can be due to the folding of the wing which may push the hypodermis and the middle membrane in such a way as to increase, at certain places, the thickness of each.

After the folding of the wing has reached its maximum (Fig. 15) certain changes have taken place. Most noticeable of these is the final disappearance of the middle membrane and of the small degenerated nuclei which it contained. After this has occurred the perpendicular strands again pass entirely across the wing and directly connect the two hypodermal layers with each other. These layers are now thinner and their nuclei are so arranged that the longitudinal axis of each lies parallel to the surface of the wing.

No marked change is noticeable in the wing after the adult insect has emerged (Figs. 16 and 17). The wing has become a little thinner and the hypodermal layers show a decrease in amount and their nuclei are smaller. The activities of the different layers have ended and there is little left within the wing of what was present during the early stages of its development and growth.

From the foregoing account it can be seen that in *Platyphylax* the term middle membrane cannot be used to designate a true membrane but rather as the name for the thin layer of protoplasm occupying a median position within the wing. As has been noted by others this layer is not continuous during the entire development and growth of the wing but disappears and is reformed in the same place. Of these two structures the latter is the more membrane like.

In the preparation of the material two or three of the commoner sublimate, acetic acid fixitives were used and the slides stained with Delafield's hæmatoxylin or with alum carmine.

BIBLIOGRAPHY.

1. **J. H. Comstock** and **J. G. Needham.** The wings of insects. Amer. Natural. Vol. XXXII, 1899.
2. **J. Gonin.** Recherches sur les métamorphoses de Lépidopteres. Bull. Soc. vaud. sc. nat. Vol. XXX, 1894.
3. **E. Kruger.** Uber dir Entwicklung der Flügel der Insekten mit besonderer Berücksichtigung der Deckflügel der Käfer. Inaug. Diss. Gottingen,1898.
4. **W. S. Marshall.** The development of the wings of a caddis-fly Platyphylax designatus. Zeit. wiss. Zool. Vol. CV, 1913.
5. **A. G. Mayer.** The development of the wing scales and their pigment in butterflies and moths. Bull. Mus. Comp. Zool. Harvard, Vol. XXIX, 1896.
6. **W. F. Mercer.** The development of the wings in the Lepidoptera. Journ. N. Y. Entom. Soc. Vol. VIII, 1900.
7. **P. B. Powell.** The development of the wings of certain beetles, and some studies of the origin of the wings of insects. Journ. N. Y. Entom. Soc. Vol. XII, 1904 and Vol. XIII, 1905.
8. **A. Rehberg.** Ueber die Entwicklung des Insektenflügels. Jahresber. Gymnas. Marienwerder Programm, 1886.
9. **C. Schaffer.** Beiträge zur Histologie der Insekten. Zool. Jahrb. Anat. Vol. III, 1889.
10. **C. Semper.** Ueber die Bildung der Flügel, Schuppen und Haare bei den Lepidopteren. Zeit. wiss. Zool. Vol. VIII, 1897.
11. **G. W. Tannreuther.** Origin and development of the wings of Coleoptera. Arch. Entwickmech. Vol. XXIX, 1910.
12. **W. L. Tower.** The origin and development of the wings of Coleoptera. Zool. Jahrb. Anat. Vol. XVII, 1903.
13. **E. Verson.** La Formanzione delle Ali nella larva del Bombyx mori. R. Stazione Bacol. Sperment. Padova, 1890.

EXPLANATION OF PLATES XX–XXII.

All figures drawn with a camera lucida.

B. M., basement membrane.
Cu., cuticula.
Hyp., hypodermis.
M. m., middle membrane.
Per. cav., peripodial cavity.
Per. mb., peripodial membrane.
Pp. s., perpendicular strands.
Tr., trichogens.

Figures eight to seventeen inclusive have been drawn with the same magnification to allow an easy comparison of the relative thickness of the wing at these different stages of development.

Plate XX.

Fig. 1. Section through one of the two layers of hypodermis that form the internal wing rudiment. This figure shows the position of the crowded nuclei as more in the basal part of the layer. ×875.

Fig. 1A. Transverse section of the entire wing rudiment from which the preceding figure was taken. × 105.

Fig. 2. The middle part only of a section through an internal wing rudiment. The outer part of each layer of the hypodermis is not drawn. The two layers have nearly come together and only a slight open space can be seen between them. The separation of the cells along their sides has started and a few of the narrow spaces between them can be seen. × 1100.

Fig. 3. Section through a wing rudiment after the two layers have come together and a narrow, lighter zone has appeared between them. × 875.

Fig. 3A. Transverse section of entire wing rudiment from which preceding figure was drawn. × 105.

Fig. 4. Median part only of a section through a wing rudiment. This shows the early formation of the middle membrane and of the perpendicular strands. × 1100.

Fig. 5. Section through a young external wing, lateral stage than preceding figure. × 1100.

PLATE XXI.

Fig. 6. Section of a wing at a later stage showing the wandering of many of the nuclei to the middle membrane in which a number of these nuclei, much reduced in size and clearness, can be seen; other nuclei are visible on the perpendicular strands. To the right a small outer portion of the hypodermis and the cuticula have not been drawn. × 1100.

Fig. 7. A small part of the same section more highly magnified to show the wandering of the nuclei from the hypodermis to the middle membrane. Only the inner edge of one layer of hypodermis is drawn and, in it, the ends of five nuclei. Opposite this is shown a part of the middle membrane and between these two the perpendicular strands on which are seen some of the wandering nuclei. The position of this view is shown by the space between the two lines at **a**, in the preceding figure. × 1700.

Fig. 8. Section of a wing at a later stage, shortly before the casting of the last larval skin. All the nuclei in the middle membrane are reduced in size and the perpendicular strands greatly elongated. × 740.

Fig. 9. Section of a wing at a still later stage of development. The middle membrane in which are seen a few of the nuclei that have wandered into it from the hypodermis is narrow and much more membrane like than in the preceding figures. × 740.

PLATE XXII.

Fig. 10. Section of a wing from a pupa after the last larval skin has been cast, the body contracted and the wings straightened. The nuclei of the hypodermis are nearly all arranged in a single row along the surface and many of the perpendicular strands extend entirely across the wing. The middle membrane is no longer continuous. × 740.

Fig. 11. A little later stage showing that at this part of the section the middle membrane has entirely disappeared. Cuticula not drawn. × 740.

Fig. 12. Section from the wing of a pupa before its final folding has commenced. The middle membrane has again formed as a continuous layer. × 740.

Fig. 13. Section of a pupal wing after the last folding has started. Cuticula not drawn. × 740.

Fig. 14. Section of another wing of about the same age. Cuticula not drawn. × 740.

Fig. 15. Section through the wing of an old pupa. The wing of this specimen is much folded and shows the entire and final disappearance of the middle membrane. The perpendicular strands again pass across the wing. Cuticula not drawn. × 740.

Fig. 16. Section of the wing of an imago shortly after its emergence. The old hypodermis is now represented by a thin layer of protoplasm containing a few shrunken nuclei. × 740.

Fig. 17. Section through the wing of an adult. × 740.

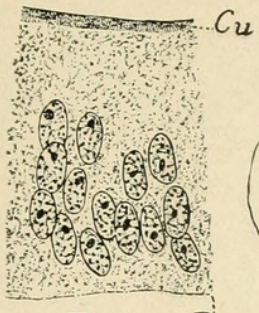
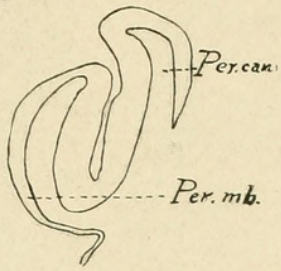


Fig. 1



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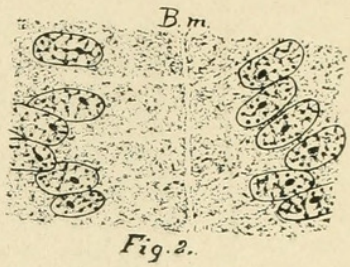

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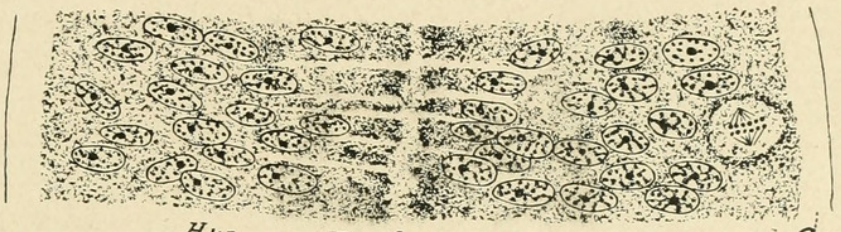

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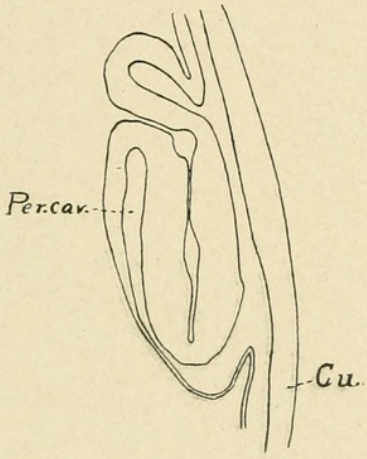

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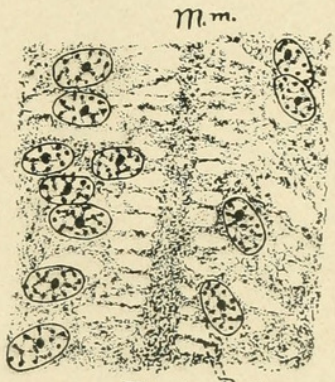

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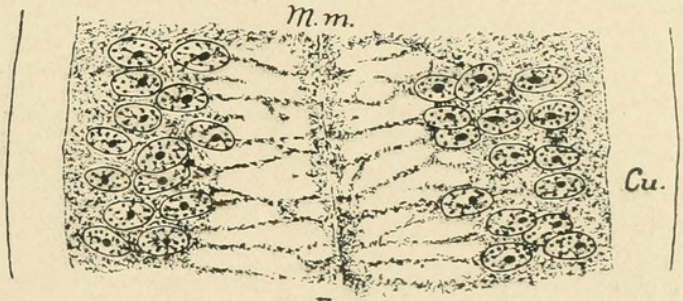

Fig. 5.

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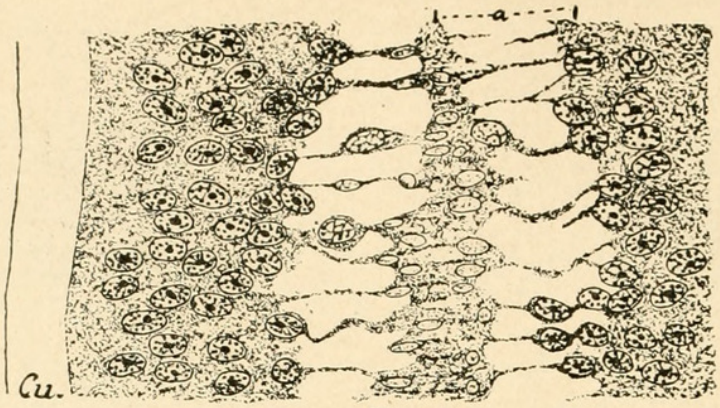

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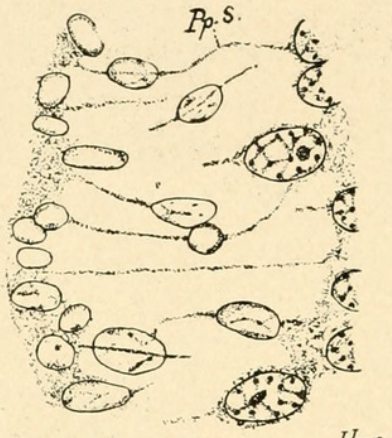

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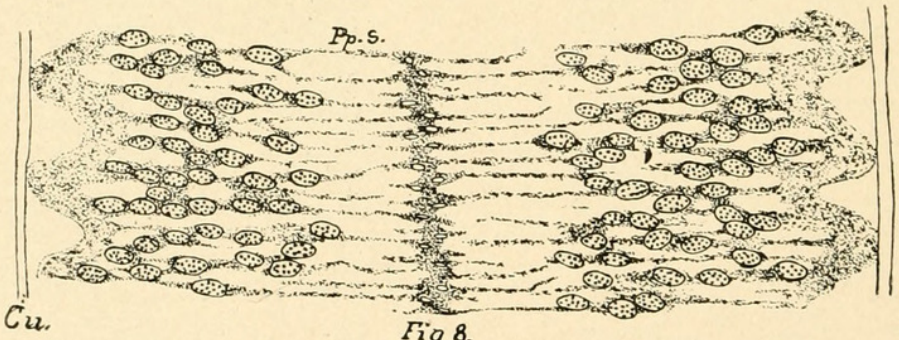

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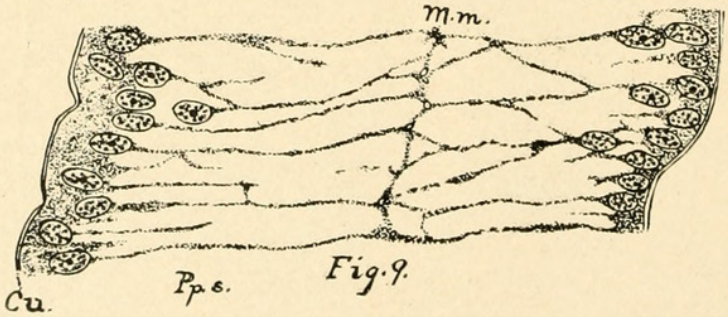

Fig. 9.

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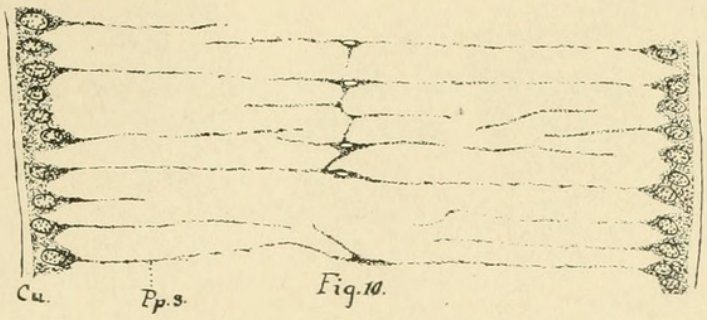

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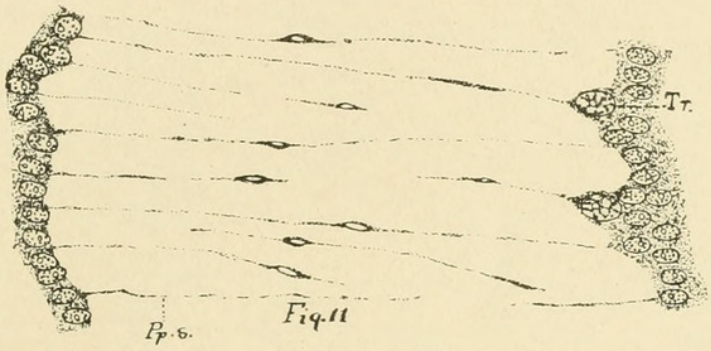

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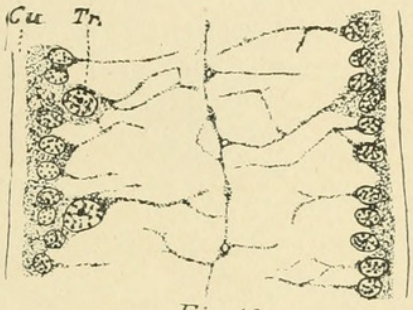

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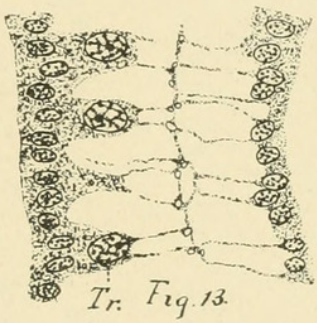

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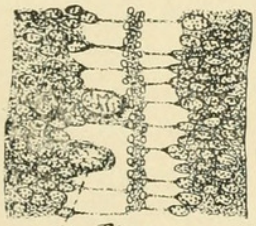

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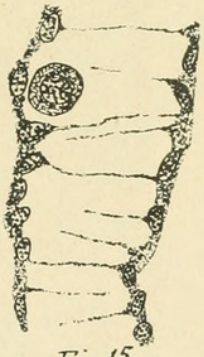

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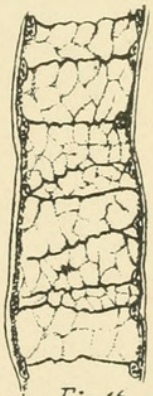

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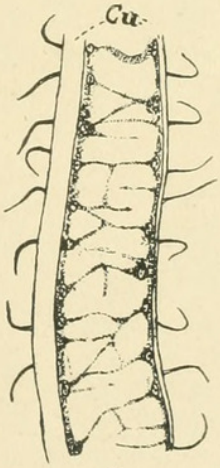

Fig. 17.

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Marshall, W S . 1915. "The Formation of the Middle Membrane in the Wings of Platyphylax Designatus Walk." *Annals of the Entomological Society of America* 8, 201–219. https://doi.org/10.1093/aesa/8.3.201.

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