

THE MORPHOLOGY OF THE TEGMINA AND WINGS IN FULGOROIDEA (Homoptera)

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Metcalf (1913) published an account of the homologies of the wing veins in certain families of the Fulgoroidea, using the nomenclature of the Comstock-Needham system as then current. Ten years later Muir (1923) briefly discussed Fulgoroid wing-venation and raised the question whether the vein generally termed the costa is not really an anterior (humeral) branch of the subcosta; he recorded that in the tegmen the first branch of the radius was never distinct and free from the remainder, and that the vein associated with the claval suture was a second main branch of the cubitus, and not the first anal vein as hitherto accepted. He considered that "the Y veins of the clavus" were formed by the first and second anal veins, and noted that in some members of the family Fulgoridae a third anal vein is present.

In view of the unsettled homology of the "costa", of the prevailing uncertainty regarding the anterior tegminal veins of the Tropiduchid genus *Alcestis* (Melichar 1914: 142, 144; Muir 1923: 225; Metcalf 1938: 383), and of recent interpretations of R, M, and the cubito-anal group of veins in other orders in the light of fossil and morphological evidence there is room for a reexamination of the morphology of the tegmina and wings of Fulgoroidea.

The relationship of the principal wing veins to those of Orthoptera may be established by reference to their antecedent tracheation, to their convexity or concavity, and to their associations with the axillary sclerites at the wing base.

The disposition of the main tracheal trunks in the tegmina and wings of all Fulgoroidea so far examined by the writer is quite uniform and is shown in Fig. 1. The material dissected included the fore and hind wing-pads of early fifth instars of the following genera: *Oliarus*, *Bothriocera* (Cixiidae), *Peregrinus* (Delphacidae), *Patara* (Derbidae), *Toropa*, *Taosa*, *Dictyophara* (Dictyopharidae), *Laternaria* (Fulgoridae), *Alcestis*, *Cyphoceratops*, *Neotangia* (Tropiduchidae), *Acanalonia* (Acanaloniidae), *Thionia*, *Colpoptera* (Issidae), *Bladina* (Nogodinidae), *Poekilloptera*, and *Ormenis* (Flatidae). The number of dissections made of material in each genus varied between two and fourteen; in the longer series some dissections were discarded because they did not satisfactorily display the oblique basal trachae from which the tracheae of the wing-pads arise. It is not uncommon for this basal trachea during dissection to become

broken between M and Cu_1 , giving rise to the illusion that the wing pads are each supplied by two distinct tracheae which give off the costo-medial group and cubito-anal group of tracheae respectively; in all cases of such apparent separation seen by the writer a careful examination of the basal trachea revealed the point of breakage between M and Cu_1 . No example was found in which the tracheae of the wing-pad truly arose from more than one basal trachea.

Another point which calls for comment is the basal union of the first two tracheae. Muir (1923: 216) refrained from pursuing his speculation that the anterior wing vein in Fulgoroidea is Sc or the humeral vein in deference to two figures given by Metcalf (1913: figs 5 and 27) of the tegmina of *Amphiscepa bivittata* Say and *Thionia simplex* Germar which show the anterior and second veins arising separately from the basal trachea. Muir recorded that in all his own dissections the anterior trachea was seen to arise from the subcosta, a condition shown in Metcalf's figures 8, 23, 28 and 48. The writer found in all dissections that the anterior and second veins join in a short common stalk before entering the basal trachea ("alar bridge" of Muir). The wing pads of fourteen specimens of *Acanalonia* spp. and of ten *Thionia* were dissected specifically to determine whether the condition figured by Metcalf for the anterior veins of *Amphiscepa bivittata* and *Thionia simplex* was typical; in all these dissections the two anterior veins were found to unite basally in a distinct common stalk, and it is concluded that the separate origin of these veins represented in the two figures already mentioned is not typical of the genera of families concerned. (*Amphiscepa bivittata* Say is currently recognized as belonging in *Acanalonia*).

The trachea of the radius and that of the media rise separately from the basal trachea as a single stem which may fork distally. The tracheae of veins Cu_1 and Cu_2 are of interest in being united basally in a common stem which curves posteriorly to lie along the basal trachea before entering it. The vein posterior to this common Cu stem is apparently always simple and curves almost parallel with the basal portion of the Cu stem and enters it at the point of its junction with the basal trachea. Posterior to this single trachea a short stem arises from the basal trachea and forks into two main branches, the posterior of which may give off a delicate ramus following the scutellar margin of the wing pad.

The anterior of these tracheae that lie behind the cubitus possesses the characteristics of the postcubital trachea of other orders in being unforked, in having a separate origin from the basal trachea and in being closely associated with the common base of Cu_1 and Cu_2 . The hindmost trachea arising from the

basal trachea represents both in its position and its bi-or trifurcate form the trachea which supplies the vannal area of the wings in orthopteroid forms.

Before homologising the tracheae of the wing pads with those of other orders it is necessary to consider the mechanical relationships of the veins of the adult wing which they respectively traverse.

The structure of the articular area of the wings has been found to be uniform in all genera examined by the writer, which include *Pintalia*, *Mnemosyne* (Cixiidae), *Bytrois* (Kinnaridae), *Delphacodes* (Delphacidae), *Derbe* (Derbidae), *Taosa* (Dictyopharidae), *Laternaria*, *Cathedra* (Fulgoridae), *Catonia* (Achilidae), *Neotangia* (Tropiduchidae), *Thionia* (Issidae), *Acanalonia* (Acanaloniidae), *Bladina* (Nogodinidae), and *Poekilloptera* (Flatidae). The elements composing the articular area, as exemplified by those found in *Taosa* and *Poekilloptera* respectively are shown in Figs. 5 and 6.

The tegula, which roofs over the axillary region of the tegmen, is attached at the middle of its inner surface to the anterior margin of the articular membrane. Just distad of this point of attachment a small lobe is developed on the anterior margin and at maturity becomes sclerotised as a semilunate plate, the *humeral plate*, sometimes bearing a minute peg-like eminence at its distal angle. The anterior wing vein, in all cases examined, was found to be approximated basally to this plate, but separated from it by a very narrow groove of flexible membrane. This vein, therefore, whether lying along the wing margin or some distance remote from it bears the anatomical relationship of the costal vein of other orders, while its tracheation agrees with that of the primitive costa as envisaged by Lameere.

There is no trace of a precostal vein in the ontology of Fulgoroidea so far studied by the writer, nor does such a vein appear to have been detected in any fossil ascribable to this superfamily.

The precostal area of the tegmina, which is found in Flatidae, Ricaniidae, Nogodinidae, Lophopidae, Eurybrachydidae, and certain Fulgoridae Tropiduchidae, and Issidae, appears to have arisen independently in each. In the Fulgorid genus *Laternaria* the narrow precostal area is formed by the dorsal sclerotised arch basally overlying the costal trachea becoming elevated, then bent forward, and finally more distally being produced in a short lamina, as shown diagrammatically in fig. 8. In the primitive Fulgoroid tegmen, as seen in *Pintalia* or *Mnemosyne*, the anterior edge of the sclerotised tract above the costal trachea is beset with a regular row of microtrichia. In forms with a precostal area this row is carried forward on the anterior margin of the expanding area but retains its association with the

haemocoelic channel in which the costal trachea lies by means of a series of channels from the haemocoel underlying the microtrichia to the peritracheal haemocoel. In *Laternaria* the channels are irregular and frequently anastomose; in the Tropicuchidae they are regular and usually oblique distally; in many species of this family which are not regarded as possessing a precostal area the separation of the microtrichous tract from the trachea in the distal portion of the costa gives rise to a series of tenuous oblique blood channels. The only difference between such channels and transverse precostal veins is that in the latter the integument overlying these channels is sclerotised to a perceptibly greater degree than that overlying the areas between the channels. The cross-veins of the precostal area in certain families such as Flatidae and Nogodinidae are traversed by slender tracheal filaments arising from the costal trachea (fig. 11). In these families the disposition of the marginal microtrichia and the regular development of the transverse sclerotised bars in the basal portion of the precostal area indicate that this area has been developed by a uniform protraction of the primitive sensillar margin without any accompanying torsion.

In the hind wing of adult Fulgoroidea the costal trachea is marginal and the overlying sclerotised arch simple. It may be noted, however, that the hind wing pads of certain Flatidae such as *Ormensis antoniae* Mel. possess a series of short transverse precostal blood channels which become obscured in the adult wing (cf. fig. 3).

It appears to have been the difficulty of accounting for the presence of a precostal area in the tegmen—"a condition recognized in no other order of insects"—that led Muir (1923: 216) to suggest that the apparent costa in Fulgoroidea is really the humeral vein or Sc, and not the homologue of the orthopteroid costa. According to this view the precostal area which lies anterior to the presumed Sc would have to be regarded as the costal cell which had persisted after the primitive marginal costal vein had disappeared. The theory, however, is beset with two difficulties: It is under the onus of demonstrating how the supposed humeral vein acquired in Fulgoroids the same relationship to the humeral plate as the costal vein bears to it in other orders of insects, and secondly it would necessitate the conclusion that in species which have a vein along the anterior margin of the tegmina the vein Sc has acquired this position as the result of a further tegminal specialization in which the costal cell has been lost in addition to the loss of the costal vein. If this were the sequence of modification then tegmina with a precostal area (the "costal cell" of the above theory) would have to be considered more primitive than those without it (where it would be presumed to have been lost). This would

imply that the tegmina of Flatidae or Ricaniidae were more primitive in this respect than those of Cixiidae or Tettigometridae, a conclusion which would not be acceptable to workers familiar with this superfamily, and would not have been acceptable to Muir, who wrote (1923: 217) "I consider that the most normal and primitive type of venation of recent Homoptera is to be found among the Cixiidae."

Some of the most curious modifications of the costa are to be found in the Tropiduchid genus *Alcestis*. In this genus platygenesis of the tegmen has been brought about by expansion of the costal cell. In some species a precostal area is developed: it is usually small and situated in the basal half of the tegmen, but in *A. lunata* Fen. the greater part of the costa is remote from the margin (fig. 7). Whatever the position this anterior vein may assume, its relation to the humeral plate remains constant. In a few Otiocerine Derbidae (e. g. *Sayiana*) the costal margin is produced near the base and more or less reflected dorsally.

The subcostal trachea, which basally forms a common stalk with that of the costa, is always approximated to the trachea of the radius in the region adjoining the anterior end of the M-Cu strut. In the tegmina of some families and in hind wings generally Sc and R lie apposed for the greater part of their length and are covered by a common sclerotised roof. At its base the sclerotised wall of the vein passes in front of the second axillary sclerite to associate with the anterior point of the first axillary, a relationship characteristic of this vein in other orders. In species having supernumerary veins in the tegmina, Sc may give off distally several secondary branches; in less specialized Fulgoroidea, however, it is either simple or forks once near the apex and typically joins the anterior margin at the apex of the costa, which may be slightly curved posteriorly, as in Cixiidae, or rather markedly so, as in Achilidae. The point where the costa and Sc meet at or near the margin is the *node* (nodus) and is of importance mechanically in being the anterior termination of the transverse line of weakness along which the relatively flexible membrane is hinged to the more coriaceous disc of the tegmen. The cell enclosed by the margin and the distal veinlets of Sc in certain families becomes differentiated as the *stigma*, either by an increase in thickness brought about by minutely vesicular sclerotisation (fig. 9) and corresponding pigmentation, as in most Cixiidae, or by increased pigmentation alone, as in Dictyopharidae; while sometimes only the basal portion of the cell may be thickened, as in some Kinnaridae, or the thickening may occur without increase in pigmentation, as in some pale Cixiidae. In Cixiidae the stigma is traversed near its posterior border by the costal trachea and a branch of the subcosta which lie side by side, the latter having

curved anteriorly at the base of the stigma to lie close to the costa; distad of this point both tracheae curve away from the margin and almost form the posterior border of the stigma.¹

In families in which supernumerary venules have been developed the distal portion of Sc breaks down into a correspondingly greater number of branches which follow the same general course as the single vein. In such cases the node occurs where the anterior venule meets or most closely approaches the costa, and this may occur at a point remote from the margin of the tegmen, as in the Fulgorid genus *Laternaria*. The stigma is usually not developed in forms with a precostal area, but its position may be indicated by a close grouping of the transverse subcostal veins, as in Nogodinidae (fig. 10). An interesting modification of this arrangement is found by the Apatesonine Achilidae, where the disto-stigmal area is traversed by a series of subcostal veinlets, though the tegminal venation as a whole is reduced. In some genera of this family the stigmal sclerotisation may occur in two adjoining marginal cells, as this part of the tegmen accommodates both a hinge and a fold-line.

The trachea of the radius is usually forked and both branches may give off veinlets distally. The anterior primary branch of this vein has been identified by Tillyard (1926: 142) as R_1 , his conclusion being based on the convexity of this branch in the fossil Scytinopteridae; the distal branches, which are primitively two, are accordingly R_{2a} and R_{1b} respectively. The posterior primary branch of the radius, which is concave in Scytinopteridae, is the radial sector and in this family reaches the margins unforked, but in recent Fulgoroidea is usually forked. The convexity of the anterior main branch of the radius has not been observed by the writer in the most primitive forms of Recent material so far examined, as in the distal portion of the tegmen, where this vein is separate, the primitive folding has been lost. The very marked convexity of the common basal stem of R , in which is included the concave Sc, indicates the presence of R_1 in this portion. The radius is associated at its origin with the second axillary sclerite.

The media arises from the basal trachea as a single stem which forks distally, usually into two main branches. The common basal stalk of this vein appears to be concave in the hind wing of such forms as *Laternaria*, and the vein would appear to represent only the posterior branch of the primitive media, the anterior convex branch having been lost. In the adult tegmen M subtends the greater part of the apical margin, and reaches its

¹Carpenter (1939) has shown that in the Archescytinidae Sc is approximated to R as far as the margin and that this common vein forms the proximal boundary of the stigma in this group while a branch of R forms its distal boundary. This is a specialization which removes the Archescytinidae from the direct line of ancestry of all recent Fulgoroidea.

greatest complexity in *Derbe*, where it gives off a series of parallel branches to the margin; in the wing it is comparatively simple, usually forking once, though occasionally, as in *Derbe*, it may be many-branched. At the base of M in the tegmen an oblique sclerotised strut, always devoid of a preceding or accompanying trachea, is developed between M and the base of Cu_1 (fig. 14). On this strut, or, in a few species, on Cu_1 near it, a vertical plate or peg is produced by heavy sclerotisation (see notes on the external wing-folding apparatus below).

The tracheae Cu_1 and Cu_2 arise from the basal trachea on an elongate stem. Cu_1 is typically forked distally (Cu_{1a} and Cu_{1b}) while in the wing secondary branching is common and this vein frequently subtends a considerable portion of the apical margin. The vein Cu_1 is strongly convex, being with R the most prominent vein in the tegmen. Cu_2 is markedly concave, and leaves Cu_1 near the base and passes without forking to the commissural margin. Cutting across its base and lying immediately anterior to it in the tegmen is the claval suture, a thin flexible line along which the clavus is hinged to the main body of the tegmen. In every specimen so far examined by the writer Cu_2 lies posterior to the suture, which anteriorly is bordered by a very narrow sclerotised band which is less conspicuous than the Cu_2 vein, and unlike the latter is not tracheate nor ornamented with macrotrichia in those species which possess them. Tillyard (1926: 158) has rather unfortunately termed the fulgoroid second cubital vein the *vena dividens* on the ground that it separates off "the very distinct anal area or *clavus* from the rest of the wing". Such a vein is not homologous with the "*vena dividens*" in the forewing of Orthoptera, nor with the true counterpart of the latter in the hind wing of certain Fulgoroidea.

The trachea which follows the Cu stem arises separately at its base and lies close against it, curving forward before turning obliquely backward and outward. This trachea is always simple, and the vein which it traverses in the mature tegmen is unattached basally and is unforked, meeting at its apex in the tegmen the vein lying close to the commissural margin to form the so-called Y vein of the clavus. Its separate tracheal origin, its close approximation to the base of Cu and its lack of attachment to the third axillary sclerite reveal this vein to be the post-cubitus of Snodgrass, a vein regarded by Comstock and Needham in Homoptera as the second anal and by Tillyard as the first anal.

In the larger Fulgoridae such as *Laternaria* or *Cathedra*, a spurious concave vein is formed in the wing between the post cubital and first anal vein. This vein is weak, devoid of a basal portion and of a corresponding trachea. Its interest lies in the fact that it is this vein which should be termed the *vena dividens*, as it is an exact counterpart, though independently

acquired, of the supernumerary vein of the same name found in Orthoptera, being adventitious, concave, and dividing off the remigial area from the vannal. No *vena dividens* of this type is developed in the tegmen.

The last of the primary wing tracheae arises from the basal trachea just posterior to the point of attachment of the post cubital, and curves outward and obliquely posteriorly, forking into two or three branches not far from its point of origin. In the mature tegmen the vein which is traversed by the anterior of these branches is firmly hinged at its base to the distal arm of the third axillary sclerite. When this tripodal sclerite rocks on its anterior and proximal points of attachment in response to the pull of the flexor muscle on its inner face the vein is pulled into parallelity with the axis of the body, thus folding the wings. By its possession of these tracheal and morphological characters this vein is established as the first anal vein of the orthopterous wing pattern. In the hind wing the first anal vein generally forks once, and behind the posterior branch lies a furrow along which the vannal portion is hinged. This is the *anal furrow*, a structure not present in the tegmen as a functional element, but perhaps vestigially represented by the line of deflexion of the commissural margin of the clavus.

The posterior trachea arising from the common anal stem traverses the second anal vein in the adult, and passes down the posterior margin of the tegmen as far as the apex of the clavus, and in the wing lies somewhat arcuately across the inner portion of the vannal area. In families where this area is large the vein gives off approximately at right angles two or three delicate atracheate struts to the inner margin of the vannal fold. In the Issid genus *Thionia*, which possesses an exceptionally large anal lobe in the wing, the second anal vein forks distally and may give off five ultimate branches to the distal margin.

The vannal area of the tegmen is not supplied with veins, and is reduced to a small triangular membranous area lying between the third axillary sclerite, the inner (scutellar) margin of the clavus and the axillary cord.

An axillary cord is present in fulgoroidea, both in the tegmina and wings, joining the inner end of the hind margin to the end of the posterior marginal fold of the respective alinota.

There are several structures in the fulgoroid wing which though of little morphological significance are functionally important. These comprise the anterior and posterior nodes, the nodal line, the accessory wing-locking mechanism, the wing coupling apparatus and, when present, the tegminal stridulatory organs.

In many families of Fulgoroidea the distal field of the tegmina, occupying very approximately one-third of the total remigial area, is thinner and more flexible than the basal area. In some

genera, such as the fulgorid *Scaralis* or the tropiduchid *Remosa*, the difference in texture between the two areas is obvious; the quasi-heteropterous condition thus produced has led systematists to adopt the terms "corium" and "membrane" for these areas. The membrane is hinged to the corium along a line from the junction of C and Sc to the apex of the clavus, where Cu_2 meets the commissural margin. This hinge is the *nodal line*. The line is frequently translucent (as in some Cixiidae), and does not interrupt the main longitudinal veins, but may be marked by a series of transverse bars which may lie in a straight line or, as is more usual, in zig-zag formation with each section being progressively displaced towards the base. Along this line sclerotised transverse struts are developed, devoid of tracheae. In some Flatidae (e. g. *Antillormenis*) the nodal series of such transverse "veins" is absent or very irregular and the line of flexion can be seen as an oblique transparent depression. The posterior end of the hinge adjoins the apex of the clavus and is developed as a *claval node* between the apex of the united Pcu and A_1 vein (the "Y vein"), the tip of Cu_2 and that of a recurrent branch of Cu_{1b} (fig. 13). In the families Fulgoridae and Achilidae Cu_2 does not approach the Pcu- A_1 common vein distally, so that the end of the clavus is open, and the clavus is terminated by the hinge line being produced beyond the claval node to the commissural margin (cf. fig. 12). In families where the tegmina are wholly coriaceous (Issidae, Acanaloniidae) or where the tegmina are much narrowed distally (Flatidae: Selizini) the nodal hinge line is absent.

Cross veins in the form of atracheate sclerotised struts appear to have been acquired independently by several families. In general they are few in small forms, or may be absent, and their number and complexity appear to be broadly correlated with the size of the tegmina and wings. They are more numerous in the tegmina than in the wings. On the corium they are usually irregularly developed and in some genera branch or anastomose; if the tegmina are heavily sclerotised the cross-veins may be absorbed into the general corial surface, though their presence is detectable by suitable illumination (examples of such modification are provided by the fulgorid *Scaralis* and Issidae such as *Thionia* or *Colpoptera* and members of the subfamily Hemisphaeriinae or by those of Calisceline Dictyopharidae or Hiracine Tropiduchidae). In the membrane, the cross veins are usually more or less at right angles to the longitudinal veins. In certain families (such as Fulgoridae, Dictyopharidae, and Tropiduchidae) there is a tendency for cross veins to be arranged progressively more regularly in the membrane in proportion as they become fewer. In the Ricaniidae, Nogodinidae and Cryptoflatine Flatidae the cross veins of the membrane generally tend to be regular, and may be confined

to a single even line subparallel to the apical margin, lying distad of the nodal line. This line is the *apical line* of Muir (1st subapical of Melichar), and terminates posteriorly at the apex of the clavus, while anteriorly it may curve basally to join the apical portion of the costa, or, as in some Cryptoflatini may end abruptly against one of the distal branches of the radius.

In Fulgoroidea the tegmen and wing of each side are coupled together during flight and form a single flight organ, with the stiff tegmen forming the remigium and the wing the functional vannus. The means by which this coupling is effected appears to be uniform throughout the superfamily: The wing margin at the apex of the costa is curved upward and looped slightly posteriorly and this engages with a minute ledge developed on the deflexed commissural margin of the clavus. In some species, a few minute spinose macrotrichia are present on the costa of the wing just basad of the marginal fold, but it is very doubtful whether these play any part in uniting the wings.

An accessory wing-locking apparatus is present on the base of each tegmen and wing ventrally and is apparently employed to adjust the wings and tegmina into their normal position of rest. It comprises (1) a vertical plate or peg developed on the ventral surface of each tegmen by a sclerotic outgrowth from the oblique strut between M and Cu₁, or on Cu₁ itself near the point of junction with this strut, and (2) an eminence on the ventral surface of Sc+R basally in the wing bearing a group of setae directed vertically downward. These setae may be sparse (about four are present in Cixiidae and as few as two in some Delphacidae), or may form a dense tuft (as in large Fulgoridae such as *Laternaria*). As the tegmina close, the tegminal plate presses on the base of the anterior wing margin and holds the latter in their folded position. The group of setae below Sc in each wing presses against the lateral field of the metanotum, and perhaps also enters a cavity below the wing base, and possibly by its resilience keeps the anterior portion of the wings in contact with the tegmen while at rest. In the genus *Derbe* and probably other Derbinae no sclerotised plate is developed on the tegmina at the base of Cu₁, and it would seem that in this genus the ventrally sclerotised base of Sc+R, which projects prominently downward, performs a similar function. The tegmina when closed are partially kept in position by the scutellar margin of the clavus fitting into the reversed notal suture of the mesonotum lying above the lateral fields of the mesoscutellum and between the mesoscutum and the posterior alinotal fold.

Organs of stridulation occur on the wings of certain derbid genera and are considered to be present also in some Araeopidae (Kirkaldy 1907: 7, 8, and Pl. XX). They are developed in both sexes. In Derbidae a portion of the inner margin of the

anal lobe of the wing is thickened and corrugated. When the wing is jerked upward this corrugated plate is rapidly scraped across a group of setae situated on the side of the third abdominal tergite (fig. 15).

The plate on the anal lobe is formed by the inward prolongation of the minute sclerotised band that binds the hind margin of the wing, and the parallel ridges on it are produced by the inward extension of every second member of the series of sclerotised loops that support the marginal band (fig. 17). The prominence of this stridulatory area varies greatly in different species; in Zoraidine Derbidae, some Derbinae, certain Cenchreini such as *Patara*, and Otiocerini (*Otiocerus*) it is conspicuous. In Cenchreine genera such as *Cedusa* and *Neocenchrea* it is obscure, and it is difficult to ascertain whether its traces are of functional value or not. In the aræopid *Perkinsiella vitiensis*, a member of a genus in which stridulation has been reported, the sclerotisation at the point where the corrugated plate occurs in Derbidae is scarcely more pronounced than elsewhere on the inner margin, while the same is true of species of *Delphacodes* seen by the writer and it would seem questionable whether in such cases effective stridulation is possible by this means. In *Derbe*, the anal border of the wing is emarginate and the basal portion projects as a rather narrow subrectangular lobe (fig. 18). This is pigmented but not appreciably thickened. The margin of the lobe is minutely spiculate, as is the whole of the posterior wing margin in this genus. A group of setae occurs on each of the lateral fields of the third abdominal tergite. It is possible that in this large species the general sclerotisation of the anal lobe is adequate for sound production. The setae over which the marginal plate is drawn are directed outward and downward (fig. 16). They are generally similar, except perhaps in point of size, to the setae sparsely scattered over the abdominal sclerites, and the group may have been formed by a local congregation of such setae.

In addition to the stridulatory organs found on the wings, many species of Derbidae bear series of large setiferous plates on the tegminal veins. These may occur on the common stem Sc+R, on M, Pcu, and A₁. In *Derbe* a row of 12 to 15 lies along Sc+R, while a series of four occupies the basal part of M. The Cenchreine genus *Patara* has them on Sc+R, Pcu and A₁, *Neocenchrea* on Pcu and A₁ only, while they are absent or very obscure in the genus *Cedusa*.

These structures occur only on the veins. Each consists of a subtriangular orifice, with the lip strongly raised on the proximal side, and a small round plate set immediately below the uppermost part of the orifice. From this plate a long slender seta projects horizontally distad, i. e., posteriorly, when the tegmina are folded (fig. 19). The tegminal veins in general are studded

with minute setae, each of which arises from an oval or rounded plate. It would seem that these larger plates have originated by an elaboration of one of the smaller type. The function of the long seta is unknown, but the plates themselves exude filaments of pearly wax. Metcalf (1938: 304,313) refers to these organs as stridulatory, but it is difficult to see against what they could be rubbed as they cannot be apposed to any other part of the body, including the tegmina of the opposite side in all positions. They are not confined to species which possess a stridulatory apparatus: they are absent or very reduced in *Otiocerus* which has stridulating organs, and abundantly present in *Neocenchrea* which has apparently none.

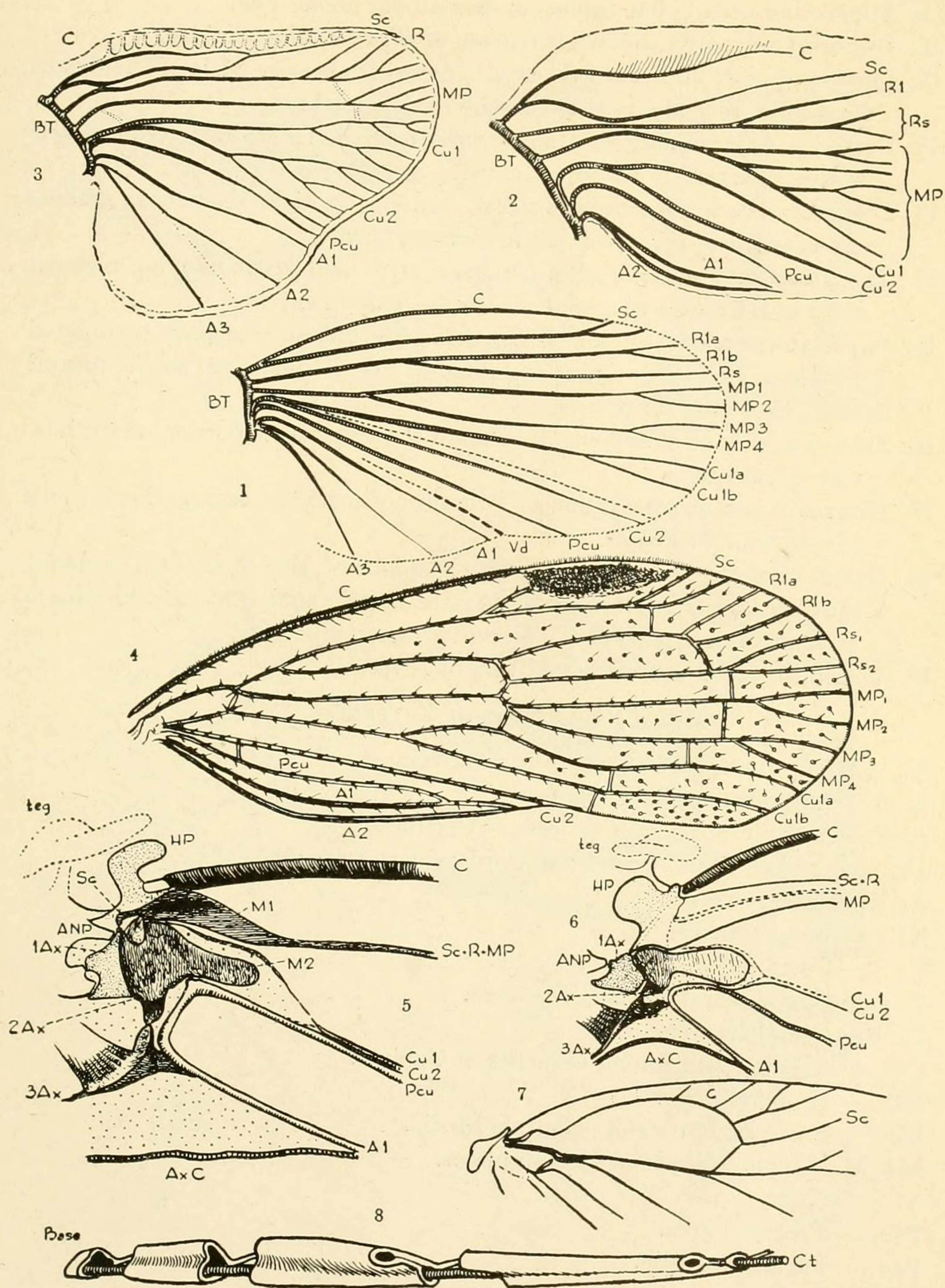
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EXPLANATION OF PLATES

(Plate 14)

1. General plan of tracheation of Fulgoroid wing.
2. Tracheae of fore wing pad of *Poekilloptera phalaenoides* (L.) (Flatidae).
3. Tracheae of hind wing pad of *Poekilloptera phalaenoides* (L.).
4. Tegmen of *Mnemosyne arenae* Fen. (Cixiidae), an example of a generalized fulgoroid wing type.
5. Base of right tegmen and axillary sclerites of *Taosa herbida* Walk.
5. Base of right tegmen and axillary sclerites of *Taosa herbida* Walk. (semi-diagrammatic).
6. Base of right tegmen and axillary sclerites of *Poekilloptera phalaenoides* (L.) (semi-diagrammatic).
7. Anterior portion of right tegmen of *Alcestis lunata* Fen.
8. Diagram showing mode of development of pre-costal area in tegmen of *Laternaria* (Fulgoridae).



(Plate 15)

9. Stigma and node in left tegmen of *Mnemosyne arenae* Fen.
10. Precostal area and node in left tegmen of *Bladina* (Nogodinidae).
11. Portion of costa and precostal area of *Ormenis antoniae* Mel. (The dotted lines show lines of great attenuation of the membrane.)
12. Posterior node at apex of Cu_{1b} in right tegmen of *Laternaria* (an example of this structure in an open clavus).
13. Posterior node between apices of Cu_1 and Cu_2 in right tegmen of *Bladina* (an example of this structure in a closed clavus).
14. The atracheate sclerotised M-Cu basal strut and accompanying pigment band in right fore wing pad of *Alcestis lunata* Fen.
15. Stridulatory apparatus of *Patara* sp. (Derbidae), showing corrugated margin of anal lobe of wing and setae on side of abdominal tergite (dorsal view, semi-diagrammatic).
16. Side view of base of abdomen of *Patara* showing setose portion of stridulatory apparatus.
17. Diagrammatic representation of structure of marginal corrugation on anal lobe of wing in *Patara*.
18. Dorsal view of portion of emarginate anal lobe of wing of *Derbe* (Derbidae), showing pigmented but not corrugated margin zone, and (below) minute setae on lateral portion of adjacent abdominal tergite.
19. Wax-bearing plate on tegminal vein of *Derbe*.

EXPLANATION OF LETTERING

- A1, A2, A3—First, second and third anal veins.
 A. m —Anterior margin of tegmen.
 ANP —Anterior notal wing process of tergum.
 1Ax, 2Ax, 3Ax—First, second and third axillary sclerites.
 Ax. C—Axillary cord.
 BT —Basal trachea.
 C —Costa.
 C. m —Commissural margin of tegmen.
 Ct —Costal trachea.
 Cu1, Cu2—First and second branches of Cubitus.
 HP —Humeral plate.
 MP —Posterior branch of primitive Media.
 M1, M2—First and second median plates.
 n —Node.
 P-c. a—Precostal area.
 Pcu —Postcubital vein.
 R —Radius.
 Rs —Radial Sector.
 Sc —Subcosta.
 teg —Tegula.
 V. d. —Vena dividens.

